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Effect of Ontogenetic Increases in Body Size on Burst Swimming Performance in Tadpoles of the Striped Marsh Frog, *Limnodynastes peronii*

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ABSTRACT

The effect of ontogenetic increases in total length on burst swimming performance was investigated in tadpoles of the striped marsh frog (*Limnodynastes peronii*) over the total-length range of 1.5–4 cm and Gosner developmental stages 25–38. The burst swimming performance of tadpoles at 10° and 24°C was determined by videotaping startle responses with a high-speed video camera at 200 Hz and analysing the sequences frame by frame. Maximum swimming velocity (U_{\max}) and acceleration (A_{\max}) increased with total length (L) at a rate that was proportionally greater than the increase in total length (i.e., positive allometry; exponents >1) and was described by the allometric equations $U_{\max} = 0.061L^{1.34}$ and $A_{\max} = 1.15L^{1.11}$ at 10°C and $U_{\max} = 0.114L^{1.34}$ and $A_{\max} = 1.54L^{1.11}$ at 24°C. Stride length increased with a total-length exponent of approximately 1 but was unaffected by temperature. Tail-beat frequency was not affected by total length and increased from 7.8 ± 0.2 Hz at 10°C to 21.7 ± 0.7 Hz at 24°C. Developmental stage did not significantly influence the relationship between total length and U_{\max} or A_{\max} . Furthermore, temperature and the associated changes in water viscosity did not affect the relationship between total length and burst swimming performance. At their U_{\max} , Reynolds numbers ranged from approximately 1,500 in the smaller tadpoles up to 50,000 for the larger animals at 24°C. We suggest the positive allometry of U_{\max} in larval *L. peronii* was due in part to the increases in tail width (TW) with total length ($TW = -1.36L^{1.66}$), possibly reflecting the increasing im-

portance of burst swimming performance to survival during larval development.

Introduction

Fish and larval anurans use fast-start swimming behaviours to escape predators (Watkins 1996; Domenici and Blake 1997). Improved fast-start performance has been correlated with improved prey capture success in fish (Beddow et al. 1995) and an increased ability to evade predators in both fish and larval anurans (Swain 1992; Watkins 1996). Not surprisingly, fast-start performance (or burst swimming) is often used in physiological studies as an ecologically relevant measure of performance and a practical method of collecting information on fitness (Huey and Stevenson 1979). Body size has a significant influence on swimming performance (Bainbridge 1958; Wardle 1975; Webb 1977) and escape success from predators (Bailey and Batty 1984; Swain 1992). Knowledge of the relationship between body size and swimming performance can reveal information about changes in vulnerability to predation during growth and development.

In adult fish, length-specific swimming velocity decreases with increasing body size (Archer and Johnston 1989; Gibson and Johnston 1995; Drucker and Jensen 1996). This negative allometry (with respect to total length) appears to be in part a function of the intrinsic contractile properties of muscle fibres (James and Johnston 1998; James et al. 1998). In contrast to adults, the length-specific swimming velocity of larval fishes appears to increase with increasing body size (Hunter 1972; Gibson and Johnston 1995; Hale 1996). This positive allometry is probably a consequence of developmental changes that correlate with increases in body length. Moreover, because of their small size, fish larvae experience low Reynolds numbers (Re) at routine swimming speeds. As a consequence, fish larvae often operate in the viscous hydrodynamic regime and their swimming performance is significantly influenced by the viscosity of water (Fuiman and Batty 1997). Because swimming speeds of different-sized larvae will be differentially influenced by water viscosity, the viscous hydrodynamic regime may also be an important factor determining the scaling relationships of swimming performance in larval fishes. Moreover, increases in viscosity that are associated with decreases in temperature may

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also exacerbate these effects of the viscous hydrodynamic regime on swimming of different-sized larvae (Fuiman and Batty 1997), thus possibly affecting the scaling relationships of swimming performance.

Burst swimming in some anuran larvae is used not only to escape predators (Watkins 1996) but also to rapidly traverse from the bottom of the pond to the surface (to ventilate the lungs) and back again, a behaviour known as "bobbing" (Wassersug and Seibert 1975; Wassersug 1992; Wong and Booth 1994). Anuran larvae usually swim in the Re range of 1,000–3,000 (Wassersug and Hoff 1985; Dudley et al. 1991) and are governed by inertial rather than the viscous hydrodynamic regime. Unlike the many studies detailing the effect of body size on locomotor performance in fish, there have been relatively few studies on larval anurans. In an unpublished study, Hoff (1987) reported that length-specific swimming velocities of anuran larvae generally decreased with increasing body length; however, scaling relationships differed between species, with the length-specific swimming velocity of at least one species of anuran larvae (*Xenopus laevis*) showing no influence of total length. Most locomotor studies of anuran tadpoles have concentrated more on the influence of ontogenetic changes in body shape and the consequences of their globose body shape rather than body-size effects on swimming performance (Wassersug and Sperry 1977; Huey 1980; Wassersug and Hoff 1985; Wassersug 1989; Brown and Taylor 1995; Liu et al. 1996, 1997).

In this study, we examined the relationship between total body length and burst swimming performance in tadpoles of the striped marsh frog (*Limnodynastes peronii*) between Gosner (1960) developmental stages 25 and 38. Like larval fishes, increases in body size of anuran tadpoles are usually correlated with developmental change. However, during the intermediate stages of tadpole development (Gosner [1960] stages 25–40), only minor changes occur in body shape or drag coefficients, with most developmental changes associated with the differentiation of the hindlimbs. Gosner (1960) stage 25 occurs when the operculum has completed development and a spiracle forms, whereas Gosner (1960) stage 40 is based on a later stage of hindlimb differentiation and occurs before the eruption of the forelimbs. We predict that the effect of total length on swimming performance of *L. peronii* tadpoles in these intermediate stages of development should be dependent on body size alone and not on developmental stage. We also examined the influence of temperature (and thus correlated changes in water viscosity) on the scaling of swimming performance in *L. peronii* tadpoles. We predict that there should be no difference in the slope of the scaling relationship of swimming performance between tadpoles tested at 10° and 24°C because the relative importance of water viscosity to tadpole swimming performance should be minimal as they operate in the inertial hydrodynamic regime.

Material and Methods

Tadpoles of the striped marsh frog (*Limnodynastes peronii*, stages 24–38, Gosner [1960]) were collected from several ponds in Brisbane, Queensland, during March 1996. Tadpoles were transported to the University of Queensland and maintained in aquaria at a density of five animals per litre and at a constant temperature of 24°C for 6 wk. Tadpoles were maintained in high densities to ensure that rapid development did not occur at 24°C and that some tadpoles remained at earlier developmental stages and at small body sizes. It is well documented that amphibian larvae kept at high densities with conspecifics have slower growth and developmental rates (Newman 1987; Tejedo and Reques 1994; Venz 1996). Tadpoles were fed boiled lettuce.

Measurement of Burst Swimming Performance

After the 6-wk period in the laboratory, 40 tadpoles over the total-length range of 1.5–4.5 cm and between Gosner (1960) developmental stages 25 and 38 were selected for measurement of their burst swimming performance. Performance was determined for 10 burst swimming sequences for each individual. The fastest sequence was taken as a measure of maximum performance. Sequences were analysed frame by frame to determine the maximum velocity (U_{max}), acceleration (A_{max}), and the time taken to reach maximum velocity ($T-U_{max}$). C -start duration (C_{dur}) was calculated as the time from when movement was initially detected until the end of the first quarter-tail-beat (straightened position). Tail-beat frequency (T_{BF}) was calculated from the time taken to complete the first full tail-beat after the C -start manoeuvre. The distance moved during this first full tail-beat was recorded to calculate stride length (S_1) and the average velocity over this stride (U_{as}). The burst swimming performance of all larvae was first examined at 24°C and then, after a recovery period of 24 h, at 10°C. The aquaria were cooled from 24° to 10°C at a rate of 4°C h⁻¹.

Burst swimming sequences were videotaped in a glass arena 30 × 30 × 5-cm-deep, water jacketed by a bath that was temperature controlled ($\pm 0.5^\circ\text{C}$). A sharp silhouette of the larvae was obtained by providing overhead illumination with an 800-W light and a background of Scotchlite reflective tape on the bottom of the filming arena. Tadpoles were videotaped by recording the image from a mirror suspended at an angle of 45° above the filming arena using an NAC-B/W high-speed video camera recording at 200 Hz (NAC, Tokyo, Japan). Burst swimming sequences were induced by a mild electric stimulus. A Panasonic AG-6300 video recorder was used to replay the recorded burst swimming sequences into the MOTION ANALYSIS VP-110 computer system, which analysed the sequences frame by frame with the Expertvision Software package (Motion Analysis, California). Only the initial 400 ms of the burst swimming responses were analysed and the raw distance data

between each frame were smoothed by using a Butterworth smoothing function set at 30 Hz for the 10°C trials and 80 Hz for the 24°C trials (see Walker 1998). The smoothed raw data were then differentiated to get velocity and then differentiated again to get acceleration data. U_{\max} and A_{\max} were calculated by using a moving average of the data over three successive frames (i.e., over 10 ms).

Re that each individual tadpole experienced at their U_{\max} and U_{as} were calculated at both test temperatures of 10° and 24°C. Re were calculated from the equation $Re = lU/n$, where l is the characteristic length of the object usually (the body length of the animal), U is the swimming speed of the animals, and n is the kinematic viscosity of the fluid. Kinematic viscosity of water at 10° and 24°C was taken from standard tables published in Touloukian et al. (1975).

After videotaping the burst swimming sequences, morphological measurements were taken from each individual. Total length (tip of snout to end of tail), head-body length (tip of snout to vent length), and tail length (T_t) were measured with Mitutoyo calipers (± 0.1 mm), and thickness of the muscle at the base of the tail (T_w) was measured with an ocular micrometer (Stemi 1000, Zeiss). The mass of each larvae was measured with an A200S Sartorius analytic balance (± 0.01 g), and stages were recorded by using the Gosner (1960) staging table.

To determine whether swimming performance was influenced by developmental stage during the early to midstages of tadpole development, length-standardised swimming performance of the tadpoles was compared between three developmental stages: 25–27, 28–30, and 31–38. The swimming performance of each individual tadpole was standardised to a body length of 2.5 cm by using the following equation:

$$\text{standardised value} = \text{actual value} \times (2.5/L)^{\text{exp}},$$

where L is total length (cm) and exp is the total-length exponent calculated in the present study (1.34 for U_{\max} and 1.11 for A_{\max}).

Statistical Analysis

Allometric scaling relationships were expressed in the form $Y = aL^b$, where a is the intercept at unity, L is the total length of the tadpoles, and b is the slope of the regression line. The equations were calculated by using log-transformed data by using least square regression techniques. The scaling relationships between different temperatures were compared by using MANCOVAs (Sokal and Rohlf 1981). If the slopes of the regression lines for each kinematic parameter were not significantly different between 10° and 24°C, then a common slope was quoted for the allometric equations at both temperatures. Multiple linear regressions were used to quantify the relationship between U_{\max} and A_{\max} and the combined effects of total length and temperature. Equations took the form

$$\log U_{\max} = a + \log L + c \times \text{temperature}.$$

The $T-U_{\max}$, C_{dur} , and T_{BF} at the different experimental temperatures were compared by using Student's t -tests or Mann-Whitney U -tests. Size-standardised U_{\max} and A_{\max} (calculated from derived equations) were compared between developmental groups by using one-way ANOVAs. All results are presented as $\bar{X} \pm \text{SE}$ errors. Statistical significance was taken at the level of $P < 0.05$.

Results

Burst swimming responses of larval *Limnodynastes peronii* were characterised by a C -start and several tail-beats resulting in a rapid acceleration to a maximum velocity. The C -start manoeuvre involved extreme caudal flexibility and allowed the tadpoles to effectively rotate their heads through 180° with very little translation.

Burst Swimming Performance

The effect of total length on several parameters of burst swimming performance were determined for larval *L. peronii* at 10° and 24°C (Table 1). U_{\max} was positively correlated with total length and was described by the allometric equations $U_{\max} = 0.061L^{1.34}$ ($n = 40$, $r^2 = 0.77$, $P < 0.001$) at 10°C and $U_{\max} = 0.114L^{1.34}$ ($n = 40$, $r^2 = 0.82$, $P < 0.001$) at 24°C (Fig. 1A). Because the total-length exponents for the allometric equations were >1 , the U_{\max} of the tadpoles increased at a rate that was proportionally greater than the increase in total length. Length-specific U_{\max} was also positively correlated with total length at 10°C ($n = 40$, $r^2 = 0.17$, $P < 0.05$) and 24°C ($n = 40$, $r^2 = 0.28$, $P < 0.01$). Temperature did not significantly affect the relationship between total length and U_{\max} (MANCOVA, $P > 0.05$); however, there was a significant stepwise change in U_{\max} with test temperature ($P < 0.01$; Fig. 1A). The Q_{10} for U_{\max} over the test temperature range of 10°–24°C, as calculated for each individual tadpole, was 1.65 ± 0.03 . An equation incorporating the effect of experimental temperature and total length on U_{\max} was calculated by using a multiple linear regression: $\log(U_{\max}) = -39.4 + 101.7 \log(L) + 1.75T$ ($n = 40$, $r^2 = 0.82$, $P < 0.001$).

As with U_{\max} , the A_{\max} of the *L. peronii* tadpoles was highly correlated with total length (Table 1) and was described by the allometric equation $A_{\max} = 1.15L^{1.11}$ ($n = 40$, $r^2 = 0.43$, $P < 0.001$) at 10°C and $A_{\max} = 1.54L^{1.11}$ ($n = 39$, $r^2 = 0.65$, $P < 0.001$) at 24°C (Fig. 1B). Temperature did not change the relationship between A_{\max} and total length (MANCOVA, $P > 0.05$), although A_{\max} increased significantly with an increase in test temperature ($P < 0.05$; Fig. 1B), with an average Q_{10} of 2.64 ± 0.11 over the temperature range of 10°–24°C. The effect of test temperature and total length on A_{\max} is described by

Table 1: Relationship between total length and various kinematic parameters of burst swimming performance in tadpoles of the striped marsh frog (*Limnodynastes peronii*) at 10° and 24°C

	Units	Water Temperature 10°C				Water Temperature 24°C			
		log a	b	r ²	P	log a	b	r ²	P
Maximum velocity (U_{max})	m s ⁻¹	.78 ± .05	1.33 ± .12	.77	<.001	1.06 ± .05	1.40 ± .11	.82	<.001
Maximum length-specific velocity	L s ⁻¹	.78 ± .05	.33 ± .12	.17	<.05	1.06 ± .05	.40 ± .11	.28	<.01
Maximum acceleration (A_{max})	m s ⁻²	-.77 ± .09	1.08 ± .21	.43	<.001	-.24 ± .06	1.21 ± .15	.65	<.001
Time to maximum velocity ($T-U_{max}$)	ms	2.09 ± .07	.22 ± .5	.02	ns	2.1 ± .12	-.35 ± .27	.02	ns
Stride length (S_L)	cm	.67 ± .03	1.35 ± .08	.90	<.001	.73 ± .04	1.05 ± .1	.76	<.001
Tail-beat frequency (T_{BF})	Hz	.93 ± .05	-.12 ± .10	.04	ns	1.42 ± .05	-.2 ± .12	.07	ns
Average stride velocity (U_{as})	m s ⁻¹	-1.44 ± .06	1.31 ± .74	.75	<.001	-.91 ± .07	.95 ± .16	.50	<.001
C-start duration (C_{dur})	ms	2.1 ± .04	-.02 ± .1	.001	ns	1.53 ± .06	.30 ± .13	.13	<.05

Note. Equations are in the form $Y = aL^b$, where a is the intercept at unity ± SEM, L is the total length of the tadpoles, and b is the slope of the regression line ± SEM. Significance was taken at the level of $P < 0.05$.

$\log(A_{max}) = -1.21 + 1.14 \log(L) + 0.04T$ ($n = 39$, $r^2 = 0.88$, $P < 0.001$).

$T-U_{max}$ was not affected by total length at both 10°C ($n = 40$, $r^2 = 0.02$, $P > 0.05$) and 24°C ($n = 40$, $r^2 = 0.02$, $P > 0.05$; Table 1). However, $T-U_{max}$ at 24°C (99.4 ± 8.3 ms) was significantly lower than at 10°C (157 ± 6.5 ms, $P < 0.001$). C_{dur} was also unaffected by changes in total length at 10°C ($n = 37$, $r^2 = 0.001$, $P > 0.05$); however, it was significantly correlated with total length at 24°C ($n = 38$, $r^2 = 0.13$, $P < 0.05$) and was described by the equation $C_{dur} = 33.9L^{0.30}$ (Table 1).

Stride length was positively correlated with total length at 10°C ($n = 37$, $r^2 = 0.90$, $P < 0.001$) and 24°C ($n = 38$, $r^2 = 0.76$, $P < 0.001$) but was not influenced by test temperature (Fig. 2A; Table 1). T_{BF} was not significantly affected by total length at either 10°C or 24°C (Table 1); however, T_{BF} significantly increased from 7.8 ± 0.2 Hz at 10°C to 21.7 ± 0.7 Hz at 24°C ($P < 0.001$; Fig. 2B). Average stride velocity was highly correlated with total length and was described by the equations $U_{as} = 0.044L^{1.17}$ at 10°C ($n = 37$, $r^2 = 0.75$, $P < 0.001$) and $U_{as} = 0.12L^{1.17}$ at 24°C ($n = 37$, $r^2 = 0.50$, $P < 0.001$; Fig. 2C; Table 1). Temperature did not affect the relationship between total length and U_{as} .

Re were calculated for individual tadpoles at their U_{max} and U_{as} at both 10° and 24°C (Fig. 3A, 3B). At their U_{max} , smaller tadpoles experienced Re of <2,000 at 10°C and approximately 5,000 at 24°C, while tadpoles >4 cm experienced Re in excess of 10,000 at 10°C and 20,000 at 24°C. At U_{as} , Re ranged from <1,000 to >5,000 at 10°C and from approximately 1,500 to >10,000 at 24°C.

Effect of Developmental Stage on Burst Swimming Performance

Length-standardised swimming performance was compared between *L. peronii* tadpoles from three Gosner (1960) developmental groups: 25–27, 28–30, and 31–38. When standardised

for total length, there were no significant differences in U_{max} and A_{max} between the different developmental groups at 10° and 24°C (Table 2). Burst swimming performance in larval *L. peronii* was dependent on total length and not on development stage.

Morphological Correlates

The relationship between total length and head-body length, tail length, and width of the tail base (T_w) was determined for the tadpoles used in the burst swimming study. Both tail length ($n = 40$, $r^2 = 0.94$, $P < 0.001$) and head-body length ($n = 40$, $r^2 = 0.94$, $P < 0.001$) significantly increased with total length. However, the increase in T_L with total length was significantly greater than the increase in head-body length (MANCOVA, $P < 0.05$; Fig. 4A). In addition, T_w increased with total length at a rate that was proportionally greater than the increase in total length and was represented by the equation $T_w = -1.36L^{1.66}$ ($n = 40$, $r^2 = 0.89$, $P < 0.001$; Fig. 4B).

Discussion

Burst swimming performance in tadpoles of *Limnodynastes peronii* between Gosner (1960) developmental stages 25 and 38 was strongly dependent on total length. Length-specific U_{max} and A_{max} significantly increased with total length over the size range of 1.5–4.5 cm. Allometric scaling relationships of burst swimming performance in larval anurans have only been described in detail in one other study. Hoff (1987) examined the scaling relationships of burst swimming in five species of larval anurans. Scaling relationships varied between species, and for all species pooled, U_{max} scaled with a length exponent of 0.64, a value considerably lower than that observed in larval *L. peronii*. U_{max} of *Bufo americanus* scaled with a length exponent of 0.69 and *Rana sylvatica* and *Rana catesbeiana* with length ex-

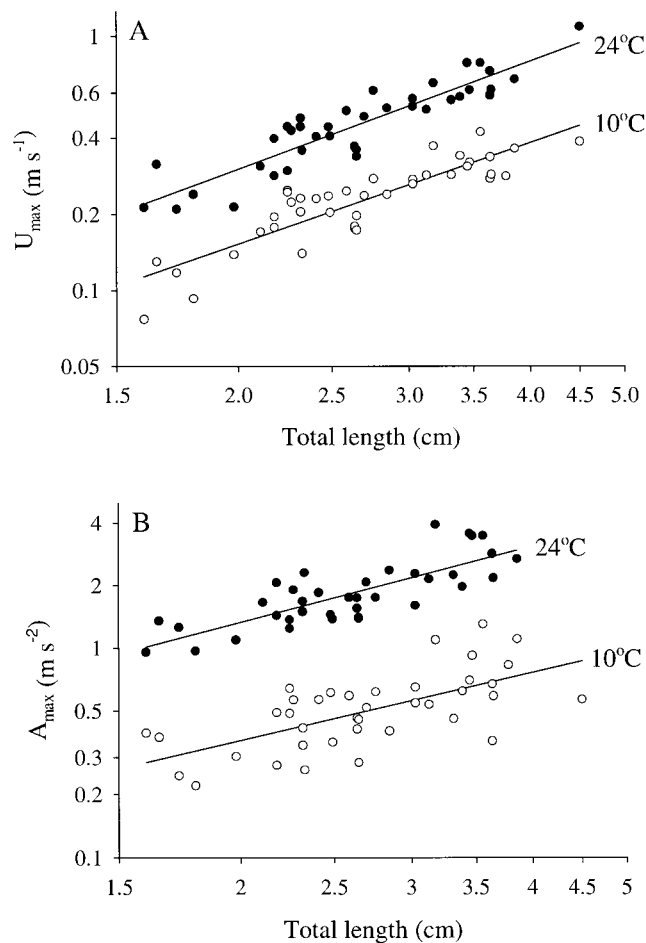


Figure 1. Relationship between total length and (A) maximum swimming velocity (U_{\max}) and (B) acceleration (A_{\max}) in tadpoles of the striped marsh frog (*Limnodynastes peronii*) at 10° and 24°C. Each line represents a first-order polynomial fitted to a set of log-log data by using least squares regression.

ponents of 0.44 and 0.43, respectively. However, the U_{\max} of larval *Xenopus laevis* scaled with a total-length exponent of 1.0. Hoff (1987) suggested this relatively high total-length exponent of U_{\max} in *X. laevis* was due to massive increases in axial muscle mass with total length. Similarly, tail width in *L. peronii* increased with total length at a rate that was proportionally greater than the increase in total length ($L^{1.66}$).

Several other studies have also reported an increase in swimming velocity with increases in total length in premetamorphic tadpoles (Wassersug and Sperry 1977; Huey 1980; Wassersug and Hoff 1985; Brown and Taylor 1995; Parichy and Kaplan 1995). Huey (1980) found average swimming velocity in tadpoles of *Bufo boreas* positively correlated with tail length between stages 31 and 41. Parichy and Kaplan (1995) also found that in the fire-bellied toad, *Bombina orientalis*, longer tails increased sprint speed. However, for both studies it is not clear whether length-specific swimming velocity increased with in-

creasing total length. In contrast, Watkins (1997) reported that U_{\max} in the Pacific tree frog, *Hyla regilla*, was independent of body size, with linear regressions of maximum speed on total length and tail length being nonsignificant. However, Watkins (1997) used a small size range of tadpoles and a simplified measure of sprint velocity that may have masked the effects of total length on maximum velocity.

Liu et al. (1997) found that both the shape of tadpoles and their kinematics during swimming created a “dead water” zone between the head-body and tail that minimised the effects of hindlimb development on tadpole swimming performance. Because the primary developmental changes between Gosner (1960) stages 25 and 38 are the eruption and differentiation of the hindlimbs, we predicted that developmental stage would not affect the swimming performance of larval *L. peronii* during these stages. Consistent with this prediction, the increase in swimming velocities with increasing total length in larval *L.*

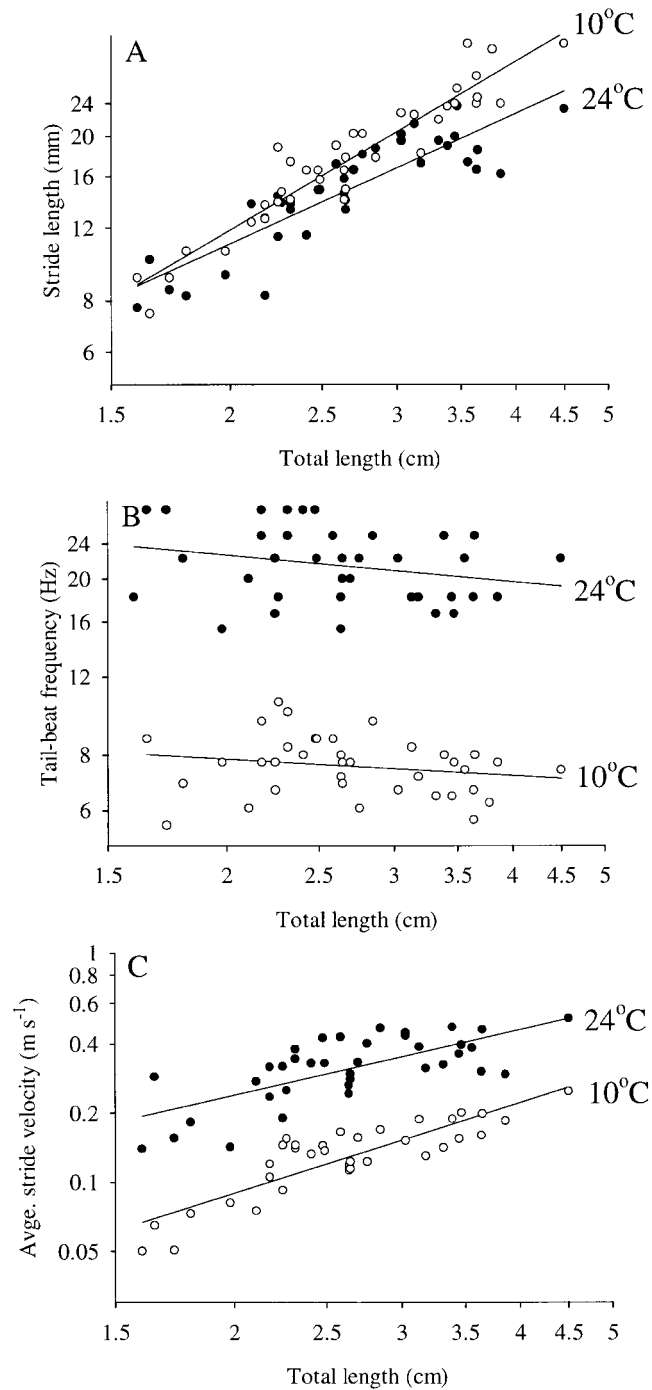


Figure 2. Relationship between total length and (A) stride length during the first full tail-beat after the C-start manoeuvre, (B) tail-beat frequency, and (C) average velocity calculated over the stride length in tadpoles of the striped marsh frog (*Limnodystes peronii*) at 10° and 24°C. Each line represents a first-order polynomial fitted to a set of log-log data by using least squares regression.

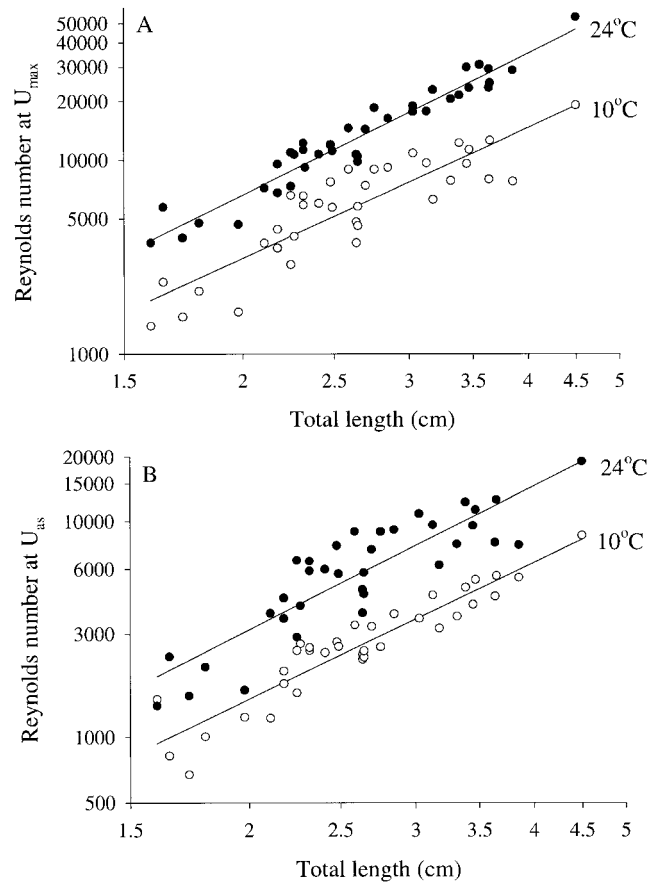


Figure 3. Relationship between total length and the calculated Reynolds number that tadpoles of the striped marsh frog (*Limnodystes peronii*) are operating at when swimming at their (A) maximum swimming velocity (U_{\max}) and (B) average velocity during the first full stride (U_{as}) after the C-start manoeuvre at 10° and 24°C. Each line represents a first-order polynomial fitted to a set of log-log data by using least squares regression.

peronii was independent of developmental stage between Gosner (1960) stages 25 and 38. Comparison of length-standardised U_{\max} and A_{\max} (by using the derived allometric equations) in larval *L. peronii* showed no differences between stages 25–27, 28–30, and 31–38. However, during the latter stages of anuran larval development, when both the forelimbs and hindlimbs increase in size, swimming velocity is significantly influenced by developmental changes, especially as a consequence of metamorphosis (Huey 1980; Dudley et al. 1991). Huey (1980) found that metamorphosis resulted in a rapid reduction in maximum burst speeds in *B. boreas*. Also, Brown and Taylor (1995) noted a significant decrease in swimming velocity at stage 43 in the wood frog, *R. sylvatica*.

Fuiman and Batty (1997) showed that ecologically relevant changes in water viscosity that were independent of temperature significantly affected the swimming performance of larval Atlantic herring (*Clupea harengus*) at Re of up to 300. Moreover, in a recent study of swimming performance in adult goldfish

(*Carassius auratus*) and guppies (*Poecilia reticulata*), Johnson et al. (1998) found that artificial increases in water viscosity at 20°C resulted in significant decreases in U_{\max} at Re of up to 3,500. Previously, it was considered that fish larvae would be unaffected by the viscous hydrodynamic regime at Re greater than 200 (Weihs 1980; Webb and Weihs 1986). Decreases in water temperature are associated with increases in the kinematic viscosity of water, which can in turn influence the scaling relationships of swimming performance in small aquatic organisms. We predicted that the scaling of swimming performance in larval *L. peronii* would be unaffected by changes in temperature because tadpoles are governed by inertial rather than the viscous hydrodynamic regime (Wassersug and Hoff 1985; Dudley et al. 1991). In larval *L. peronii*, temperature did not significantly influence the relationship between swimming performance and total length (allometric exponent). At their U_{\max} , larval *L. peronii* between 1.5 and 4.5 cm experienced Re between 1,500 and 50,000 and were unlikely to be influenced

Table 2: Effect of developmental stage (Gosner 1960) on length-standardised maximum velocity (U_{\max}) and maximum acceleration (A_{\max}) in the striped marsh frog, *Limnodynastes peronii*

Gosner (1960) Developmental Stage	Water Temperature 10°C		Water Temperature 24°C	
	U_{\max} (m s ⁻¹)	A_{\max} (m s ⁻²)	U_{\max} (m s ⁻¹)	A_{\max} (m s ⁻²)
25–2722 ± .43 (12)	.47 ± .15 (12)	.41 ± .15 (13)	1.81 ± .14 (13)
28–3021 ± .39 (15)	.49 ± .15 (15)	.43 ± .19 (15)	1.64 ± .15 (15)
31–3820 ± .07 (13)	.47 ± .17 (13)	.41 ± .24 (12)	1.80 ± .15 (12)

Note. Results are $\bar{X} \pm \text{SEM}$ (N). There was no significant difference in U_{\max} or A_{\max} with developmental stage. Total length of each individual tadpole was standardised to 2.5 cm by using the allometric scaling exponents determined in this study (1.34 for U_{\max} and 1.11 for A_{\max}).

by changes in the viscosity of the water because of temperature. However, at their U_{as} , larval *L. peronii* were swimming at Re as low as 500 at 10°C. Although there were no significant changes in the scaling relationships of U_{as} with temperature, when a curvilinear regression was fitted to the U_{as} versus total length data for tadpoles at 10°C, the correlation coefficient increased by 0.15. It is possible that at 10°C, U_{as} of the smaller tadpoles may have been affected by the viscous hydrodynamic regime, which in turn may have influenced the relationship between total length and U_{as} .

There is a limited data set on the scaling of U_{\max} in fish. The generality appears to be that length-specific swimming velocity decreases with increasing total length (Archer and Johnston 1989; Videler and Wardle 1991; Gibson and Johnston 1995; James and Johnston 1998). In juvenile turbot, *Scophthalmus maximus*, U_{\max} scaled to $L^{0.74}$ in fish 0.88–8.0 cm at 18°C (Gibson and Johnston 1995), whereas in the Antarctic fish *Notothenia coriiceps*, U_{\max} scaled to $L^{0.66}$ (Archer and Johnston 1989). In a recent study, James and Johnston (1998) also found that length-specific U_{\max} during escape responses in the short-horned sculpin, *Myoxocephalus scorpius*, decreased proportionally to total length ($L^{0.47}$). These decreases in length-specific swimming velocity with increasing total length have been attributed to the contractile properties of the muscles powering burst swimming (Wardle 1980; James et al. 1998). In studies on fish muscle, maximum unloaded contraction velocity becomes slower and activation and relaxation times for isometric twitch and tetanic contractions become longer with increasing total length (Altringham and Johnston 1990; Anderson and Johnston 1992; James et al. 1998). Similar results have been reported for amphibian and mammalian muscle contractile properties, and it appears that as animal size increases, muscles become slower (Rome et al. 1990; Seow and Ford 1991; Marsh 1994; Altringham et al. 1996). Positive allometry of tail width (presumably correlated with axial muscle mass) in larval *L. peronii* would help to offset the negative allometry of the intrinsic contractile velocities of muscle and may contribute to

the observed scaling relationships of burst swimming performance.

In contrast to the scaling of U_{\max} in adult fish, length-specific swimming velocity appears to increase with increasing total length in larval fish. Length-specific U_{\max} of both larval chinook salmon (*Oncorhynchus tshawytscha*; Hale 1996) and larval winter flounder (*Pleuronectes americanus*; Williams and Brown 1992) increases with total length. Moreover, when the scaling data from Gibson and Johnston (1995) on the swimming performance of *S. maximus* are examined, it appears that the smaller size range of fish scale with a length exponent >1, whereas the larger size range scale with an exponent <1. This positive allometry is probably, in part, a consequence of developmental changes that correlate with increases in body length, including changes in body shape and the development and functioning of the musculoskeletal and nervous system. Moreover, because larval fish often swim within the viscous hydrodynamic regime, small changes in body length significantly influence the effect of water viscosity on swimming performance, which may in turn bias the scaling relationship of swimming performance toward positive allometry. Re can change by several orders of magnitude during the development and growth of fish larvae (Batty and Blaxter 1992; Müller and Videler 1996).

Unlike larval fish, the increase in length-specific U_{\max} with total length in larval *L. peronii* is not due to the effects of developmental stage or the effects of viscous forces and may be ecologically related. Larval *L. peronii* have an increased reliance on aerial respiration throughout development. The frequency of air breaths in larval *L. peronii* increases between Gosner (1960) development stages 25 and 35, resulting in an increase in surfacing behaviour and open-water activity (Wong and Booth 1994). Thus, as *L. peronii* tadpoles become larger and their dependence on aerial respiration increases, bouts of surfacing behaviour become more frequent. This increase in activity in the open water may increase their vulnerability to open-water predators throughout larval development and also

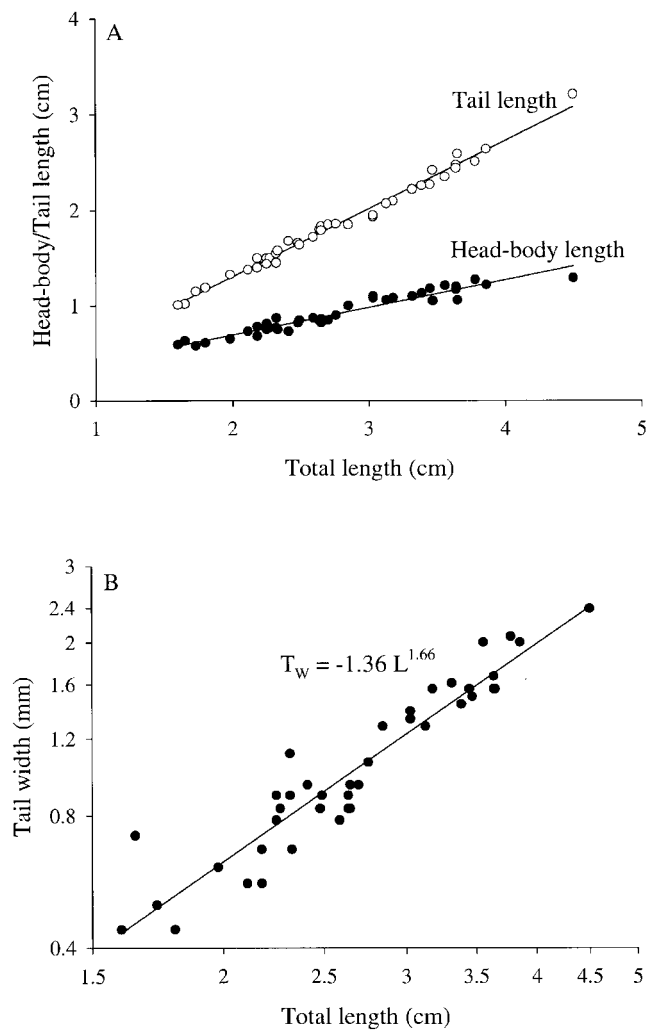


Figure 4. Relationship between total length and (A) head-body length, tail length (both linear regressions), and (B) tail width at the base in tadpoles of the striped marsh frog (*Limnodynastes peronii*). Regression line for tail width data represents a first-order polynomial fitted to a set of log-log data by using least squares regression.

may increase the importance of burst swimming performance to survival.

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Literature Cited

- Altringham J.D. and I.A. Johnston. 1990. Scaling effects in muscle function: power output of isolated fish muscle fibres performing oscillatory work. *J Exp Biol* 151:453–467.
- Altringham J.D., T. Morris, R.S. James, and C.I. Smith. 1996. Scaling effects of muscle function in fast and slow muscles of *Xenopus laevis*. *Exp Biol Online* 1:6. <http://link.springer.de/link/service/journals/00898/index.htm>.

- Anderson M.E. and I.A. Johnston. 1992. Scaling of power output in fast muscle fibres of the Atlantic cod during cyclical contractions. *J Exp Biol* 157:381–389.
- Archer S.D. and I.A. Johnston. 1989. Kinematics of labriform and subcarangiform swimming in the Antarctic fish *Notothenia neglecta*. *J Exp Biol* 14:195–210.
- Bailey K.M. and R.S. Batty. 1984. Laboratory studies of predation by *Aurelia aurita* on larvae of cod, flounder, plaice and herring: development and vulnerability to capture. *Mar Biol* 83:287–291.
- Bainbridge R. 1958. The speed of swimming of fish as related to size and to the frequency and amplitude of the tail beat. *J Exp Biol* 35:109–133.
- Batty R.S. and J.H.S. Blaxter. 1992. The effect of temperature on the burst swimming performance of fish larvae. *J Exp Biol* 170:187–201.
- Beddow T.A., J.L. Van Leeuwen, and I.A. Johnston. 1995. Swimming kinematics of fast starts are altered by temperature acclimation in the marine fish *Myoxocephalus scorpius*. *J Exp Biol* 198:203–208.
- Brown R.M. and D.H. Taylor. 1995. Compensatory escape mode trade-offs between swimming performance and maneuvering behaviour through larval ontogeny of the wood frog, *Rana sylvatica*. *Copeia* 1995:1–7.
- Domenici P. and R.W. Blake. 1997. The kinematics and performance of fish fast-start swimming. *J Exp Biol* 200:1165–1178.
- Drucker E.G. and J.S. Jensen. 1996. Pectoral fin locomotion in the striped surfperch. II. Scaling swimming kinematics and performance at a gait transition. *J Exp Biol* 199:2243–2252.
- Dudley R., V.A. King, and R.J. Wassersug. 1991. The implications of shape and metamorphosis for drag forces on a generalized pond tadpole (*Rana catesbeiana*). *Copeia* 1991:252–257.
- Fuiman L.A. and R.S. Batty. 1997. What a drag it is getting cold: partitioning the physical and physiological effects of temperature on fish swimming. *J Exp Biol* 200:1745–1755.
- Gibson S. and I.A. Johnston. 1995. Scaling relationships, individual variation and the influence of temperature on maximum swimming speed in early settled stages of the turbot *Scophthalmus maximus*. *Mar Biol* 121:401–408.
- Gosner K.L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 16:183–190.
- Hale M.E. 1996. The development of fast-start performance in fishes: escape kinematics of the chinook salmon (*Oncorhynchus tshawytscha*). *Am Zool* 36:695–709.
- Hoff K.V.S. 1987. Morphological Determinants of Fast-Start Performance in Anuran Tadpoles. PhD diss. Dalhousie University.
- Huey R.B. 1980. Sprint velocity of tadpoles (*Bufo boreas*) through metamorphosis. *Copeia* 1980:537–540.
- Huey R.B. and R.D. Stevenson. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Am Zool* 19:357–366.
- Hunter J.R. 1972. Swimming and feeding behavior of larval anchovy, *Engraulis mordax*. *Fish Bull U S* 70:821–838.
- James R.S., N.J. Cole, M.L.F. Davies, and I.A. Johnston. 1998. Scaling of intrinsic contractile properties and myofibrillar protein composition of fast muscle in the fish, *Myoxocephalus scorpius* L. *J Exp Biol* 201:901–912.
- James R.S. and I.A. Johnston. 1998. Scaling of muscle performance during escape responses in the fish, *Myoxocephalus scorpius* L. *J Exp Biol* 201:913–923.
- Johnson T.P., A.J. Cullum, and A.F. Bennett. 1998. Partitioning the effects of temperature and kinematic viscosity on the C-start performance of adult fishes. *J Exp Biol* 201:2045–2051.
- Liu H., R.J. Wassersug, and K. Kawachi. 1996. A computational fluid dynamics study of tadpole swimming. *J Exp Biol* 199:1245–1260.
- . 1997. The three-dimensional hydrodynamics of tadpole locomotion. *J Exp Biol* 200:2807–2819.
- Marsh R.L. 1994. Jumping ability of anuran amphibians. Pp. 51–111 in J.H. Jones, ed. *Advances in Veterinary Science and Comparative Medicine*. Vol. 38B. Academic Press, New York.
- Müller U.K. and J.J. Videler. 1996. Inertia as a “safe harbour”: do fish larvae increase length growth to escape viscous drag? *Rev Fish Biol Fish* 6:353–360.
- Newman R.A. 1987. Effects of density and predation on *Scaphiopus couchii* tadpoles in desert ponds. *Oecologia* 71:301–307.
- Parichy D.M. and R.H. Kaplan. 1995. Maternal investment and developmental plasticity: functional consequences for locomotor performance of hatchling larvae. *Funct Ecol* 9:606–617.
- Rome L.C., A.A. Sosnicki, and D.O. Goble. 1990. Maximum velocity of shortening of three fiber types from horse soleus muscle: implications for scaling with body size. *J Physiol* 431:173–186.
- Seow C.Y. and L.E. Ford. 1991. Shortening velocity and power output of skinned muscle fibres from mammals having a 25,000 fold range of body mass. *J Gen Physiol* 97:541–560.
- Sokal R.R. and F.J. Rohlf. 1981. *Biometry*. 2d ed. W. H. Freeman, New York.
- Swain D.P. 1992. The functional basis of natural selection for vertebral traits of larvae in the stickleback *Gastrosteus aculeatus*. *Evolution* 46:987–997.
- Tejedo M. and R. Reques. 1994. Plasticity in metamorphic traits of natterjack tadpoles: the interactive effects of density and pond duration. *Oikos* 71:295–304.
- Touloukian Y.S., S.C. Saxena, and P. Hestermans. 1975. *Viscosity. Thermophysical Properties of Matter*. Vol. 11. Plenum, New York.
- Venz M. 1996. Plasticity in the Larval Traits of Brown-Striped Marsh Frogs (*Limnodynastes peronii*): Interactive Effects of

- Larval Density with Pond Size, and Habitat Drying. Unpub. honours thesis. University of Queensland.
- Videler J.J. and C.S. Wardle. 1991. Fish swimming stride by stride: speed limits and endurance. *Rev Fish Biol Fish* 1: 23–40.
- Walker J.A. 1998. Estimating velocities and accelerations of animal locomotion: a simulation experiment comparing numerical differentiation algorithms. *J Exp Biol* 201:981–995.
- Wardle C.S. 1975. Limit of fish swimming speed. *Nature* 255: 725–727.
- . 1980. Effect of temperature on the maximum swimming speeds of fishes. Pp. 519–531 in M.A. Ali, ed. *The Environmental Physiology of Fishes*. Plenum, New York.
- Wassersug R. 1989. Locomotion in amphibian larvae (or “Why aren’t tadpoles built like fishes?”). *Am Zool* 29:65–84.
- . 1992. The basic mechanics of ascent and descent by anuran larvae (*Xenopus laevis*). *Copeia* 1992:890–894.
- Wassersug R. and K.V.S. Hoff. 1985. The kinematics of swimming in anuran larvae. *J Exp Biol* 119:1–30.
- Wassersug R.J. and E. Seibert. 1975. Behavioral responses of amphibian larvae to variation in dissolved oxygen. *Copeia* 1975:86–103.
- Wassersug R.J. and D.G. Sperry. 1977. The relationship of locomotion to differential predation on *Pseudacris triseriata* (Anura: Hylidae). *Ecology* 58:830–839.
- Watkins T.B. 1996. Predator-mediated selection on burst swimming performance in tadpoles of the Pacific tree frog, *Pseudacris regilla*. *Physiol Zool* 69:154–167.
- . 1997. The effect of metamorphosis on the repeatability of maximal locomotor performance in the Pacific tree frog, *Hyla regilla*. *J Exp Biol* 200:2663–2668.
- Webb P.W. 1977. Effects of size on performance and energetics of fish. Pp. 315–331 in T. J. Pedley, ed. *Scale Effects in Animal Locomotion*. Academic Press, New York.
- Webb P.W. and D. Weihs. 1986. Functional locomotor morphology of early life history stages of fishes. *Trans Am Fish Soc* 115:115–127.
- Weihs, D. 1980. Energetic significance of changes in swimming modes during growth of larval anchovy *Engraulis mordax*. *U S Fish Wildl Ser Fish Bull* 77:597–604.
- Williams P.J. and J.A. Brown. 1992. Development changes in the escape response of larval winter flounder *Pleuronectes americanus* from hatch through metamorphosis. *Mar Ecol Prog Ser* 88:185–193.
- Wong S. and D.T. Booth. 1994. Hypoxia induces surfacing behaviour in brown-striped frog (*Limnodynastes peronii*) larvae. *Comp Biochem Physiol A Mol Integr Physiol* 109:437–445.