

THE KINEMATICS OF VOLUNTARY STEADY SWIMMING OF HATCHLING AND ADULT AXOLOTLS (*AMBYSTOMA MEXICANUM* SHAW, 1789)

KRISTIAAN D'AOÛT (*) AND PETER AERTS

Department of Biology, University of Antwerp (U.I.A.),
Universiteitsplein 1, B-2610 Antwerpen (Wilrijk), Belgium
e-mail : kdaout@uia.ua.ac.be

Abstract. Axolotls swim throughout post-hatching ontogeny. This coincides with an approximately twentyfold range in total body length (L), which may imply unfavourable differences in encountered flow regime (viscous *versus* inertial) during ontogeny. Using high-speed video (500 fields s^{-1}), we analysed the kinematics, mechanical efficiency, swimming speeds and flow regime of swimming hatchlings (approximately 0.01 m L , «stage 1»), 2 week old animals (approximately 0.02 m L , «stage 2») and 20 week old animals (approximately 0.08 m L , «stage 3»), and compared the data with similar data from adults (0.135-0.238 m L , «stage 4»).

All stages swim by passing waves of lateral curvature down the body. The kinematics, described by the characteristics of this wave (speed, frequency, length, amplitude) are largely comparable in all four stages: within each stage, swimming speed is increased by increasing the wave frequency only. Mechanical swimming efficiency, estimated by means of Lighthill's elongated-body theory, is about 5% lower in hatchlings than in adults.

The most striking result is that the observed, voluntary absolute swimming speeds from stage 1 to stage 4 are much more similar than would be expected given the twenty-fold L range. Possible explanations are ecological and/or hydrodynamical. Firstly, predator escape success increases as the swimming speed increases. Secondly, by adopting high speeds, axolotls increase Reynolds numbers, and thus avoid having to swim in the unfavourable viscous flow regime.

Key words: *Ambystoma mexicanum*, axolotl, swimming, ontogeny, flow regime.

INTRODUCTION

Axolotls, being neotenic salamanders, maintain a larval habitus throughout ontogeny (BRUNST, 1955). Total body length (L), however, ranges from about 0.01 m (post-hatching) to 0.25 m or more for adults. This paper deals with the effect of body size on locomotion and, more specifically, with the mechanical consequences of swimming at the full range of post-hatching body lengths.

(*) Present address: Laboratory for Functional Morphology, Department of Biology, University of Antwerp (U.I.A.) Universiteitsplein 1, B-2610 Antwerpen (Wilrijk), Belgium

The thrust and drag (which are quantitatively equal in the case of steady swimming) during swimming arise from two different forces acting on the animal's body and in the water close to the body (WEBB, 1975): inertial forces and viscous forces. Their ratio (inertial/viscous forces) is the Reynolds number (Re). Re indicates the governing flow regime and is of crucial importance to an understanding of the dynamic environment in which the animal moves. It is calculated as follows:

$$Re = \frac{L \cdot U}{\mu/\rho} \quad (1)$$

with L being a relevant length (mostly, and in this paper, total body length), U the swimming speed, μ the viscosity and ρ the density of the medium. The ratio μ/ρ is the kinematic viscosity and equals $1.002 \cdot 10^{-6} \text{ m}^2\text{s}^{-1}$ for fresh water at 20°C (calculated from μ and ρ data in WEAST, 1974). Changes in the kinematic viscosity result from changes in water salinity (e.g. typically 3.5% lower in sea water than in fresh water) and more importantly, from changes in temperature (FUIMAN & BATTY, 1997). However, for most biological studies, Re is estimated from L and U only, keeping kinematic viscosity constant. At low Re (< 1), viscous forces dominate and inertial forces can be neglected (this is the case for small and slow animals, e.g. swimming bacteria, sperm cells). At high Re (e.g. swimming fish, Re typically around 10^4 - 10^5), inertial forces dominate, and viscous forces are only quantitatively important in the animal's boundary layer (WEBB, 1975). Briefly, low Re indicates a «viscous» flow regime, high Re an «inertial» flow regime, with the threshold around a Reynolds number of 200 (WEIHS, 1980; WEBB & WEIHS, 1986). Theoretical (WEIHS, 1980) and experimental (VYMEN, 1974) studies indicate that swimming in the two flow regimes is accompanied not only by considerable differences in swimming style, but also in body morphology (e.g., see MÜLLER & VIDELER, 1996), because constructional demands also change with the flow regime (cf. OSSE, 1990, and references therein). Therefore, if larvae could swim in an inertial flow regime, they would be subject to similar physical constraints as the adults (WEBB & WEIHS, 1986), and design changes (which likely require a lot of energy) would be unnecessary.

Throughout their ontogeny, axolotls are likely to encounter a wide range of Reynolds numbers, because their L varies approximately 20-fold. D'AOÛT & AERTS (1997) found that adult axolotls voluntarily swim at approximately 1 L/s. If this remains true for larvae of 0.01-0.015 m, Re would range from 80 to 200, and axolotls would have to switch from viscous to inertial swimming very soon after hatching, when energy allocation is crucial and predation pressure high.

Many fish larvae hatch in the viscous flow regime and reach the inertial flow regime around first feeding (MÜLLER & VIDELER, 1996). MÜLLER & VIDELER (1996) found that larvae from all analysed species do not, however, adapt to their flow regime, but grow disproportionately in length to escape from the viscous regime into the «safe harbour» (SHINE, 1978) of inertial swimming as fast as possible.

Apart from increasing body length, there is another way to reach the inertial flow regime: increasing swimming speed. D'AOÛT & AERTS (1997) found that, within the limited observed size range of adults (0.135-0.238 m), small individuals swim relatively faster than big individuals. If this trend holds true for larvae, they may indeed escape from the viscous flow regime by swimming faster. This would, apart from the hydrodynamic

advantages, also have an ecological advantage, which is absent in the case of increased length growth: the higher the animal's speed, the higher its escape success will be (GARLAND, 1994). High relative locomotor speed (in body lengths per second) would further enhance escape probability of larvae in a stage where it is especially prone to predation (VAN DAMME & VAN DOOREN, 1999).

This paper focuses on swimming kinematics and speeds, and investigates the following points: (1) does the swimming style of larval and adult axolotls differ, (2) do larvae swim relatively faster than adults and (3) do they succeed in escaping the viscous flow regime?

MATERIALS AND METHODS

Experimental animals

Prior to experiments, Mexican axolotls, *Ambystoma mexicanum* Shaw, 1789 (Amphibia: Caudata: Ambystomatidae), were kept in an aerated freshwater tank at room temperature. After spawning of one individual, eggs were transferred to another tank and regularly checked. Dead or fungus-infected eggs were immediately removed. About 80% of the eggs hatched.

First-day hatchlings, defined here as «stage 1» individuals, were randomly selected and used for video recordings. After 2 and 20 weeks, a random selection of individuals was made (defined here as «stage 2» and «stage 3» individuals, respectively) and these were again used for video recordings (see also Table 1). «Stage 4» animals are adults from 0.135-0.238 m total body length, previously analysed by D'AOÛT & AERTS (1997). In this way, early post-hatching stages (stages 1 and 2, see aims in the Introduction) can be compared with adults (stage 4) and with specimens of smaller body size, but with an adult habitus (stage 3).

Recording of the swimming sequences

During recording sessions, animals were placed in an appropriate set-up consisting of a petri dish (diameter 0.19 m, depth 0.03 m; stages 1 and 2) or of two open aquaria, interconnected by a closed glass tunnel (height = 0.1 m; width = 0.15 m; length = 1 m; stages 3 and 4). Both set-ups included reference grids. Animals were video-taped in dorsal view at 500 fields s⁻¹ using a NAC-1000 high-speed video system equipped with a Fujinon 12.5-75 mm zoom lens. In the cases of the stage 1 or 2 animals, B&H (Schneider-Kneuznach) close-up diopters were fitted to the lens to increase magnification. Animals were sometimes stimulated to swim by gently touching them with a fine probe, but they were free to select their swimming speed («preferred» or «voluntary» speed) as they were not chased, or made to swim against an externally induced flow.

Water temperature was 20 ± 2 °C during both the acclimatisation and the experiments. Kinematic viscosity differences in this range are about ± 5% and are neglected; for Re calculations the kinematic viscosity value of 1.002 10⁻⁶ m²s⁻¹ was used (see Introduction).

Analysis of the high-speed video sequences

For analysis, only rectilinear swimming trials consisting of at least three complete cycles were used. Three representative swimming bouts from each stage were thus selected for a complete analysis and compared with 28 «stage 4» sequences (D'AOÛT & AERTS, 1997).

All animals swam at the bottom in all analysed sequences, representing the normal behaviour in aquaria (pers. obs.) and most likely also in nature, where axolotls live at the bottom of lakes (SMITH & SMITH, 1971). For each frame, the dorsal midline was digitised using a NAC-1000 XY coordinator connected to a PC. For details about further data processing, we refer to D'AOÛT & AERTS (1997). The dorsal midlines of the animals are described by 20 segments of 0.05 L, delimited by 21 points (the «body points», BP), point 1 being the snout tip and point 21 being the tail tip.

We studied the following parameters: (1) swimming speed U (m/s), the forward speed of the animal calculated as the displacement of the snout tip divided by the corresponding time period; (2) wave speed V (m/s), the speed of the wave of propulsion, relative to the animal's body (thus, not to the external frame of reference); (3) wave frequency f (Hz), the reciprocal value of the wave period, *i.e.* the duration of one complete cycle; (4) stride length, the distance travelled in one complete cycle (*i.e.* with one tailbeat; VIDELER, 1993), (5) wave length λ , the length of the propulsive wave on the body, and (6) the amplitudes A (m) of the 21 body points (BP). The maximal amplitude A (= maximal lateral deflection from the mid-position) was determined for every body point; the graph representing these amplitudes as a function of position along the body is further referred to as the amplitude profile. To allow comparison of U , A and λ different-sized animals, these parameters were scaled to the total body length yielding specific speed U_{sp} , specific amplitude A_{sp} and specific wave length λ_{sp} .

Because of the range of animal sizes (L) and swimming speeds, fluid dynamical regimes may differ drastically. To account for differences in flow regime, Reynolds numbers (Re) were calculated (see Introduction). In addition, dimensionless frequency was calculated as follows:

$$f_{di} = \frac{f \cdot L^2}{U \cdot \rho} \quad (2)$$

In this way, dimensionless frequency (f_{di}) times dimensionless stride length (the distance travelled with exactly one complete cycle, normalised for L) yields Re .

Based on the kinematical data, the (hydro)mechanical efficiency of swimming was calculated, *i.e.* the ratio of propulsive power to the mechanical power produced by the swimming animal. LIGHTHILL's (1960) elongated body theory is widely used and has, for tadpoles of *Rana catesbeiana*, proven to give accurate estimations in quantitative terms (*e.g.*, LIU *et al.*, 1996). The elongated-body theory has a number of inherent limitations (for details, see D'AOÛT & AERTS, 1997) but, since the body shape of larval and adult axolotls does not change drastically, this theory can be used to compare mechanical swimming efficiencies. Also propeller efficiency (or slip factor), defined as U/V , was calculated. Since V is always greater than U during steady swimming, the propeller efficiency can range from zero to values close to the theoretical maximum of one.

In order to have a wider range of swimming speeds and frequencies for stage I larvae, 30 rectilinear, steady sequences of 3-9 cycles were randomly selected (in addition to the three analysed in detail, see above), and mean U and mean f were calculated. These additional data extended the data set on Reynolds numbers of hatchling axolotls.

TABLE I

Overview of the kinematic variables and calculated efficiencies for three sequences of stages 1-3. Data can be compared with literature data on stage 4 (D'AOÛT & AERTS, 1997). For details, we refer to the Material and Methods section. L , total body length (m); U , swimming speed (m/s); U_{sp} , specific swimming speed (L/s); V , wave speed (m/s); f , swimming frequency (Hz); wave length λ (m); A_{sp} , specific tail tip amplitude (L); U/V (dimensionless), propeller efficiency (slip factor; dimensionless); EBT, efficiency using LIGHTHILL's (1960) elongated-body theory (dimensionless); $strl$, stride length (m); $strl_{sp}$, specific stride length (bodylengths); λ_{sp} , specific wave length (bodylengths).

<i>seq</i>	<i>stage</i>	L	U	U_{sp}	V	f	λ	A_{sp}	U/V	EBT	$strl$	$strl_{sp}$	λ_{sp}
d54	1	0.010	0.106	10.2	0.190	18.7	0.010	0.368	0.563	0.782	0.006	0.549	0.976
d58	1	0.010	0.104	10.0	0.211	19.3	0.011	0.289	0.500	0.750	0.005	0.520	1.038
d53	1	0.011	0.115	10.8	0.242	23.1	0.010	0.199	0.494	0.747	0.005	0.470	0.937
	mean	0.010	0.108	10.3	0.214	20.37	0.010	0.285	0.519	0.760	0.006	0.513	0.984
	s.e.	0.0006	0.0059	0.416	0.026	2.39	0.0006	0.085	0.038	0.019	0.00058	0.040	0.0509
d55	2	0.018	0.078	4.29	0.156	9.13	0.017	0.276	0.504	0.752	0.009	0.470	0.956
d56	2	0.018	0.097	5.39	0.217	13.0	0.016	0.156	0.451	0.726	0.007	0.414	0.874
d57	2	0.022	0.097	4.33	0.198	10.9	0.019	0.183	0.499	0.750	0.009	0.399	0.855
	mean	0.0193	0.091	4.67	0.190	11.0	0.017	0.205	0.485	0.743	0.008	0.428	0.895
	s.e.	0.0023	0.011	0.62	0.031	1.94	0.0015	0.063	0.029	0.014	0.001	0.037	0.054
d50	3	0.066	0.271	4.10	0.553	11.7	0.049	0.186	0.492	0.746	0.023	0.349	0.748
d52	3	0.085	0.151	1.78	0.306	5.75	0.047	0.082	0.496	0.748	0.026	0.309	0.548
d51	3	0.088	0.132	1.50	0.248	4.50	0.068	0.105	0.534	0.767	0.029	0.333	0.767
	mean	0.080	0.185	2.46	0.369	7.32	0.055	0.124	0.507	0.754	0.026	0.330	0.688
	s.e.	0.012	0.075	1.43	0.162	3.85	0.012	0.055	0.023	0.012	0.003	0.020	0.121

RESULTS

According to BREDER's (1926) definition, axolotls of all stages have an anguilliform swimming mode, characterised by a wave of curvature travelling down the body faster than the animal's swimming speed (Fig. 1).

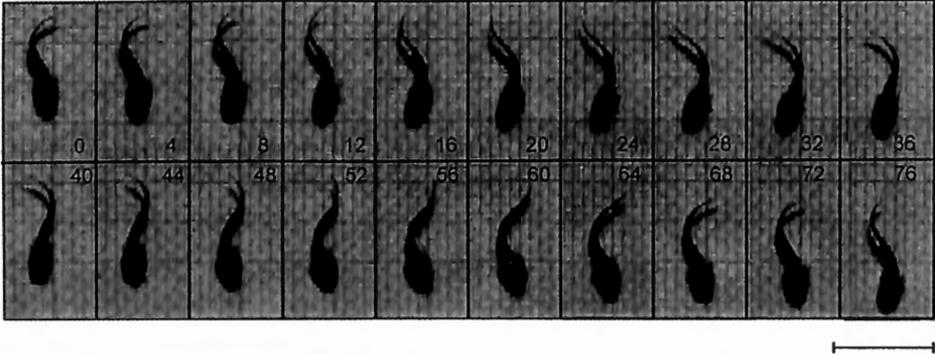


Fig. 1. – Dorsal-view video images illustrating approximately one swimming cycle of a stage 1 individual of *Ambystoma mexicanum*. The time interval between successive frames is 4 ms, the scale bar is 0.01 m. The swimming style of this hatchling animal is qualitatively similar to adults (see fig. 2 in D'AOÛT & AERTS, 1997).

The amplitude of the wave of propulsion is not constant, but changes as a function of the location along the body: the head region oscillates least, although still considerably (e.g. approximately 10% L in stage 1), and the amplitude increases to reach a maximum at the tail tip (Fig. 2). Maximal specific tail tip amplitudes decrease during ontogeny and are approximately 0.285 L for stage 1, 0.205 L for stage 2, 0.124 L for stage 3 (Table 1) and 0.097 L for

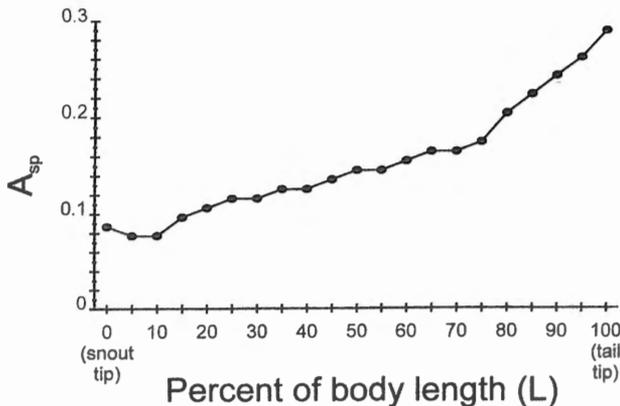


Fig. 2. – Specific amplitude as a function of position along the body, for a representative sequence of a stage 1 individual. Amplitude is smallest (but not zero) in the head region and increases towards the tail, where amplitude is maximal.

stage 4 (D'AOÛT & AERTS, 1997). Specific stride length is clearly higher in stages 1 and 2 (0.513 and 0.428, respectively), than in stages 3 and 4 (0.330 and 0.345, respectively).

In stages 1 to 3, the frequency of the propulsive wave (f) increases linearly with U_{sp} (Fig. 3), as it does in the size range represented by stage 4 (D'AOÛT & AERTS, 1997). It is, however, important to focus on dynamically similar conditions when kinematic variables between different-sized animals at different speeds are compared. Therefore, we plotted the dimensionless frequency as a function of Reynolds number, for all available data of the four stages (after log-log transformation, see Fig. 4). Clearly, f_{di} relates directly to Re , and the previously observed linear relationship between frequency and speed remains valid when the fluid dynamical regime is taken into account. Note that early stages have a low Re , but high U_{sp} (compare Figs 2 and 3).

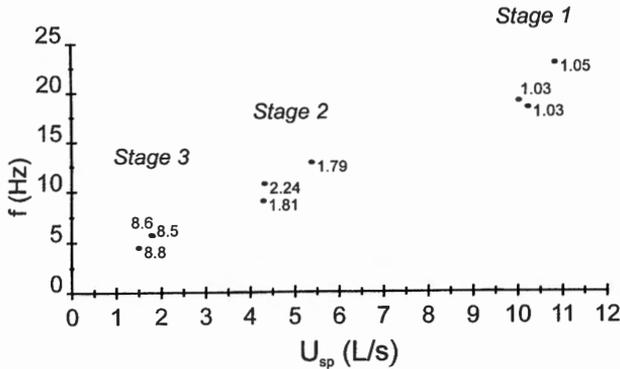


Fig. 3. – Swimming frequency as a function of specific swimming speed for 3 sequences each of stage 1-3 axolotls. L (cm) is indicated at the data point. Note that smaller individuals have higher specific swimming speeds. As in adult axolotls (stage 4), specific swimming speed is directly related to frequency.

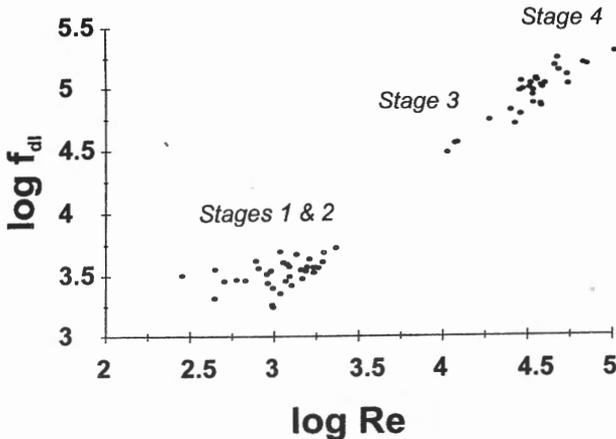


Fig. 4. – Dimensionless frequency as a function of Reynolds number (log-log transformed) for stage 1-4 individuals (including the 30 sequences of stage 1 that were not analysed in more detail). Animals with a 20-fold range in body length have a similar relationship between dimensionless values (Re resp. f_{di}).

Absolute voluntary swimming speed increases from stage 1 to stage 4 (Fig. 5 and Table 1), but it should be noted that the ontogenetic variation in swimming speeds is much smaller than the differences in body length between the four stages. Fig. 6 and Table 1 show that U_{sp} (which accounts for L differences) reaches much higher values for small larvae (stages 1, 2) than for large larvae and adults (stages 3 and 4, respectively).

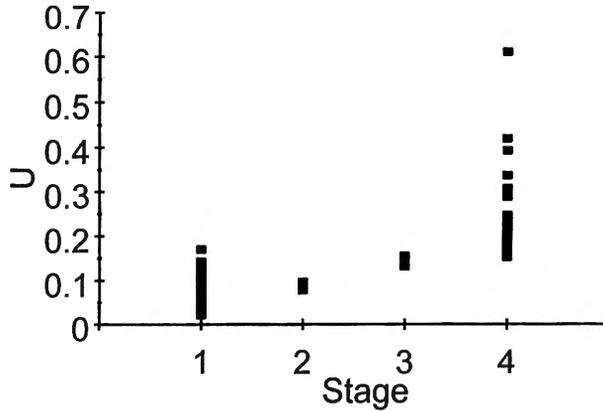


Fig. 5. – Observed swimming speeds (U) for stage 1-4 axolotls. Larval axolotls clearly swim more slowly than adults, but the difference is less than the 20-fold difference in L .

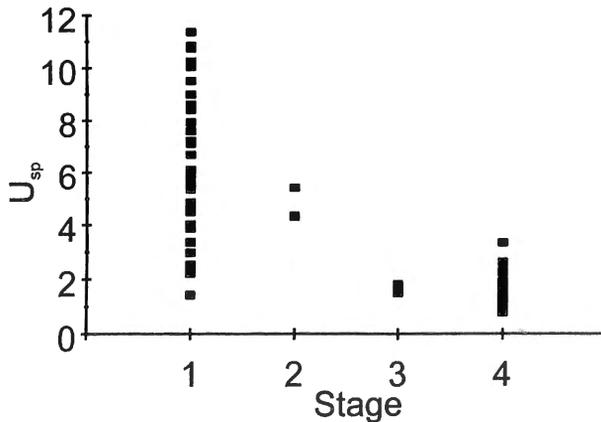


Fig. 6. – Observed specific swimming speeds (U_{sp}) for stage 1-4 axolotls. Larvae can swim at much higher specific swimming speeds than adults.

Fig. 7 depicts the observed log-transferred Reynolds numbers for the different stages. Reynolds numbers range from $2.48 \cdot 10^2$ to $1.98 \cdot 10^3$ for stage 1 ($N = 36$), and from $1.59 \cdot 10^4$ to $8.63 \cdot 10^4$ for adults ($N = 28$). Stages 2 and 3 have intermediate Reynolds numbers ($N = 3$, for both stages).

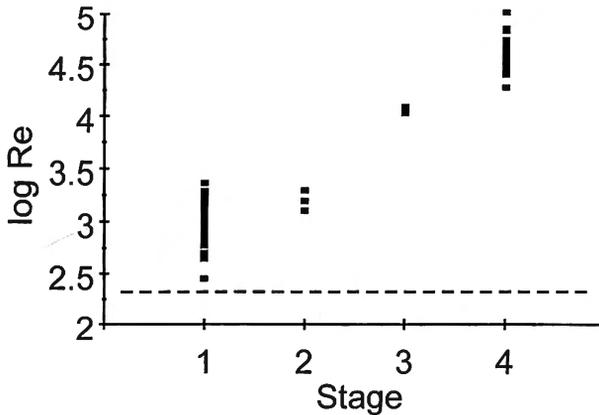


Fig. 7. – Observed Reynolds numbers (Re) for stage 1-4 axolotls. Note that, even for the slowest observed sequences of stage 1 animals, Re is higher than 200. As a consequence, axolotls swim in the inertial flow regime throughout ontogeny.

Mechanical swimming efficiencies, estimated by LIGHTHILL's (1960) elongated-body theory, differ little between stages 1 to 3, and are, with mean values of 0.743 to 0.760, slightly (respectively, 4.5% to 6.7%) lower than the mean efficiency of stage 4 animals.

DISCUSSION

In this paper, we compared the swimming style, efficiency, speeds and flow regime of larval versus adult axolotls. Qualitative comparison (Figure 1) and analysis of several kinematic variables show that the swimming style of axolotls remains remarkably similar throughout ontogeny and can be compared with literature data of other anguilliform swimmers (e.g. adult axolotls, D'AOÛT & AERTS, 1997; *Siren intermedia*, GILLIS, 1997; *Anguilla rostrata*, GILLIS, 1998). Axolotls of all post-hatching ontogenetic stages have a largely comparable swimming style, characterised by the presence of a body wave, travelling from head to tail with increasing amplitude. The specific swimming speed correlates linearly with wave frequency, as in most fishes (VIDELER, 1993). A striking difference, however, is the amplitude of this wave, which is larger for larvae than for adults (see Table 1). This causes an important head yaw due to angular recoil forces (BATTY, 1981), also found in anuran tadpoles (WASSERSUG, 1989).

Using LIGHTHILL's (1960) elongated-body theory, we have shown that larval stages (1-3) swim slightly less efficient (by approximately 5%) than do adults, and about 10% less efficient than do anuran tadpoles (WASSERSUG & HOFF, 1985). A puzzling finding, however, is that relative stride length is clearly longer for larvae than for adults (see Table 1). While adults need about three cycles to travel their own body length (specific stride length 0.345, D'AOÛT & AERTS, 1997), stage 1 larvae need only about two (specific stride length 0.513, Table 1). Since the slip factor (or propeller efficiency), and elongated-body efficiency of all stages are similar, this finding has to be the result of differences in specific wave length λ_{sp} . Indeed, the specific wavelength decreases from about 0.98 at stage 1 (this

paper) to 0.60 at stage 4 (D'AOÛT & AERTS). Thus, less waves are present on the larval body (approximately 1) than on the adult body (approximately 1.7) at any instant of the swimming cycle. Evidently, since the slip remains the same, a wave that travels down the full length of the body within one cycle, propels the animal further than a similar wave that travels over only 0.6 of the body length (Table 1).

Apart from similarities in swimming style, small axolotls were observed to swim at much higher specific swimming speeds (up to 11.4 L/s) than adults (up to 3.3 L/s). Since, at all stages, a linear relationship was observed between preferred specific swimming speed and frequency, frequencies of larvae are much higher, accordingly. This is in contrast to fish larvae, the swimming speeds of which increase linearly with size (BLAXTER, 1986), so that specific swimming speed remains approximately constant.

The relatively high swimming speed of larvae has important consequences in relation to the flow regime the animal encounters, since Reynolds number increases linearly with swimming speed (Equation 1). Like fish larvae, axolotl larvae can, at first glance, be assumed to swim in the viscous flow regime ($Re < 200$), which is most likely not beneficial (see Introduction). WEBB & WEIHS (1986) argued that most biological functions in fish larvae occur at higher Re (> 200), because then, constraints towards hydrodynamical activities (feeding, breathing, swimming) would remain similar throughout ontogeny. Fish larvae acquire relatively high Re by increased length growth (MÜLLER & VIDELER, 1996; see also WEBB & WEIHS, 1986; FUIJMAN, 1983; OSSE, 1990), or by kick-and-glide swimming (WEIHS, 1980). Axolotl larvae acquire $Re > 200$ from the moment of hatching because of their high swimming speed. Thus, both fish and axolotl larvae succeed in escaping from the viscous flow regime, but by different means. Axolotls swim in the inertial flow regime from the instant of hatching, so they do not have to switch from viscous to inertial swimming during ontogeny. Hence, physical constraints towards the swimming mode would remain similar, and similar forms would correlate with similar (swimming) behaviour (WEBB & WEIHS, 1986).

Escaping the viscous flow regime by speed increase has an advantage, of an ecological nature, that length increase does not offer: increased escape success. Larvae are highly predated, and mortalities are high (e.g. see PEPIN, 1991, for fish larvae). Obviously, a higher absolute speed will increase the chance of escape from a predator (GARLAND, 1994). Since axolotl larvae are able to swim at least as fast as the preferred speed of adults (Fig. 5, and D'AOÛT & AERTS, 1997), they would likely have good escape chances. Recent evidence (VAN DAMMEN & VAN DOOREN, 1999) argues that specific speed is an even better predictor of escape success than absolute speed. In this case, escape success of axolotl larvae would increase even more, since specific speeds are very high (Fig. 6).

To conclude, the relatively high swimming speed acquired by axolotl larvae is both hydrodynamically and ecologically beneficial, i.e. to escape the viscous flow regime, and to increase the chances of successful escape from predators.

ACKNOWLEDGEMENTS

We gratefully acknowledge Dr. Frits De Vree for the support during the work in his lab. Dr. R. Van Damme, Dr. A. Herrel and four anonymous referees made valuable comments on an earlier version of the manuscript. We explicitly thank Dr. J. Mees for the editing of this paper. This research

was supported by a University of Antwerp research grant (BOF UA 1996, project number 2882) to P.A., who is a research director from the Fund for Scientific Research - Flanders (F.W.O.).

REFERENCES

- BATTY, R.S. (1981) – Locomotion of plaice larvae. *Symp. Zool. Soc. Lond.*, **48**: 53-69.
- BLAXTER, J.H.S. (1986) – Development of sense organs and behaviour of teleost larvae with special reference to feeding and predator avoidance. *Trans. Am. Fish. Soc.*, **115**: 98-114.
- BREDER, C.M. (1926) – The locomotion of fishes. *Zoologica*, **4**: 159-297.
- BRUNST, V.V. (1955) – The axolotl (*Siredon mexicanum*). I. As material for scientific research. *Lab. Invest.*, **4**: 45-64.
- D'AOÛT & P. AERTS (1997) – Kinematics and efficiency of steady swimming in adult axolotls (*Ambystoma mexicanum*). *J. Exp. Biol.*, **200**: 1863-1871.
- FUIMAN, L.A. (1983) – Growth gradients in fish larvae. *J. Fish. Biol.*, **23**: 117-123.
- FUIMAN, L.A. & BATTY, R.S. (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.
- GARLAND, T. JR. (1994) – Phylogenetic analyses of lizard endurance capacity in relation to body size and body temperature. In: *Lizard ecology*. VITT, L.J. & E.R. PIANKA (Eds.). Princeton University Press, Princeton: 237-260.
- GILLIS, G.B. (1997) – Anguilliform locomotion in an elongate salamander (*Siren intermedia*): effects of speed on axial undulatory movements. *J. Exp. Biol.*, **200**: 767-784.
- GILLIS, G.B. (1998) – Environmental effects on undulatory locomotion in the American eel *Anguilla rostrata*: Kinematics in water and on land. *J. Exp. Biol.*, **201**: 949-962.
- LIGHTHILL, M.J. (1960) – Note on the swimming of slender fish. *J. Fluid Mech.* **9**: 305-317.
- LIU, H., R.J. WASSERSUG & K. KAWACHI (1996) – A computational fluid dynamics study of tadpole swimming. *J. Exp. Biol.*, **199**: 1245-1260
- MÜLLER, U.K. & J.J. VIDELER (1996) – Inertia as a «safe harbour»: Do fish larvae increase length growth to escape viscous drag? *Reviews in Fish Biology and Fisheries*, **6** (3): 353-360.
- OSSE, J.W.M. (1990) – Form changes in fish larvae in relation to changing demands of function. *Neth. J. Zool.*, **40** (1-2): 362-385.
- PEPIN, P. (1990) – Effect of temperature and size on development, mortality, and survival of pelagic early life history stages of marine fish. *Can. J. Fish. aquat. Sci.*, **48**: 503-518.
- SHINE, R. (1978) – Propagule size and parental care: the «safe harbor» hypothesis. *J. theor. Biol.*, **75**: 417-424.
- SMITH, H.M. & R.B. SMITH (1971) – *Synopsis of the herpetofauna of Mexico, vol. 1, Analysis of the literature on the Mexican Axolotl*. Augusta: Lundberg Press.
- VAN DAMMEN, R. & T.J.M. VAN DOOREN (1999) – Absolute versus per unit body length speed of prey as an estimator of vulnerability to predation. *Anim. Behav.*, **57**: in press.
- VIDELER, J.J. (1993) – *Fish swimming*. London: Chapman & Hall.
- VLIMEN, W.J. (1974) – Swimming energetics of larval anchovy, *Engraulis mordax*. *Fish. Bull. nat. mar. Fish. Serv. U.S.*, **72**: 885-899.
- WASSERSUG, R.J. (1989) – Locomotion in amphibian larvae (or Why aren't tadpoles built like fishes?). *Am. Zool.*, **29**: 65-84.
- WASSERSUG, R.J. & K. HOFF (1985) – The kinematics of swimming in anuran larvae. *J. Exp. Biol.*, **119**: 1-30.

- WEAST, R.C. (1974) – *Handbook of chemistry and physics. A ready-reference book of chemical and physical data*. Cleveland: CRC Press.
- WEBB, P.W. (1975) – Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Bd Can.*, **190**: 1-158.
- WEBB, P.W. & WEIHS, D. (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*. *Fish. Bull. nat. mar. Fish. Serv. U.S.*, **77**: 597-604.