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Estimation of swimming performance of juvenile *Tilapia mossambica* (Jones and Sarojini, 1952) under controlled environment

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Abstract: **Overall physical ability of a fish can be evaluated by the estimation of the swimming performance under controlled environment. The critical swimming speed of juvenile *Tilapia mossambica* (Fork length 1.1cm±0.1, mean±S.D., N=8) was estimated using customized Brett type swimming tunnel with controlled water velocity. The critical swimming speed ($U_{crit.}$) of juvenile *T. mossambica* was 8.8 BL S^{-1} (body length) with average swimming duration was 46.25±13.1 minute (mean±S.D.) and average travelled distance was 198.8±22.68 meter (mean±S.D.). The length of undulatory caudal region of *T. mossambica* was 43.68%±2.10 and 37.48%±1.30 (mean±S.D.) against FL (Fork Length) and SL (Standard Length) respectively. The mechanistic model of the caudal fin propulsion gives assumptions of the basic swimming dynamics and metabolic expenses during the carangiform type of swimming in *T. mossambica*.**

Keywords: **Swimming performance, *Tilapia mossambica*, Critical swimming speed, Aspect ratio.**

I. INTRODUCTION

Different types of swimming pattern can be seen during fish swimming according to their shape, size, fin structures, behaviour and habitat [19]. Swimming helps fish for their locomotion or survival by fulfilling their routine needs like feeding, predator prey interaction, reproduction etc. Studying fish swimming performance may help in understanding their ecology and overall physiology [1] [6] [12]. The fish swimming performance can be analyzed for three different types of swimming *viz;* sustained swim, prolonged swim and burst swim [19]. The main objectives of swimming tests are the observation of fish swimming pattern at controlled speed and its relation with metabolic costs during swimming [16] [18] [30]. We can also get the other relative information's like propulsive pattern of fins, swimming kinematics, behaviour etc. [8] [10] [15] from fish swimming analysis. The overall swimming performance analysis of a fish also may provide important information's about the disease, effects of changes in surrounding environments, etc. [7] [21]. The analysis of dynamics of fish swimming is one of the growing fields of scientific robotics and under water vehicles development research [15]. A fish can show accelerating, cruising and manoeuvring pattern of swimming [26]. Most fishes show accelerating, by generating thrust using their backward moving propulsive wave of muscular body and caudal fin [26] where manoeuvring and stability mostly depends on median or pectoral fin movements [32]. Undulatory or oscillatory motions are the basic movement characteristics of fin propulsion. Fish uses both types of motion of fins synergistically, to achieve their swimming. Fish bend their muscular tail to produce undulatory motion of caudal region, which depends on the aerobic and anaerobic muscle energetics [23]. The oxidative red muscle helps in sustain and prolonged swimming and glycolytic white muscle helps in burst or rapid swimming [16]. According to thrust generating region or propulsive elements of fish trunk and caudal region, the swimming patterns of fish can be categorized as anguilliform, subcarangiform, carangiform, thunniform and ostraciiform swimming etc. [17] [26]. Fish belongs to order Perciformes also considered as labriform swimmer, which shows oscillatory movements of pectoral fin to generate thrust [8] [30]. In this present study, we estimated overall swimming performances of *Tilapia mossambica* by critical swimming (U_{crit}) analysis [14] [28] for its physiology and prolonged swimming test [5] [33] for caudal fin propulsive pattern analysis, also will help to find the basic mechanistic properties of swimming of *T. mossambica*.

II. MATERIALS AND METHODS

A. Experimental organism

Late larval stage [13] of Juvenile *Tilapia mossambica* was collected from local fish farm. Collected *T. mossambica* were kept in stocking glass aquarium, measured (L×W×H: 18×10×10 inch) in laboratory condition for seven days to recover from transportation stress. The water of the stocking tank was aerated with a low flow air pump (210 L/hour) continuously with maintained day night length (12D:12N hr) using standard aquarium light. The water of stocking tank was partially (~15%) replaced with fresh water daily. The juvenile fish were feed twice a day with crusted common aquarium fish food floating pallets. The feeding was completely stopped 24 hrs before the experiment. The early juvenile stage (15-20 dpf; day post hatch) of *T. mossambica* (N=8) with fork length 1.15 ±0.1 cm mean±S.D. was used for this study.

B. Instrumental setup

The experiment was carried out using small Brett type swimming tunnel (Fig. 1) [2] [3] [5] prepared in laboratory with small glass tube, micro DC water pump, microcontroller, PWM (Pulse Width Modulation) motor driver and hall sensor based flow meter [24]. The glass tube with inside diameter was 0.9 cm and length was 5cm, serves as swimming area (Fig. 2A & 3A). The flow of the tunnel was controlled by controlling the rotational speed of the impeller of the micro pump motor using microcontroller with PWM control (Fig. 2C). Water flow through the test chamber was monitored using the digital velocity data obtained from the water flow sensor (Sea-YF-S401- Flow pulse characteristics: Flow= (98xQ)±2%; Q=Liter/minute) attached to the same microcontroller (Fig 2. A). Water flow was also calibrated manually by measuring the amount of water passing through the test chamber for unit time. The swimming area was covered from both side by removable flow straighter made with small circular thin plastic tubes, which can be placed in position after entering the test fish inside the test chamber (Fig 2. A). Testing area was fully submerged inside water holding tank (L×W×H: 10×4×4 inch) (Fig. 3B), where water was continuously circulated through test chamber during experiment.

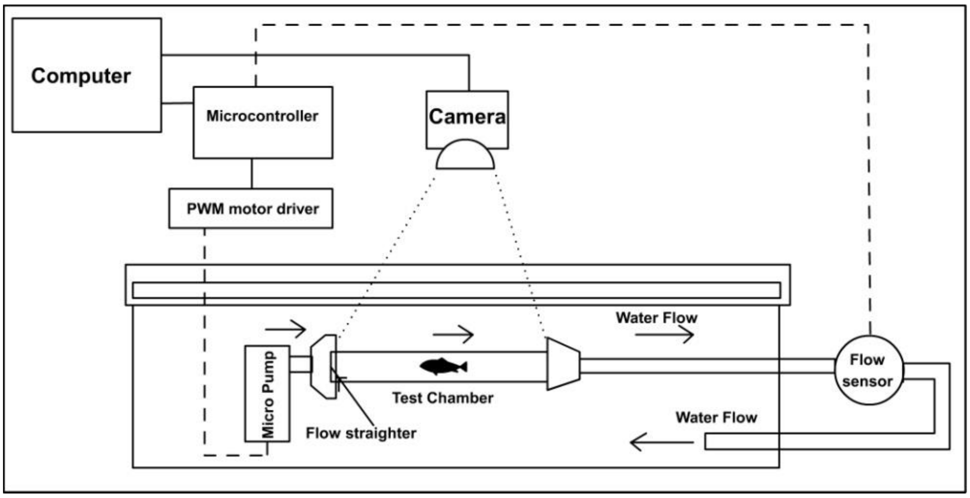

Figure 1: Schematic representation showing the instrumental setup

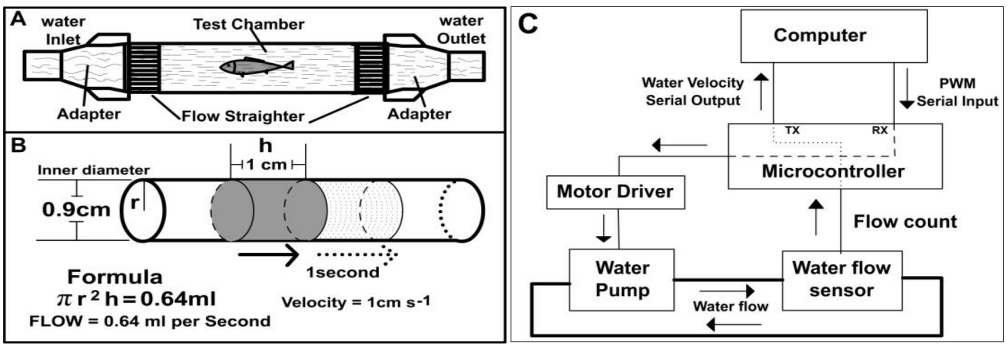

Figure 2: Schematic representation showing; A- Test chamber, B- Velocity calculation C- Work flow model of the instrument.

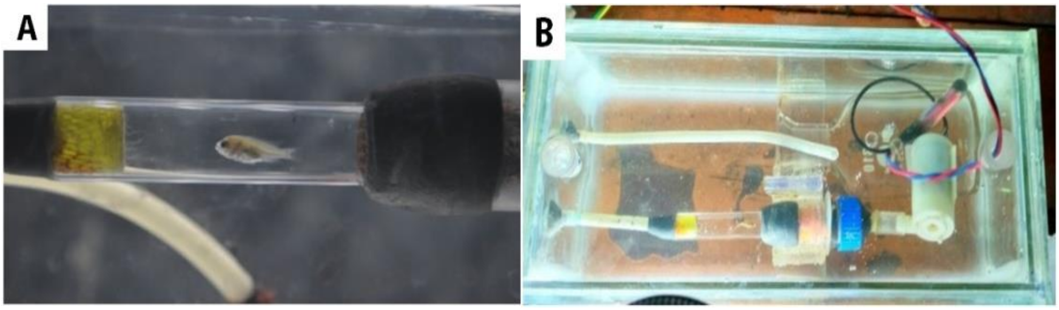

Figure 3: The actual setup of the experiment.

A. The experiment fish inside the test chamber.

B. Test chamber inside the water holding tank.

C. Experimental design

After introducing the fish inside the test chamber, fish was acclimated for 20-30 minutes with minimum velocity less than one Body Length per second (BL S^{-1}) to reorient fish according to flow and the test chamber. After acclimation, prolonged swimming performance of the fish was tested to get the critical swimming speed and caudal fin propulsive information. The velocity was increased step wise in multiples of 1.5 cm s^{-1} (step height). Duration of each step was five minutes for first six steps, after that, each step length was increased for 20 minutes from step number seven and onwards for U_{crit} analysis (Fig. 4A) [4] [25] [26]. With slight modification in prolong swim test, caudal fin propulsion was analyzed, where the step height and step length were remain same i.e.; 1.5 cm s^{-1} and 5min for each step respectively up to 10^{th} step (Fig. 4B). This was near the maximum velocity in which test organism can hold itself at liner position against the test chamber. The tail beat frequency (TBF) in Hz, and stride depth (StD) (2h) was considered as the basic propulsive parameter of the caudal fin of the juvenile fish. In every step the continuous video of swimming pattern of the fish was recorded with 24 fps (frame per second) at least for one minute by DSLR camera (Nikon-D5000). Same experiments were repeated in similar condition with replicates for statistical analysis of critical swimming, tail beat frequency and stride depth analysis.

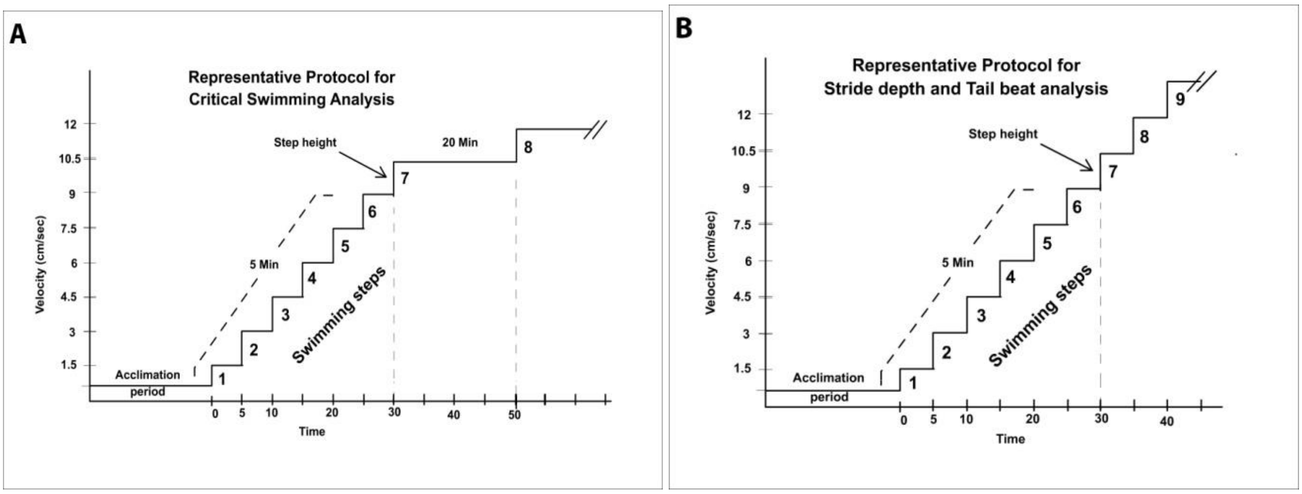

Figure 4: Diagram of the experimental protocols.

A. Protocol for U_{crit} analysis.

B. Protocol for caudal fin propulsion analysis.

Swimming test was terminated when fish could not able to swim against the water flow and attached to the back wall of swimming chamber at least for 3-5 seconds and time was recorded for calculation of critical speed. The taken video was saved with proper ID for further analysis by using WINDOWS based image analysis software’s. The critical swimming was calculated using the formula [27]

$U_{crit} = U_f + U_s \times (t_f/t_s)$

where,

($U_{crit} =$ Critical swimming speed, U_f= velocity of the last completed step, $U_s =$ step hight,

$t_f =$ time spent in last step, $t_s =$ step length.).

A. Image analysis

At first the video was splits with duration of one second and randomly selected at least five seconds (N=5) for further analysis. Image analysis was carried out with the help of Kinovea (Ver. 0.8.15.), ImageJ (Ver. 1.49m) and Icy (Ver. 1.9.3.2) [11] for image analysis. Sequence of images from the clip was used to make "montage" (Fig. 6A). The "montage" was used for tail beat frequency and kinematic model [17][10] analysis. Stride depth (2h) was measured from the length of deflection of caudal fin tip against the central line of the body (Fig. 5 & 6B). Line and angle tools were used for detail image analysis of caudal fin propulsion (Fig. 6B & 7D). Line tool was calibrated before every image analysis against the fixed internal diameter of swimming test chamber (0.9cm) in the same image during analysis (Fig. 6B). The midline tracing model generated with the help of approximately 24 sequential images to trace the midline of the fish body (Total Length). The aspect ratio (A) of the caudal fin was calculated from the formula, $A=h^2/s$; where, 's' is the surface area of the fin and 'h' is the height of the fin [25]. Similarly adult the aspect ratio of adult T. mossambica was carried out in order to compare with juvenile. The measurements were saved manually in the Microsoft datasheet for further analysis. The mean value and standard deviation (S.D.) ware obtained and used to produce charts from the saved measured data.

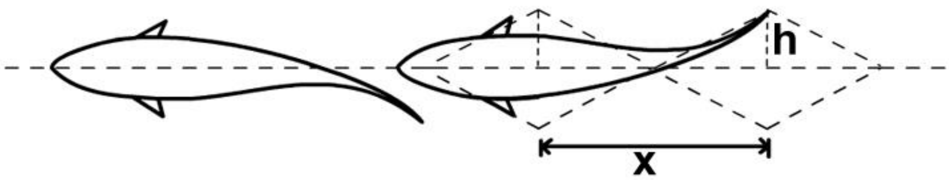

Figure 5: Model schematic representation showing the caudal fin propulsive parameters.

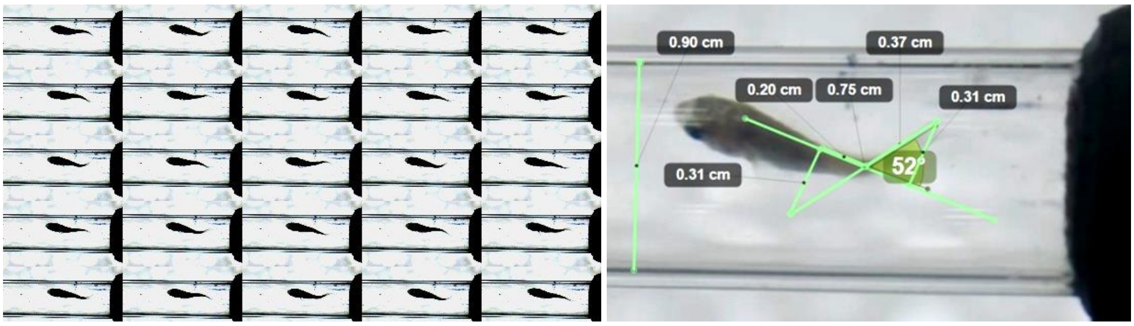

Figure 6: The Screen Shot of image analysis during the experiment.

A. Image montage to find TBF (Tail Beat Frequency).

B. Image frame wise analysis of StD (stride depth) etc.

III. RESULT

Total eight fishes were tested (Fork length 1.15 ±0.1 cm mean±S.D. at the time of the experiment) for the critical swimming test, tail beat frequency and stride length and aspect ratio analysis. We found average completed swimming step by juvenile *Tilapia mossambica*, was 7^{th} and average traveled distance was 198.8±22.68 meter (mean±S.D.) (Table 2). The average Critical swimming velocity of juvenile *T. mossambica* was measured as 10.5±0.76 cm s^{-1} (mean±S.D.) and average total swimming duration was 46.25±13.10 minute (mean±S.D.) (Table. 2). The aspect ratio of caudal fin was measured 1.20±0.13 (mean±S.D.) (Table 1) in juvenile and 1.9±0.20 (mean±S.D.) in adult *T. mossambica.* We found highest tail beat frequency (TBF) of juvenile *Tilapia mossambica* was 11.7±0.6 s^{-1} (mean±S.D.) at 10^{th} step (12.6 BL S^{-1}) and highest stride depth (StD) was 0.9±0.05cm (2h) (mean±S.D.) at 8^{th} step (10 BL s^{-1}). The average tail beat frequency

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and stride depth during entire experiment was 9.8±1.1 s^{-1} and 0.73±0.11cm (mean±S.D.) respectively. A value of stride depth was increased linearly up to first 6^{th} step, then it shows irregular trend may be due to transition of energy source from red muscle to white muscle of test organism.

TABLE 1: Measurements of morphological lengths and caudal fin aspect ratio

Parameters	Juvenile	
	Average	S.D.
Total Length (TL) (cm)	1.30	0.05
Fork Length (FL) (cm)	1.15	0.07
Standard Length (SL) (cm)	1.03	0.08
% Undulatory Caudal Region according to FL	43.68	2.10
% Undulatory Caudal Region according to SL	37.48	1.30
Aspect ratio (A) of the caudal fin	1.20	0.13

TABLE 2: Result of Critical swimming test

Average Completed Step	Total minute	Total Traveled in (Meter)	Critical swimming velocity (cms^{-1})
Step 7th	46.25±13.10	198.8±22.68	10.5±0.76

TABLE 3: Tail beat frequency and Stride Depth (2h).

Velocity			Average Tail Beat per Second (TBF)	Average Tail beat per Minute	Average Stride Depth (StD) (cm)
Step Number	Rate of water flow in Cm S^{-1}	Rate of water flow at avg. BL S^{-1} of test fish			
1	1.5	1.3	8±0.0	480	0.50±0.02
2	3.0	2.5	9.0±1.0	540	0.62±0.03
3	4.5	3.8	9.7±0.6	580	0.68±0.02
4	6.0	5.0	9.7±0.6	580	0.72±0.02
5	7.5	6.3	9.7±0.6	580	0.72±0.05
6	9.0	7.5	9.0±1.0	540	0.84±0.06
7	10.5	8.8	10.0±0.0	600	0.78±0.11
8	12.0	10.0	10.7±0.6	640	0.90±0.05
9	13.5	11.3	11.0±1.0	660	0.84±0.05
10	15.0	12.6	11.7±0.6	700	0.72±0.11
	During entire experiment		9.8±1.1	590	0.73±0.11

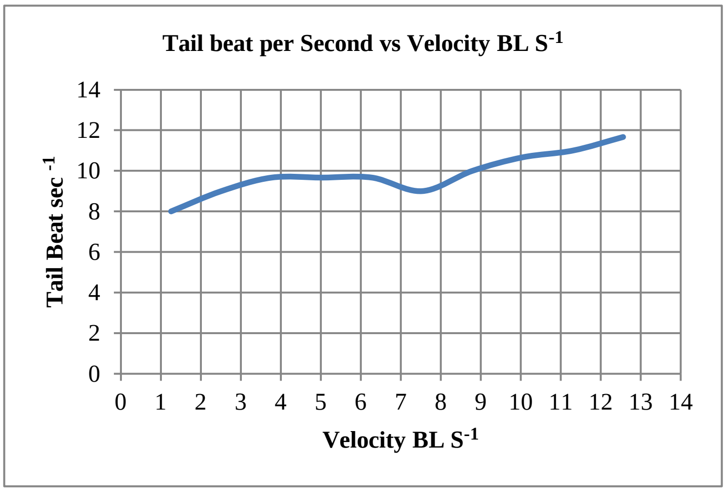

Chart 1: Shows the relationship between Tail beat frequency and Velocity .

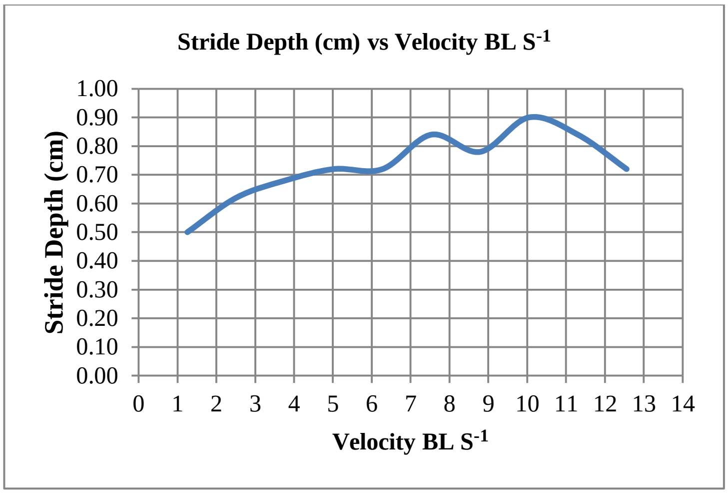

Chart 2: Shows the relationship between Stried depth and Velcity.

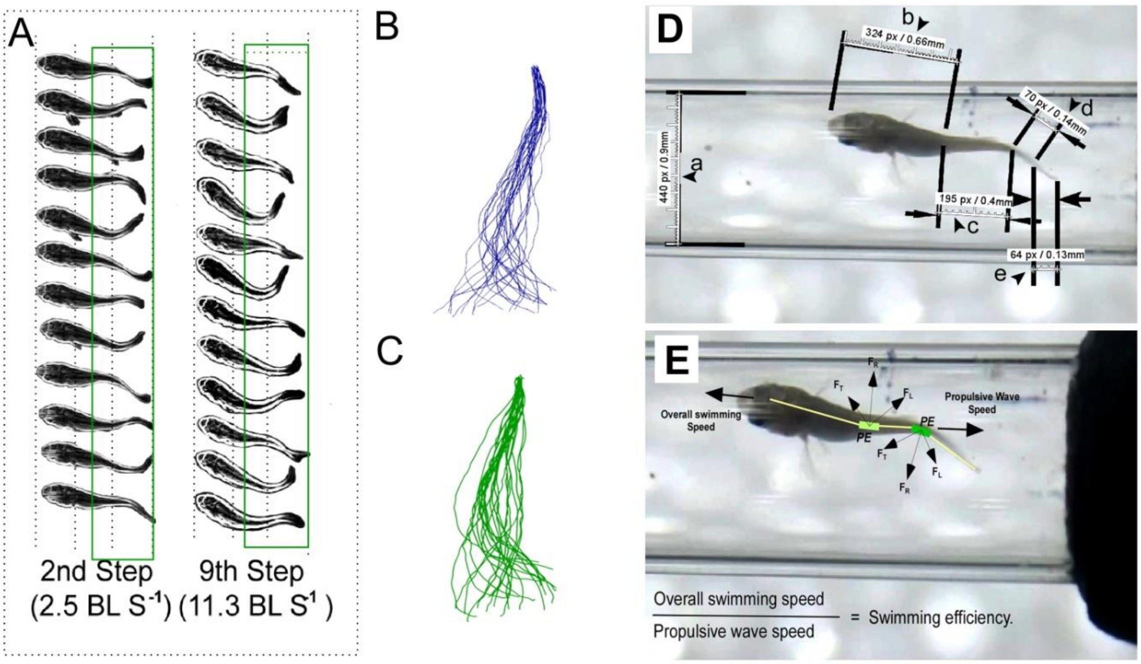

Figure 7: The kinematic model of swimming of juvenile *T. mossambica*.

A: Carangiform type of swimming: green box shows undulatory caudal region of juvenile tilapia.

B & C: Midline tracing model: amplitude of the body wave. B- At 2th step. C- at 9nd step.

D: Length measurement of fish: a- Calibration, b+c= Standard length (SL),

b+c+d= Fork length (FL), b+c+d+e= Total length (TL).

E: Generalized model of two propulsive element (*PE*) of a undulatory caudal region

(Forces: F_L- Lateral component, F_T- Thrust component, F_R- Reaction component).

IV. DISCUSSION & CONCLUSION

The overall objective of this study was to evaluate the critical velocity of swimming and physical ability of juvenile *Tilapia mossambica* under controlled environment. The result suggests that the critical swimming velocity of juvenile *T. mossambica* was around 7th step (8.8 BL S^{-1}) according to the standard U_{crit} test protocol [5] [27]. Several experiments on aspect ratio of caudal fin in different fish group revealed that family Carcharhinidae, Clupeidae, Salmonidae, Cyprinidae, Gadidae, Scombridae ranging between 2.3-3.5, 1.8-2, 2.2-3, 1.5 -2.2, 0.1- 1.3, 6.5-7 respectively [25]. Where the lowest and highest aspect ratio can be found in family Gobiidae and Scombridae ranging from 0.6 to 7 [25]. In juvenile *T. mossambica* we found the aspect ratio of caudal fin was 1.2±0.13 (Table. 1) and in 4 cm long (TL) adult it was and 1.9±0.20 (mean±S.D.). The aspect ratio we found in juvenile *T. mossambica*, was quite lower than the fish groups with fast swimming viz. Scrombridae. But the aspect ratio 1.9±0.2 (mean±S.D.) we found in adult T. mossambica shows some closeness with certain moderately fast swimming groups like Carcharhinidae, Clupeidae, Salmonidae, Cyprinidae etc. Juvenile *T. mossambica* shows little higher swimming capacity in relation to caudal fin aspect ratio, because the juvenile fish can generally attain more relative swimming speed than the larger fish [25]. Fish reaches to the U_{crit} when it was exhausted by depletion of muscle metabolic fuel, swimming capacity might increase during only prolonged swimming test designed with smaller step length. The metabolic expenditure of swimming could be calculated on the basis of fin beat frequency [29]. Similarly, we can predict supply energy for prolonged type of swimming is sufficient up to 5th (6.3 BL S^{-1}) and 6th (7.5 BL S^{-1}) step respectively for TBF and StD. The caudal beat frequency drops (chart 1) at 6th step (7.5 BL S^{-1}) (Chart. 1) may due to the energy depletion in the red oxidative muscle, which helps them in prolonged swimming. After which, fish may start using the white glycolitic muscle which generally helps during burst swimming. The gradual increase in the beat frequency starts after 7th (8.8 BL S^{-1}) step up to the end of the experiment. After the 10th step (12.6 BL S^{-1}) the fish irregularly lost its stability due to high water current. Therefore in the present study, we only consider prolonged type of swimming which was terminated at 10th step. The caudal fin stride depth was decreased at 7th (8.8 BL S^{-1}) step (Chart. 2), due to fast movement of the caudal fin with highest frequency achieved in expense of major metabolic cost provided by red muscle during swimming. During step 8th the StD increased up to maximum (0.90±0.05 cm), when test fish starts using white muscle fuel and shifted from prolonged to burst swimming mode. Continuous drop of StD, after 8th (10.0 BL S^{-1}) step reflects rapid depletion of white muscle fuel, as fish can continue its burst swimming mode lasts for very short time. After step 9th (11.3 BL S^{-1}), the fish was not able to manage the movement of caudal fin with enough StD to generate enough thrust to remain stable at high water current. So, the combined effect of TBF and StD is responsible for this caudal fin base swimming. The overall swimming efficiency of a fish depends on the ratio between overall swimming speed and propulsive wave speed [26]. From the basic kinematics [17] of propulsion of caudal region of *T. mossambica*, we found, the both propulsive elements (*PE*) [24] were situated at muscular caudal region (Fig. 7E). In generally, involvement of one third portion of caudal region for undulatory or oscillatory motion during swimming is the basic characteristics of carangiform type of swimming [4]. Juvenile *T. mossambica* uses the muscular caudal region to produce thrust generating undulatory motion (Fig. 7A), where the length of undulatory caudal region of *T. mossambica* was 43.68%±2.10 and 37.48%±1.30 (mean±S.D.) against the FL and SL of the fish respectively (Fig. 7D). This suggests the *T. mossambica* as a carangiform type of swimmer. The midline tracing model (Fig. 7B & C) indicates the amplitude of caudal fin propulsion [10] and suggests that juvenile *T. mossambica* shows the carangiform type of swimming. This mechanistic model of the caudal fin propulsion provides the basic assumptions of metabolic expenses during carangiform type of swimming in juvenile *Tilapia mossambica*.

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REFERENCES

[1] Beamish, F. W. H. (1978). Swimming capacity. *In Fish Physiology (ed. W. S. Hora and D. J. Randall). New York, NY: Academic Press*. **7**: 101-187.

[2] Beecham, R. V., *et al.* (2014). Design and Calibration of a Tilting Tunnel Respirometer to Study Non-horizontal Swimming in Fishes. *Science and Technology*. **4**(2): 22-29.

[3] Blažka, P., Volf, M., and Čepela, M., (1960). A new type of respirometer for the determination of the metabolism of fish in an active state. *Physiol.Bohemoslov.* **9**: 553-558.

[4] Borazjani I., and Sotiropoulos, F. (2008). Numerical investigation of the hydrodynamics of carangiform swimming in the transitional and inertial flow regimes. *The Journal of Experimental Biology*. **211**: 1541-1558. doi:10.1242/jeb.015644.

[5] Brett, J.R., (1964). The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Board Can.* **21**: 1183-1226.

[6] Budick S. A., and O'malley, D. M. (2000). Locomotor repertoire of the larval zebrafish: swimming, turning and prey capture. *The Journal of Experimental Biology*. **203**: 2565–2579.

[7] Deslauriers, D., and Kieffer, J. D. (2012). The effects of temperature on swimming performance of juvenile shortnose sturgeon (*Acipenser brevirostrum*). *J. Appl. Ichthyol*. 1–6.

[8] Drucker, E. G., and Lauder, G. V. (2000). A hydrodynamic analysis of fish swimming speed: wake structure and locomotor force in slow and fast labriform swimmers. *The Journal of Experimental Biology*. **203**: 2379–2393.

[9] Drucker, E. G., and lauder, G. V. (2001). Locomotor function of the dorsal fin in teleost fishes: experimental analysis of wake forces in sunfish. *The Journal of Experimental Biology*. **204**. 2943–2958.

[10] Elder, H. Y., and Trueman, E. R. (1980). Aspects of animal movement. *Society for Experimental Biology: Seminer Series*. **5**: 125-150.

[11] Elwardany, S.H., El-Sayed, W.H., and Ali, M.F. (2015). Reliability of Kinovea Computer Program in Measuring Cervical Range of Motion in Sagittal Plane. *Open Access Library Journal*. **2**: e1916.

[12] Fish, F. E. (1993). Power output and propulsive efficiency of swimming bottlenose dolphins (*Tursiops truncatus*). *J. exp. Biol.* **185**: 179–193.

[13] Fujimura, K., and Okada, N. (2007). Development of the embryo, larva and early juvenile of Nile tilapia Oreochromis niloticus (Pisces: Cichlidae). Developmental staging system. Develop. *Growth Differ.* **49**: 301–324.

[14] Hoover, J. J., *et. al.* (2011). Critical swimming speeds of adult shovelnose sturgeon in rectilinear and boundary layer flow. *J. Appl. Ichthyol*. **27**: 226–230.

[15] Marras S., and Porfiri, M. (2012). Fish and robots swimming together: attraction towards the robot demands biomimetic locomotion. *J. R. Soc. Interface*. **9**: 1856–1868.

[16] Marras, S. *et. al.* (2013). Relationships among Traits of Aerobic and Anaerobic Swimming Performance in Individual European Sea Bass *Dicentrarchus labrax*. *PLoS ONE*. **8**(9): e72815.

[17] Muller, U. K., and Leeuwen, J. L. (2006). Undulatory fish swimming: from muscles to flow. *Fish and Fisheries.***7**: 84–103.

[18] Ohlberger, J. (2005). Modelling Energetic Costs of Fish Swimming. *Journal of Experimental Zoology*. **303A**:657–664.

[19] Peake, S. (2004). An Evaluation of the Use of Critical Swimming Speed for Determination of Culvert Water Velocity Criteria for Smallmouth Bass. *Transaction of American fisheries society*. **133**: 1472-1479.

[20] Plaut, I. (2000). Effects of fin size on swimming performance, swimming behavi our and routine activity of zebrafish *Danio rerio*. *The Journal of Experimental Biology* **203:** 813–820

[21] Pettersson, A., Pickova, J., and Brännäs, E. (2010). Swimming performance at different temperatures and fatty acid composition of Arctic charr (*Salvelinus alpinus*) fed palm and rapeseed oils. *Aquaculture* **300**: 176–181.

[22] Quintella, B. R., *et. al.* (2010). Critical swimming speed of yellow- and silver-phase European eel (*Anguilla anguilla*), *J. Appl. Ichthyol.* **26**: 432–435.

[23] Roche, D. G. *et. al.,* (2014). Unsteady flow affects swimming energetics in a labriform fish (*Cymatogaster aggregata*). *The Journal of Experimental Biology*. **217**: 414-422.

[24] Russel, K., Haque, M. B. (2012). Microcontroller Based DC Motor Speed Control Using PWM Technique. *International Conference on Electrical, Computer and Telecommunication Engineering.* **Dec. 01-02**: 519-522.

[25] Sambilay, V. C. (1990). Inter relationships between swimming speed, caudal fin aspect ratio and body length of fishes. *Fishbyte.***8**(3):16-20.

[26] Sfakiotakis M., et. al., (1999). Review of Fish Swimming Modes for Aquatic Locomotion. *IEEE Journal of Oceanic Engineering.* **24**(2): 237-252.

[27] Tierney, K. B., and Farrell, A.P. (2004). The relationships between fish health, metabolic rate, swimming performance and recovery in return-run sockeye salmon, *Oncorhynchus nerka* (Walbaum). *J. Fish Dis*. **27**: 663-671.

[28] Tierney, K.B. (2011). Swimming Performance Assessment in Fishes. *J. Vis. Exp*. (**51**): e2572. doi:10.3791/2572 (2011).

[29] Tudorache C. *et. al.* (2008). Pectoral fin beat frequency predicts oxygen consumption during spontaneous activity in a labriform swimming fish (*Embiotoca lateralis*). *Environ Biol Fish.* **84**:1211-8. DOI 10.1007/s10641-008-9395-x.

[30] Tudorache, C., Boeck, D. G., and Claireaux, G. (2013). Forced and Preferred Swimming Speeds of Fish: A Methodological Approach. *Swimming Physiology of Fish.* 81-107. DOI: 10.1007/978-3-642-31049-2_4.

[31] Tytell, E. D. *et. al.* (2010). Disentangling the Functional Roles of Morphology and Motion in the Swimming of Fish. *Integrative and Comparative Biology*. **50**(6): 1140–1154.

[32] Videler, J. J., and Wardle, C. S. (1991). Fish swimming stride by stride: speed limits and Endurance. *Reviews in Fish Biology and Fisheries*. **1**: 23-40.

[33] Walker, J. A., Alfaro, M. E., Noble, M. M., and Fulton, C. J. (2013). Body Fineness Ratio as a Predictor of Maximum Prolonged-Swimming Speed in Coral Reef Fishes. *PLoS ONE* **8**(10): e75422. doi: 10.1371/ journal. pone.0075422.