

**SWIMMING IN FOUR GOLDFISH (*CARASSIUS AURATUS*)  
MORPHOTYPES: UNDERSTANDING FUNCTIONAL DESIGN AND  
PERFORMANCE THROUGH ARTIFICIAL SELECTION**

by

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## ABSTRACT

Although artificially selected goldfish exhibit swimming performance decrements, with the most derived morphotypes more affected, they can be utilized to explore functional design and movement pattern principles in aquatic vertebrates. Drag, steady swimming kinematics (tailbeat frequency, amplitude, stride length), energetics (standard and active metabolic rate), fast-start performance (average and maximum velocity and acceleration), stability in yaw and roll and propulsive muscle ultrastructural characteristics (mitochondrial volume density and spacing, myofibril diameter and capillary to fibre ratio in red and white muscle) were measured for four morphotypes: common, comet, fantail and eggfish, of comparable length ( $\approx 5$  cm). A performance “pairing” (common and comet; fantail and eggfish) was a recurrent theme for most performance parameters. Vertebral numbers (30), segment lengths ( $\approx 0.85$  mm) and standard metabolic rates ( $\approx 140$  mg O<sub>2</sub> kg<sup>-1</sup> hr<sup>-1</sup>) are exceptions where values are the same. Fantail and eggfish drag and drag coefficients (referenced to frontally projected area  $\approx 0.6 - 0.9$ ) were higher (requiring more thrust at any given velocity) than those for the more streamlined common and comet ( $\approx 0.3 - 0.6$ ;  $P < 0.05$ ). This is reflected in kinematics; tailbeat frequency and stride length at any given velocity for the common and comet are lower and higher respectively than that of the fantail and eggfish ( $P < 0.05$ ). Common and comet fatigue times are not significantly different from that of their ancestor, Crucian carp ( $P > 0.05$ ), and are lower than those of the fantail and eggfish ( $P < 0.05$ ). The cost of transport of the common and comet ( $\approx 0.6$  mg O<sub>2</sub> kg<sup>-1</sup> m<sup>-1</sup>) is accurately predicted from the mass scaling relationship for fish ( $P > 0.05$ ), but values for the fantail and eggfish ( $\approx 1.3$  mg O<sub>2</sub> kg<sup>-1</sup> m<sup>-1</sup>) are not ( $P < 0.05$ ). Eggfish steady

swimming (dorsal fin absent) was characterized by rolling and yawing motions associated with significant energy losses. Common and comet fast-start performance (average velocity  $\approx 0.45 \text{ m s}^{-1}$ , maximum velocity  $\approx 1.2 \text{ m s}^{-1}$ , average acceleration  $\approx 7.5 \text{ m s}^{-2}$ , maximum acceleration  $\approx 35 \text{ m s}^{-2}$ ) was similar to that of other locomotor generalists (e.g. trout). Eggfish maximum acceleration ( $\approx 5 \text{ m s}^{-2}$ ) is poor due to the absence of inertial and lifting contributions to thrust from the dorsal fin and energy wasting rolling motions. Artificially selected fish can bear upon fitness related adaptations associated with form and movement, providing insights into the “performance envelope” of natural systems subject to ecological speciation.

# TABLE OF CONTENTS

ABSTRACT.....	ii
TABLE OF CONTENTS.....	iv
LIST OF TABLES.....	vi
LIST OF FIGURES .....	vii
ACKNOWLEDGEMENTS.....	viii
1 INTRODUCTION .....	1
2 MATERIAL AND METHODS.....	7
2.1 Morphometrics.....	7
2.2 Drag.....	8
2.3 Fatigue time and critical swimming speed.....	8
2.4 Oxygen consumption .....	10
2.5 Steady swimming kinematics .....	10
2.6 Fast-starts .....	12
2.7 Propulsive musculature and vertebral column.....	15
2.8 Statistics .....	16
3 RESULTS .....	17
3.1 Morphometrics and drag.....	17
3.2 Steady swimming kinematics and oxygen consumption .....	20
3.3 Fast-starts .....	24
3.4 Musculature and vertebral column.....	28
4 DISCUSSION .....	32

4.1 Drag.....	32
4.2 Steady swimming.....	33
4.3 Fast-starts .....	38
4.4 Dynamic stability in yaw and roll.....	40
5 CONCLUSIONS .....	42
REFERENCES .....	43
APPENDIX 1.....	57
APPENDIX 2.....	58

## LIST OF TABLES

<b>Table 1:</b> Morphometric characteristics of four <i>Carassius auratus</i> morphotypes. ....	18
<b>Table 2:</b> Kinematic data of S1 and S2 fast-starts for four <i>Carassius auratus</i> morphotypes .....	26
<b>Table 3:</b> Average segmental and total inertial added mass and lifting forces and the resultant turning moment for S1 and S2. ....	27
<b>Table 4:</b> Mitochondrial volume density, surface density, mitochondrial spacing, myofibril diameter and capillary to fiber ratio in goldfish red and white muscle. ....	29
<b>Table 5:</b> Data table for velocity, power and efficiency components of goldfish steady swimming.....	37

# LIST OF FIGURES

<b>Figure 1:</b> Timeline for the domestication of the common goldfish..	3
<b>Figure 2:</b> Schematic drawing of a propulsive section during fast-start. ....	14
<b>Figure 3:</b> Drag versus velocity ( <b>A</b> ) and frontal drag coefficient versus Reynolds number ( <b>B</b> ). ....	19
<b>Figure 4:</b> Steady swimming centerlines ( <b>A</b> ). Roll and yaw angles versus time ( <b>B</b> ). ....	21
<b>Figure 5:</b> Tailbeat frequency ( <b>A</b> ), amplitude ( <b>B</b> ) and stride length ( <b>C</b> ) versus velocity..	22
<b>Figure 6:</b> Fatigue time ( <b>A</b> ) and total oxygen consumption rate ( <b>B</b> ) versus velocity..	23
<b>Figure 7:</b> Centrelines during fast-starts.....	25
<b>Figure 8:</b> Fast-start curvature versus axial location. ....	30
<b>Figure 9:</b> Transmission electron micrographs of propulsive red and white muscles.....	31
<b>Figure 10:</b> Fatigue time for goldfish domesticates and a variety of small fishes that include body and caudal fin and pectoral fin swimmers.....	34
<b>Figure 11:</b> Cost of transport versus body mass for goldfish domesticates and a variety of other fishes .....	36

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# 1 INTRODUCTION

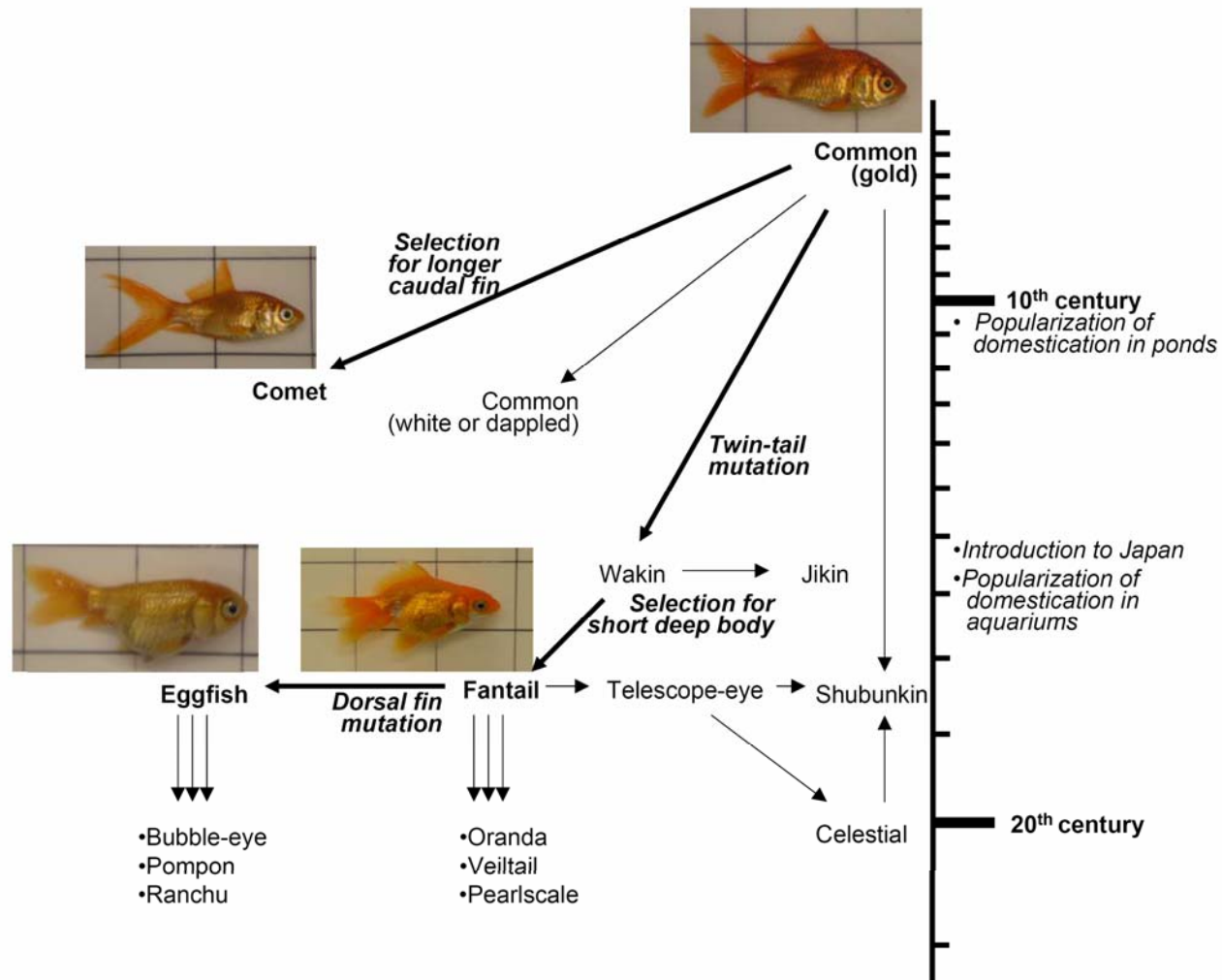
Divergent evolution occurs in nature (natural selection) and under domestication (artificial selection). Variation under domestication was emphasized in Darwin's 1844 Essay (Darwin, 1909) and in the "The Origin of Species by Means of Natural Selection" (Darwin, 1859), which opens with a chapter on the subject. To date, little consideration has been given to domestication with a view to understanding aquatic vertebrate functional design in an ecological context. Given the strictures pertaining to current definitions and criteria of domestication, this is not surprising. For example, Clutton-Brock (1999) defines a domestic animal as "one bred in captivity for purposes of economic profit to the human community that maintains total control over its breeding, organization of territory and food supply". Focusing on fish, Balon (1995, 2004) ascribes the following characteristics of a truly domesticated organism: the individual is valued and kept for a specific purpose, its breeding is subject to human control, its behaviour is different from that of the wild ancestor, its morphology and physiology exhibit variations never seen in the wild and some individuals at least would not survive without human protection. Therefore, it is understandable that domesticates have received little attention with regard to assessments of functional morphology and movement. However, behavioural (e.g. anti-predator responses, aggression, reproductive behaviour) and physiological (e.g. nutritional, hormonal) differences in cultured fishes (principally salmonids) have been considered (Hungtingford, 2004; Thorpe, 2004).

*Cyprinus* and *Carassius* are sister taxa that diverged 1.7 - 5.5 million years ago (Zhou, 1989). The genus *Cyprinus* contains about 15 species including the common carp *Cyprinus carpio*. *Carassius* contains only two species, crucian carp *C. carassius* and

common goldfish *C. auratus* (Holopainen et al., 1997). Selective breeding of goldfish has led to the development of many morphotypes (schematically summarized in Fig. 1). *C. auratus* was domesticated from the crucian carp between the 3<sup>rd</sup> and 5<sup>th</sup> centuries A.D. during the Tsin dynasty in China (Chen, 1925; Matsui, 1934). The comet (12<sup>th</sup> century; long deeply forked caudal fin) and wakin (late 16<sup>th</sup> century; twin-tail) were both directly derived from the common goldfish (Chen, 1956; Smartt, 2001). Fantails (twin-tail with short deep body) emerged from the wakin in the early 18<sup>th</sup> century (Chen, 1925, 1956). The eggfish (twin-tail, no dorsal fin) was selectively bred from the fantail in 1726 (Chen, 1925; Smartt and Bundell, 1996).

Goldfish varieties are produced by two major mechanisms: mutational changes in a single or few genes (oligogenes) and interactions between a large number of genes (polygenes). The xanthic color mutation in goldfish is an example of the former, originating from an alteration in the dominance relationship of oligogenes (Kajishima, 1977; Smartt, 2001). Most goldfish varieties are produced by polygenes, as the interaction between a large numbers of genes allow for additive effects on the character (e.g. selected breeding for longer caudal fin, short deeper body and absence of a dorsal fin in the comet, fantail and eggfish respectively) (Smartt, 2001).

Artificial selection for different goldfish forms is a reversible process. For example, the twin-tail of the fantail (a recessive trait) is reversible by crossing with a homozygous single-tail morphotype (Hance, 1924; Matsui, 1934). The fantail morphotype can also be produced when heterozygous single-tail forms are crossed (Hance, 1924). Reduced dorsal fin forms, intermediate between the fantail and eggfish, occur from time to time, and the eggfish morphotype can be derived by crossing these



**Figure 1:** Timeline for the domestication of the common goldfish. Data from Chen (1956) and Smartt (2001).

individuals followed by further selection (Chen, 1925; Smartt and Bundell, 1996). The bifurcated caudal fin of the comet is a dominant trait, and the common can be derived by crossing the heterozygous form (Smartt, 2001).

In addition to goldfish, a few other forms have been domesticated as ornamentals by aquarists, including zebrafish (Cyprinidae), swordtails, guppies, platys, mollies (Poeciliidae), neon tetra (Characidae), discus and angelfishes (Cichlidae). However, most studies of form in relation to swimming performance in these fish have focused on the wild type (e.g. oxygen consumption rates in *Brachydanio rerio* (Plaut and Gordon, 1994), swimming endurance in *Xiphophorus nigrensis* (Ryan, 1988), *X. helleri* (Royle et al., 2005) and *Poecilia reticulata* (Nicoletto, 1991), energy cost of swimming in male *X. montezumae* (Basolo and Alcaraz, 2003), fast-start swimming performance in *X. helleri* (Royle et al., 2006)).

Domestication offers a system for exploring the relationships between functional morphology and swimming performance in fish in steady swimming (e.g. speed and stamina, kinematics, energetics and cost of transport), unsteady swimming (e.g. fast-start kinematics, duration, velocity and acceleration) and stability and manoeuvrability (e.g. control forces in steady swimming, role of fins as effectors, reactions to perturbations and disturbances, turning radii). However, only a few studies with a limited focus have utilized domesticates. Plaut (2000) showed that the critical swimming speed and routine activity levels of wild-type zebrafish exceeds that of “long finned” and “no tail” domesticates. Robinson and Rowland (2005) used a number of behavioural indices to show a reduced startle response in domesticates compared to wild-type *B. rerio*. A

reduced startle response is also characteristic of hatchery reared brown trout *Salmo trutta* (Alvarez and Nicieza, 2003).

A broad range of form and performance issues can be addressed by selecting representative, distantly related wild-types for comparison (e.g. Blake, 1983, 2004; Videler, 1993; Webb, 1988, 1998, 2006; Harper and Blake, 1990; Gerstner, 1999; Webb and Gerstner, 2000; Korsmeyer et al., 2002; Wakeling, 2006), by comparative studies within a family (e.g. Bellwood and Wainwright, 2001; Fulton et al., 2001) and at a finer phylogenetic scale with incipient species (e.g. Law and Blake, 1996; Blake et al., 2005) and morphs within a species (e.g. Skúlason et al., 1989). Comparisons based on phylogenetically distant fishes that evolved over a long period can reflect large form variations but may be confounded by differences in internal anatomy (e.g. vertebral number and segment lengths, arrangement of propulsive musculature) and physiology (e.g. muscle energetics, metabolic rate). Incipient species and naturally occurring morphs that evolved over a relatively short period show fewer confounding issues but less morphological difference. Domesticates offer diverse forms (due to the actions of polygenes) that produce large scale morphological differences at the intra-specific level which may be rapidly bred with fewer internal anatomical and physiological confounding differences for comparative biomechanical assessments of form without recourse to invasive procedures (e.g. fin amputation).

Amputation as a means of understanding fin function in fish (e.g. Breder, 1926; Gray, 1933, 1968; Horak, 1969; Webb, 1973, 1977) is ineffective due to compensation following fin removal. Dorsal, pelvic, pectoral, anal and adipose fin removal has also been shown to have no effect on steady swimming performance (Horak, 1969). Caudal

fin amputation in rudd and whiting was compensated for by movements of other fins and the body with no significant effect on speed (Breder, 1926; Gray, 1933). Webb (1973) measured kinematic variables and oxygen consumption rates in sockeye salmon *Oncorhynchus nerka* in which the trailing edge depth and caudal fin area were reduced by partial caudal fin amputation and found no significant difference in critical swimming speed between intact fish and fish with either the epaxial or hypaxial caudal fin lobes removed. However, for fast-starts, median fin amputation in rainbow trout *O. mykiss* is associated with decreasing performance with progressive reductions in fin and body area, particularly when the caudal fin was amputated (Webb, 1977). Arguably, this implies no effective scope for compensation when forces are dominated by unsteady lifting (sharp edges of fins) and inertial (added mass) forces. High propulsive muscle strain (Goldbogen et al., 2005) and maximal power output (Frith and Blake, 1995) during escape fast-starts likely leaves little scope for kinematic compensation (e.g. increased tailbeat frequency and amplitude).

There can be no doubt that artificial selection of goldfish has brought about decrements in swimming performance underlain by kinematic differences that are attributable to sub-optimal functional design (body form) and propulsive musculature, with the most derived morphotypes being more affected. Our purpose is to utilize the goldfish domesticates as a practical experimental system to explore functional design (significance of overall body morphology, fin development and placement, propulsive muscle ultrastructural characteristic) and movement pattern (steady and fast-start performance, stability and manoeuvrability) in fish.

## 2 MATERIAL AND METHODS

### 2.1 Morphometrics

Four goldfish morphotypes *Carassius auratus* L. (common, comet, fantail and eggfish;  $n = 10$  per morphotype) were obtained from a local commercial dealer and transported to a holding tank ( $0.60 \times 0.30 \times 0.40$  m) with a gravel bottom and natural plants containing fresh aerated dechlorinated water at  $25 \pm 1^\circ\text{C}$ . Fish were euthanized (overdose of MS222), weighed in air ( $W_a$ ) and water ( $W_s$ ) (Mettler PK300 scale,  $\pm 0.001$  g, with manufacture suspension apparatus; Columbus, Ohio, U.S.A.). Standard length ( $L_s$ , tip of rostrum to posterior of the caudal peduncle) and body length ( $L$ , tip of the rostrum to the trailing edge of the caudal fin) were measured (caliper, 30 cm, Helios  $\pm 0.05$  cm; Mebtechnik, Germany). The pectoral, anal, dorsal and caudal fins were dissected, stained with methylene blue and photographed (Olympus IR-500 digital camera, Center Valley, PA, U.S.A.). Their planform area was determined using ImageJ (National Institutes of Health; <http://rsb.info.nih.gov/ij/>). Frontally projected body area ( $A$ ) was measured from digitized tracings (Houston Instruments Hipad digitizer, Houston, Texas, U.S.A.) of “head on” photographs. The centre of mass (CM) of the fish was determined by suspending from the mouth and marking with the vertical line of gravity; this procedure was repeated with suspension from the cloaca. The CM was where the two points crossed.

## **2.2 Drag**

Drag ( $D$ ) was determined from terminal velocity ( $V_t$ ) measurements obtained by dropping dead fish down a water filled Plexiglass column (10 cm x 10 cm x 45 cm) against a grid (1 cm x 1 cm). The fish were stabilized by a dart flight attached to the end of a fine steel wire that ran through the length of the fish stiffening the body and caudal fin. The pectoral, dorsal and anal fins were removed to eliminate fin flutter (Webb, 1975; Blake, 1983). A  $V_t$  range was obtained by changing the buoyancy of the fish by placing lead pellets into their mouth. The falling fish was filmed at 60 Hz (Troubleshooter high-speed camera, Model TS500MS, Fastec Imaging, San Diego, CA, U.S.A.). Terminal velocity was always achieved, and only fish that fell straight were analyzed. Fish drag at  $V_t$  was calculated by subtracting the drag of the stabilizer from that of the stabilizer and fish together. At terminal velocity, drag is equal to the submerged weight:  $D = W_s = 0.5\rho AC_D V_t^2$  where  $\rho$  and  $C_D$  are water density ( $1000 \text{ kg m}^{-3}$ ) and the drag coefficient ( $C_D = 2D(\rho A V_t^2)^{-1}$ ) respectively.

## **2.3 Fatigue time and critical swimming speed**

Fish ( $n = 8$  per morphotype) were acclimated for 1 hour in a Blazka-type swim tunnel (Blazka et al., 1960) (length = 0.50 m; inner cylinder diameter = 0.06 m; outer cylinder diameter = 0.10 m; volume = 2.50 ℓ) submerged in a water bath ( $25 \pm 1^\circ\text{C}$ ). Flow was generated by a pump (Model 3E-12NT, Little Giants Pump Company, Oklahoma City, Oklahoma, U.S.A.) with an adjustable speed motor (Model 3PN501B, Staco Energy Products, Dayton, Ohio, U.S.A.). Flow was calibrated by a small velocity probe (Nixon



Streamflow 422,  $\pm 0.01$  m/s, Cheltenham, U.K.). A flow-rectifying grid made of straws was located in front of the pump.

Fish were not fed the day before experimentation to ensure a post-absorptive state (Beamish, 1964). The time to fatigue ( $F_t$ , when the fish ceased swimming and fell back against the downstream grid) was measured (stopwatch,  $\pm 0.05$  s) for speeds ranging from 0.15-0.35 m s<sup>-1</sup> at 0.05 m s<sup>-1</sup> intervals and was determined for each fish at one velocity per day ( $N = 160$ ) allowing a day for recovery.

Critical swimming speed ( $V_{crit}$ ; Brett, 1964, 1967; reviewed by Beamish, 1978; Hammer, 1995; Kolok, 1999; Plaut, 2001; Blake, 2004) was also determined in the swim tunnel ( $n = 8$  per morphotype):  $V_{crit} = V_f + \left[ \Delta V (t_f t_i^{-1}) \right]$  where  $V_f$ ,  $\Delta V$ ,  $t_f$  and  $t_i$  are highest swimming velocity maintained for 20 minutes, velocity increment, time elapsed at fatigue velocity (when the fish could not maintain position against the current) and the prescribed time interval of 20 minutes respectively. Prior to the experiments, the fish swum against a current of 0.5 L s<sup>-1</sup> for 1 hr to allow for recovery from handling stress (Kolok, 1991; Peake et al., 1997). Five trials (constituting one data point) were repeated for each fish with a day's rest in the holding tank between trials ( $N = 160$ ). Following Brett (1964), speed increments were established in preliminary tests to allow for a uniform standard for comparison of 60 min fatigue time. The speed increments were 1.56 L s<sup>-1</sup>, 1.17 L s<sup>-1</sup>, 0.68 L s<sup>-1</sup> and 0.49 L s<sup>-1</sup> every 20 min from initial velocities of 3.1 L s<sup>-1</sup>, 3.0 L s<sup>-1</sup>, 0.9 L s<sup>-1</sup> and 0.8 L s<sup>-1</sup> for the common, comet, fantail and eggfish respectively.  $V_{crit}$  was corrected for fish cross-sectional area blocking ( $V_{crit}$ ) as:  $V_{crit} = V_s (1 + A_i / A_{ii})$ , where  $V_s$  is the velocity in the absence of the fish,  $A_i$  is the cross-sectional area of the fish and  $A_{ii}$  is the cross-sectional area of the tunnel (Smit et al., 1971):  $V_s / V_{crit} \approx 0.97$ .

## **2.4 Oxygen consumption**

Oxygen consumption was measured by an oxygen probe (air-calibrated; YSI-58, YSI 5905 BOD oxygen probe; Yellow Springs Instruments, Yellow Springs, Ohio, U.S.A.) that entered the swim tunnel through a cylindrical port (diameter = 2.5 cm, length = 2.3 cm) placed just forward of the rectifying grid. There was no measurable background oxygen consumption without a fish over a period of 20 min. Total oxygen consumption rate ( $\dot{M}_{O_2}$ ) is:  $\dot{M}_{O_2} = \Delta[O_2] v \alpha_w (mt)^{-1}$  where  $\Delta[O_2]$ ,  $v$ ,  $m$ ,  $\alpha_w$  and  $t$  are the change in oxygen saturation, volume of water in the swim tunnel, fish mass, solubility constant for oxygen in water (8.3 mg  $\ell^{-1}$  at 25°C) and duration of 20 min respectively (Alsop and Wood, 1997).

Standard metabolic rate (SMR;  $n = 8$  per morphotype; 5 trials per fish) was measured over 1 hr in the flow tank without flow by the same oxygen probe following an acclimation period of 24 hr.

## **2.5 Steady swimming kinematics**

Continuous steady swimming was recorded (60 Hz; Troubleshooter high-speed camera, Model TS500MS, Fastec Imaging, San Diego, CA) during critical swimming speed and oxygen consumption rate measurements ( $n = 8$  per morphotype; 5 trials per fish). A grid (0.5 cm x 0.5 cm) was placed at the bottom of the water bath below the swim tube and the camera positioned directly above, giving a clear undistorted view of the fish against the grid. Video segments in which the fish swam steadily with no perceptible movement relative to the grid through 10 complete tailbeats were selected for

analysis (constituting one trial). Tailbeat frequency (excursion of the tail from one side of the body to the other and back again divided by duration), amplitude (distance between the lateral most positions of the tip of the tail during one complete tailbeat cycle) and stride length (speed divided by tailbeat frequency) were measured.

Propulsive wave velocity and wavelength were determined following published methods (Dewar and Graham, 1994; Donley and Dickson, 2000). The time between peaks in lateral displacement at the tip of the snout and tail was measured (lateral displacement over time for the wave of undulation to pass); this was repeated 10 times for each trial to obtain a mean progression time. Propulsive wave velocity was calculated by dividing the body length by the mean progression time, and wavelength was obtained by dividing propulsive wave velocity with tailbeat frequency.

The angle of rolling motions ( $\gamma$ ; angle between the X and Z axis) for two dimensional movements in the vertical plane was calculated following Zelenin et al. (2003). A black dot was made with a permanent marker on the dorsal midline of the fish at the level of insertion at the pectoral fins. The rolling angle is:  $\gamma = \tan^{-1}(d_d / d_p)$  where  $d_d$  and  $d_p$  are the maximum distance of the marker from the x-axis and the body depth at the level of the pectoral fin respectively. The yaw angle in the X, Y plane of oscillations at the tip of the snout ( $\chi$ ) was:  $\chi = \tan^{-1}(a_h / L)$  where  $a_h$  is the maximum amplitude of the motions.

## 2.6 Fast-starts

Fast-start escape responses are fixed action patterns consisting of two stages. A unilateral contraction of the axial musculature bends the fish into a C-shape, stage 1 (S1), followed by a propulsive stroke of the tail in the opposite direction, stage 2 (S2) (Domenici and Blake, 1997).

Fish ( $n = 10$  per morphotype) in a tank ( $0.30 \times 0.30 \times 0.25$  m; water depth = 30 cm;  $25 \pm 1^\circ\text{C}$ ) acclimatized to filming lights (three Berkey Coloran Halide, 650 W bulbs) by feeding with the lights on a week before experiments (Law and Blake, 1996). Feeding ceased the day before experimentation to ensure post-absorptive digestive state (Beamish, 1964). Fish were acclimated for 1 hr prior to experiments. Fast-start induced by striking the side of the tank with a plastic bulb attached to a 1 m pole. The tank walls were covered with black paper so that the fish could not anticipate the approaching stimulus. The top view of the fish was filmed (250 Hz; Troubleshooter high-speed camera, Model TS500MS, Fastec Imaging, San Diego, CA) against a 2 cm x 2 cm reference grid on the bottom of the tank. The CM of the stretched straight fish was used as a reference point (Table 1). Fish outlines were digitized with ImageJ. Only fish out of wall proximity were analyzed. Instantaneous distance versus time data were smoothed by a moving five-point regression (Lanczos, 1956) and differentiated to obtain velocity and acceleration.

The S1 turning angle ( $\phi$ ; angle between the initial and final orientation of the fish) for two dimensional movement in the horizontal plane (Law and Blake, 1996) was calculated using dot products between one vector at the CM (e.g. position  $x_2, y_2$  to position  $x_3, y_3$ ) and the previous vector ( $x_1, y_1$  to  $x_2, y_2$ ). The initial turning direction was considered positive, with subsequent turning angles signed negative if in the opposite

direction relative to the initial turn. The horizontal angular velocity was obtained by employing a five-point moving regression (Lanczos, 1956) of the angle-time data. Distance moved ( $d$ ) and  $\phi$  for the CM for S1 were used to calculate the turning radius ( $R$ ):  $R = 2d \cos(\phi/2)$ . The rolling angle was determined for fast-starts in the same way as for steady swimming.

Fish curvature was determined by digitizing the dorsal projected outline of fish on each frame with ImageJ. The dorsal midline was divided into 51 equidistant coordinates

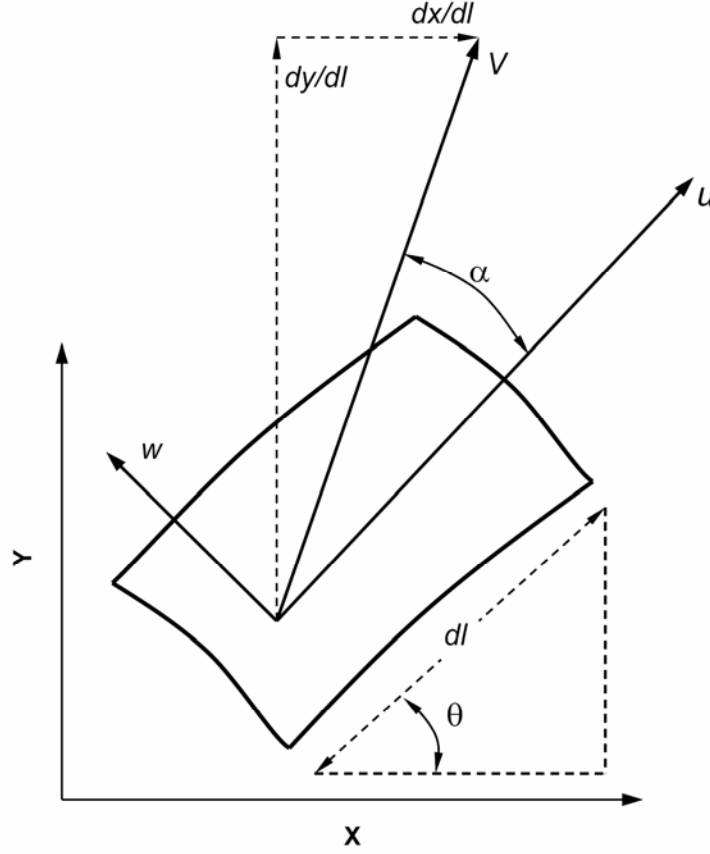
(i.e. 50 equal segments) to determine local curvature ( $\kappa$ ) as:  $\kappa = \frac{\delta x}{\delta d'} \frac{\delta^2 y}{\delta d'^2} - \frac{\delta y}{\delta d'} \frac{\delta^2 x}{\delta d'^2}$

where  $x$  and  $y$  are coordinates of a midline point and  $d'$  is the distance from the tip of the snout to that point along the midline (Jayne and Lauder, 1995; Tytell and Lauder, 2002).

Forces and moments generated during fast-starts are calculated based on Weihs' (1972) model, following the application procedures of Frith and Blake (1991). The model assumes that thrust in the direction of motion ( $F_M$ ) is generated by the acceleration of the added mass of the body and lift forces from the caudal, dorsal and anal fins:

$$F_M = \frac{d \int_0^L m_a w (dy/dl) dl}{dt} + \sum_{i=1}^k 0.5 \rho S_i V_i^2 C_{L\alpha_i} \alpha_i$$

The first term on the right hand side of the equation represents the contribution of the inertial forces generated by the body, where  $m_a$ ,  $w$ ,  $dy/dl$  and  $dl$  are the added mass, velocity component for a propulsive section perpendicular to the fish's backbone, sine of the angle between the propulsive section and fish's direction of motion and the length of a propulsive segment respectively (Fig. 2). The added mass is:  $m_a = 0.25 \pi \rho d_s^2 \beta$ , where



**Figure 2:** Schematic drawing of a propulsive section of length  $dl$ :  $\mathbf{V}$  is the velocity vector for the section and  $w$  is the component perpendicular to the backbone and  $u$  is the tangential component.  $\mathbf{V}$  can also be described by the vector components  $dy/dt$  and  $dx/dt$  where  $\alpha$  is the angle between the  $\mathbf{V}$  and  $u$  and  $\theta$  is the angle subtended by the tangent to the propulsive section and the x-axis.

$d_s$  is the depth of a propulsive section and  $\beta$  is a shape factor ( $\approx 1$ ; Lighthill, 1970). The

perpendicular velocity component ( $w$ ) is:  $w = \frac{dy}{dt} \frac{dx}{dl} - \frac{dx}{dt} \frac{dy}{dl}$ , where  $dy/dl$  and  $dx/dl$  are

the sine and cosine of a section's angle relative to the direction of motion and  $dy/dt$  and  $dx/dt$  are velocity vectors for a propulsive section normal and tangential to the fish's direction of motion respectively (Lighthill, 1971).

The second term on the right hand side of the equation represents the contribution of the lift forces generated by the fins, where  $S_i$ ,  $\mathbf{V}_i$ ,  $C_{L\alpha_i}$  and  $\alpha_i$  are the sectional fin

area, its absolute velocity, the rate of change of the lift coefficient with angle of attack ( $\alpha_i$  describes the angle between the fin section  $i$  and its velocity vector  $V_i$ ) respectively, and  $k$  is the total number of fins. The rate of change of the lift coefficient relative to the angle of attack for steady motion is:  $C_{L\alpha} = \pi AR(1 + 0.5AR)^{-1}$  (Robinson and Laumann, 1956), where  $AR$  is fin aspect ratio ( $\text{span}^2/\text{planform fin area}$ ; Table 1). Values of  $C_{L\alpha}$  were corrected for unsteady motions using:  $C_L / C_{L\infty} = (1 + \Gamma)(2 + \Gamma)^{-1}$  where  $C_L$  and  $C_{L\infty}$  are the instantaneous lift coefficient and steady state lift coefficient respectively and  $\Gamma \equiv V_i t / c$  where  $V_i$  is the forward velocity,  $t$  is time and  $c$  is fin chord (Weihs, 2002).

## ***2.7 Propulsive musculature and vertebral column***

The total red and white propulsive musculature was dissected out of five fish of each morphotype (euthanized by overdose of MS222), blotted dry with a paper towel and weighed (Mettler PK300 scale,  $\pm 0.001$  g; Columbus, Ohio, U.S.A.). Muscle fibre fine structure, red and white muscle fibre fine structure were dissected from one fish of each morphotype at the tenth myotome from the tail ( $0.8 L$ ). Muscle strips were cut into blocks ( $\approx 2$  mm squares), fixed in 2.5% glutaraldehyde (0.1 M cacodylate buffer) for 8 hours, washed with 0.1 M sodium cacodylate buffer overnight and immersed in 1 % osmium tetroxide (0.1 M cacodylate buffer) for 1 hour. Samples were dehydrated through a series of sequential 10 minute washes in 70%, 75%, 85%, 95%, 100% and 100% ethanol and embedded with epoxy resin for 3 days. T.E.M. micrographs ( $\times 12,000$ ;  $N = 75$  for each of the red and white muscle) were analyzed. The mitochondrial volume density ( $V_V$ ; volume of mitochondrial cellular components per unit volume of fibre), mitochondrial

surface density ( $S_V$ ; area of outer membrane per unit volume of muscle tissue), mitochondrial spacing ( $\lambda_a = 4(1 - V_V)/S_V$ ), myofibril diameter ( $M_d$ ) and capillary to fibre ratio ( $C:F$ ) (Weibel, 1980; Tyler and Sidell, 1984) were analyzed with ImageJ.

Vertebral counts (number of intervertebral joints) and segment lengths (Linear Vernier Microscope,  $\pm 0.01$  mm; Griffin and George Ltd, U.K.) for five fish of each morphotype were determined.

## **2.8 Statistics**

The effects of morphotype on morphometrics, steady swimming wavelengths, fast-start kinematics (duration, distance, average velocity, maximum velocity, average acceleration, maximum acceleration), vertebral segment lengths, proportions of white and red muscle mass and measurements of fine structure from T.E.M. micrographs were determined using ANOVA (SPSS 13.0 for Windows). The locations of any significant differences were obtained (Tukey-HSD test). Slopes and intercepts for drag, steady swimming kinematics (frequency, amplitude, stride length), fatigue time and total oxygen consumption rates were compared by ANCOVA. Differences between measured and extrapolated standard metabolic rates for each morphotype were determined using two-sample  $t$ -tests. The null hypothesis was rejected at  $P < 0.05$  in all cases.



## 3 RESULTS

### 3.1 Morphometrics and drag

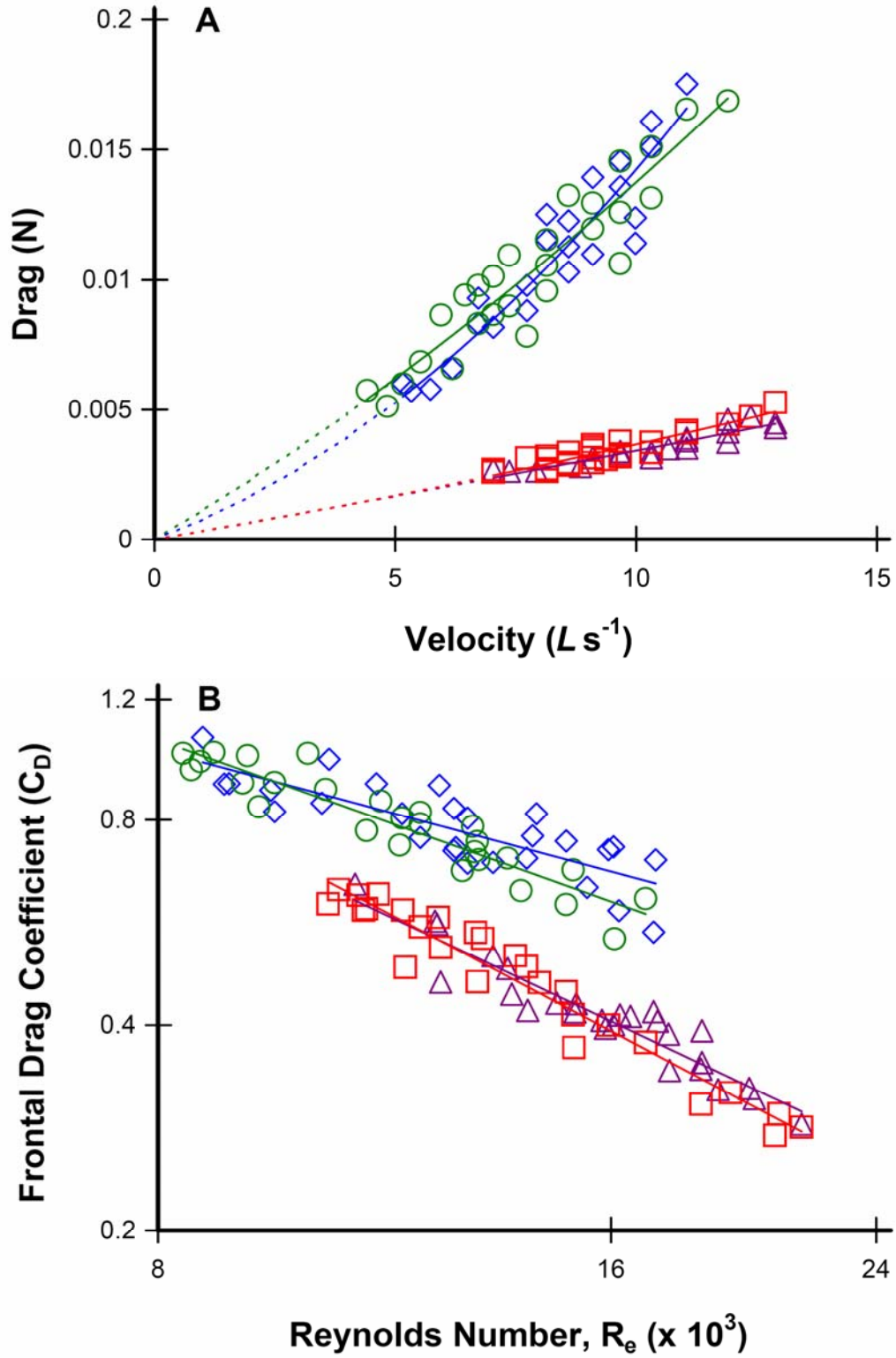
Table 1 shows that for fish of comparable length ( $P > 0.05$ ): 1. Body mass of the common and comet were significantly lower than that of the fantail and eggfish ( $P < 0.05$ ). 2. The frontally projected area and total body surface area of the fantail and eggfish was higher than the common and comet ( $P < 0.05$ ). 3. Fineness ratio ( $L_s/d_m$  where  $d_m$  is the maximum depth of the fish) for the eggfish and fantail were significantly lower than those of the common and comet ( $P < 0.05$ ). 4. Dorsal and anal fin area, aspect ratio, chord length and span length were not significantly different among common, comet and fantail ( $P > 0.05$ ). 5. Caudal fin area, chord length, span and aspect ratio were significantly different among the morphotypes ( $P < 0.05$ ).

Drag ( $D$ ) increased with the square of water velocity ( $D = aV^2 + bV + c$  and  $r^2 > 0.85$  for all morphotypes). Slopes and intercepts for drag versus velocity and drag coefficient versus Reynolds number ( $Re = LV\nu^{-1}$ , where  $\nu$  is kinematic viscosity of water  $1.003 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$  at  $25^\circ\text{C}$ ) of common and comet were significantly lower than that of fantail and eggfish ( $P > 0.05$ ; Fig. 3).

**Table 1:** Morphometric characteristics of four *Carassius auratus* morphotypes.

	Common	Comet	Fantail	Eggfish
<i>N</i>	10	10	10	10
Body mass (g)	2.1 ± 0.4 <sup>a</sup>	2.3 ± 0.4 <sup>a</sup>	4.4 ± 0.5 <sup>b</sup>	5.5 ± 0.5 <sup>b</sup>
Stretched straight centre of mass	0.31±0.01 <i>L</i> <sup>a</sup>	0.33±0.01 <i>L</i> <sup>a</sup>	0.40±0.01 <i>L</i> <sup>b</sup>	0.41±0.01 <i>L</i> <sup>b</sup>
Standard length <i>L<sub>s</sub></i> (cm)	4.1 ± 0.2 <sup>a</sup>	4.2 ± 0.3 <sup>a</sup>	3.6 ± 0.4 <sup>a</sup>	4.0 ± 1.6 <sup>a</sup>
Body length <i>L</i> (cm)	5.1 ± 0.2 <sup>a</sup>	5.7 ± 0.5 <sup>a</sup>	5.7 ± 0.5 <sup>a</sup>	5.3 ± 0.2 <sup>a</sup>
Fineness ratio ( <i>L<sub>s</sub>/d<sub>m</sub></i> )	2.8 ± 0.2 <sup>a</sup>	2.8 ± 0.2 <sup>a</sup>	2.1 ± 0.2 <sup>b</sup>	1.7 ± 0.2 <sup>b</sup>
Maximum depth of section <i>d<sub>m</sub></i> (cm)	1.8 ± 0.1 <sup>a</sup>	1.8 ± 0.1 <sup>a</sup>	2.9 ± 0.1 <sup>b</sup>	1.8 ± 0.1 <sup>a</sup>
Total frontally projected area (cm <sup>2</sup> )	1.1 ± 0.1 <sup>a</sup>	1.0 ± 0.1 <sup>a</sup>	1.6 ± 0.2 <sup>b</sup>	1.7 ± 0.2 <sup>b</sup>
Total body surface area (cm <sup>2</sup> )	16.8 ± 1.5 <sup>a</sup>	17.3 ± 1.7 <sup>a</sup>	23.4 ± 1.5 <sup>b</sup>	23.8 ± 1.6 <sup>b</sup>
Dorsal fin planform area (cm <sup>2</sup> )	0.8 ± 0.1 <sup>a</sup>	0.8 ± 0.1 <sup>a</sup>	0.6 ± 0.2 <sup>a</sup>	NA
Dorsal fin aspect ratio	0.7 ± 0.2 <sup>a</sup>	0.7 ± 0.2 <sup>a</sup>	0.5 ± 0.2 <sup>a</sup>	NA
Dorsal fin chord length (cm)	1.7 ± 0.1 <sup>a</sup>	1.7 ± 0.1 <sup>a</sup>	1.5 ± 0.1 <sup>a</sup>	NA
Dorsal fin span length (cm)	0.8 ± 0.1 <sup>a</sup>	0.8 ± 0.1 <sup>a</sup>	0.9 ± 0.1 <sup>a</sup>	NA
Caudal fin planform area (cm <sup>2</sup> )	1.1 ± 0.2 <sup>a</sup>	1 ± 0.2 <sup>a</sup>	1.7 ± 0.2 <sup>b</sup>	1.1 ± 0.2 <sup>a</sup>
Caudal fin aspect ratio	3.4 ± 0.2 <sup>a</sup>	4.5 ± 0.2 <sup>a</sup>	1.5 ± 0.1 <sup>b</sup>	2.3 ± 0.2 <sup>c</sup>
Caudal fin chord length (cm)	1.2 ± 0.1 <sup>a</sup>	2.3 ± 0.1 <sup>b</sup>	2.3 ± 0.1 <sup>b</sup>	1.6 ± 0.1 <sup>c</sup>
Caudal fin span (cm)	1.9 ± 0.1 <sup>a</sup>	2.1 ± 0.1 <sup>b</sup>	1.5 ± 0.1 <sup>c</sup>	1.5 ± 0.1 <sup>d</sup>
Anal fin planform area (cm <sup>2</sup> )	0.5 ± 0.1 <sup>a</sup>	0.5 ± 0.1 <sup>a</sup>	0.6 ± 0.1 <sup>a</sup>	0.6 ± 0.1 <sup>a</sup>
Anal fin aspect ratio	1.3 ± 0.2 <sup>a</sup>	1.3 ± 0.2 <sup>a</sup>	1.3 ± 0.2 <sup>a</sup>	1.3 ± 0.2 <sup>a</sup>
Anal fin chord length (cm)	0.7 ± 0.1 <sup>a</sup>	0.7 ± 0.1 <sup>a</sup>	0.6 ± 0.1 <sup>a</sup>	0.6 ± 0.1 <sup>a</sup>
Anal fin span (cm)	0.8 ± 0.1 <sup>a</sup>	0.8 ± 0.1 <sup>a</sup>	0.9 ± 0.1 <sup>a</sup>	0.9 ± 0.1 <sup>a</sup>
Pectoral fin planform area (cm <sup>2</sup> )	0.3 ± 0.1 <sup>a</sup>	0.3 ± 0.1 <sup>a</sup>	1.0 ± 0.1 <sup>b</sup>	1.0 ± 0.1 <sup>b</sup>

Means were compared using ANOVA with *post hoc* sequential Tukey-HSD test. Significant differences ( $P < 0.05$ ) among the four groups are indicated by different superscript letters. Values are mean ± 2 S.E.



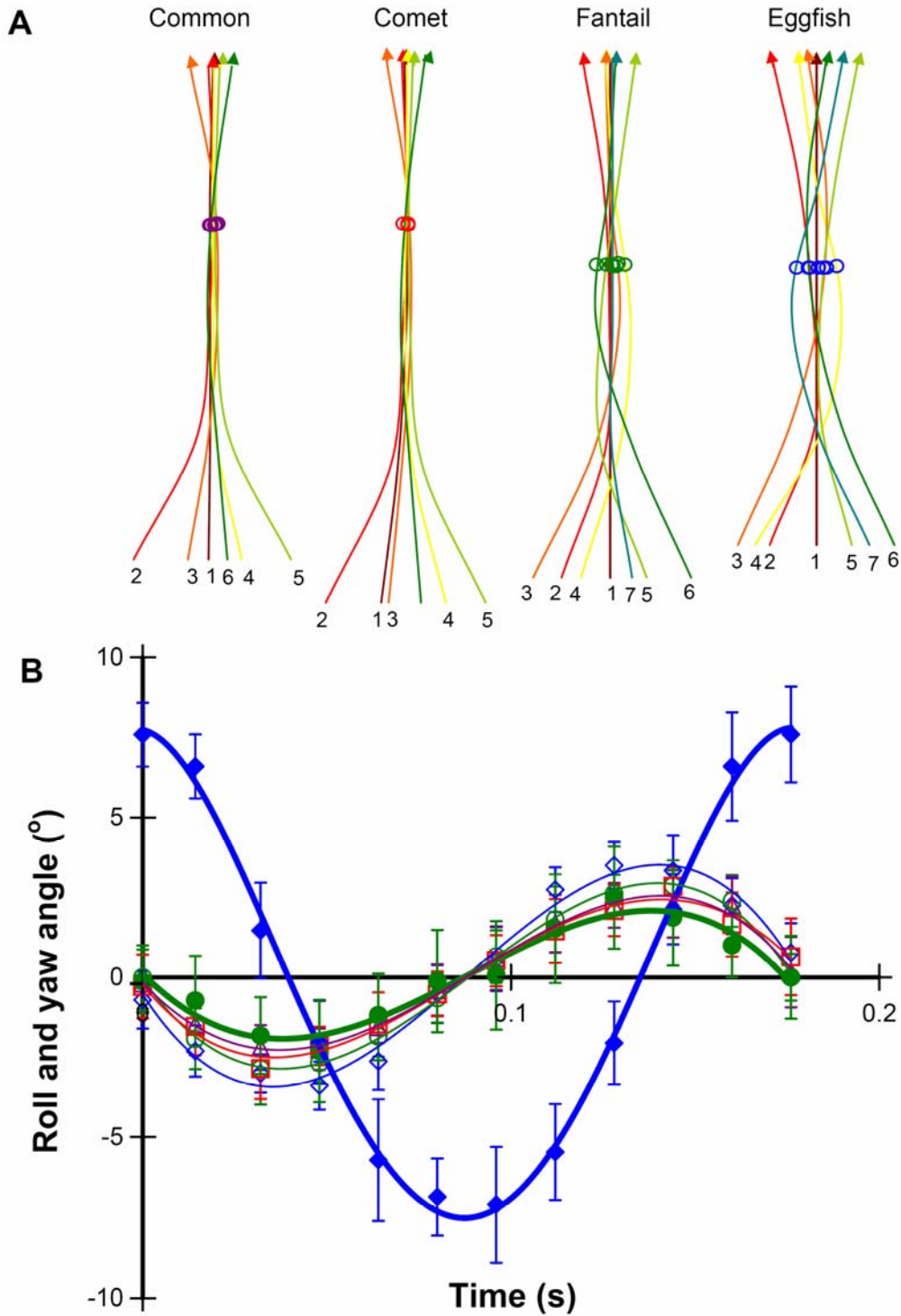
**Figure 3:** Drag versus velocity (A) and frontal drag coefficient versus Reynolds number (B) (common, purple triangle; comet, red square; fantail, green circle; eggfish, blue diamond).

### **3.2 Steady swimming kinematics and oxygen consumption**

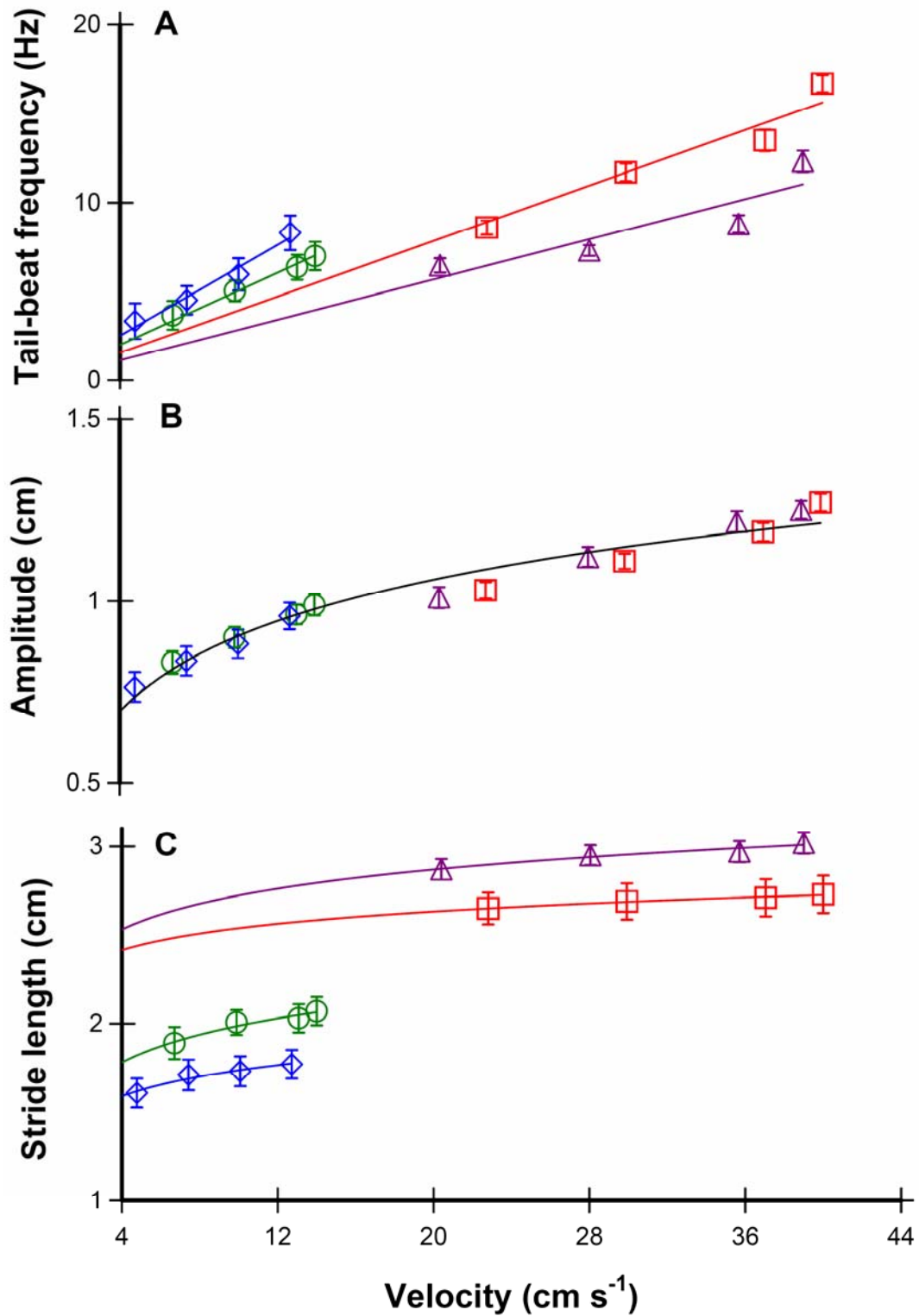
All morphotypes swam in the subcarangiform mode (Breder, 1926; Webb, 1975; Lindsey, 1978; Blake, 1983) with a specific wavelength (wavelength of the body waves divided by body length)  $< 1.0 L$  and amplitude increasing rapidly over the posterior one-third of the body (Fig. 4). Wavelengths ( $4.5 \pm 0.1$ ,  $4.4 \pm 0.1$ ,  $3.8 \pm 0.1$  and  $3.7 \pm 0.1$  cm (mean  $\pm$  2S.E.) for common, comet, fantail and eggfish respectively) were velocity independent and significantly higher for the common and comet ( $P < 0.05$ ). The slopes of tailbeat frequency and stride length versus velocity for the common and comet were significantly lower and higher respectively than those of the fantail and eggfish ( $P < 0.05$ ; Fig. 5). Slopes were not significantly different between the common and comet and between the fantail and eggfish ( $P > 0.05$ ). The slopes of tail-beat amplitude versus velocity for the four morphotypes were not significantly different ( $P > 0.05$ ).

Fatigue time and  $V_{crit}$  for the common and comet were significantly higher than those for the fantail and eggfish ( $P < 0.05$ ; Fig. 6). Slopes of oxygen consumption rate versus swimming velocity for the common and comet were significantly lower than those for fantail and eggfish ( $P < 0.05$ ). The y-intercepts were not significantly different ( $P < 0.05$ ). The standard metabolic rates for common, comet, fantail and eggfish ( $135 \pm 12$ ,  $138 \pm 9$ ,  $145 \pm 15$  and  $148 \pm 13$  mg O<sub>2</sub> kg<sup>-1</sup> hr<sup>-1</sup> (mean  $\pm$  2S.E.) respectively) were higher than extrapolated values (119, 125, 132 and 136 mg O<sub>2</sub> kg<sup>-1</sup> hr<sup>-1</sup> respectively).

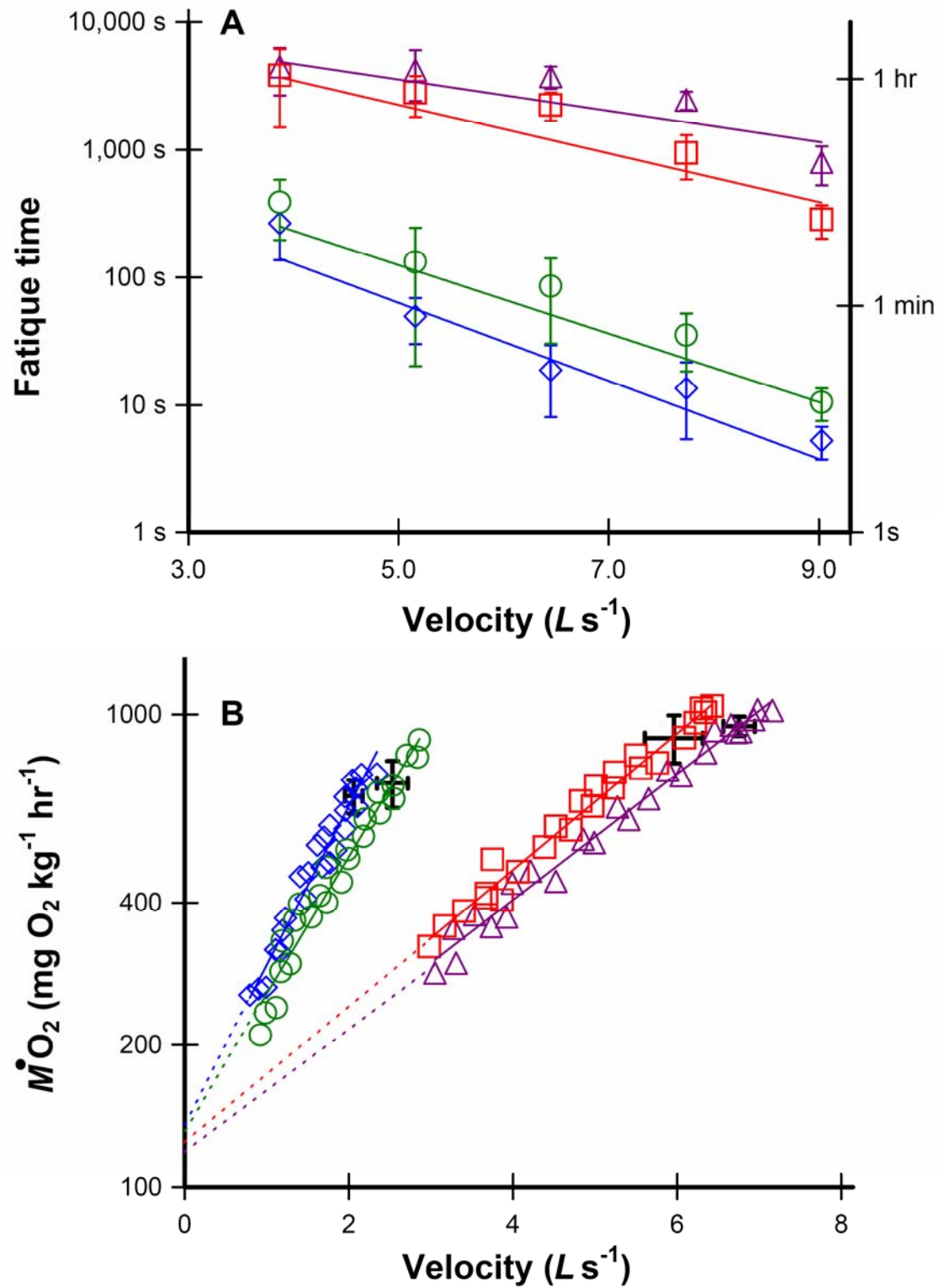
Roll angle of the eggfish was significantly higher than that of the fantail ( $P < 0.05$ ) and negligible in the common and comet. Yaw angles were highest for the eggfish but were not significantly different for the four morphotypes ( $P > 0.05$ ).



**Figure 4:** Steady swimming centerlines (**A**) indicated by successive numbers, the tip of the snout (arrowheads) and centre of mass (circles) for the common, comet, fantail and eggfish at intervals of 0.017 s, 0.017 s, 0.033 s and 0.033 s respectively. Roll (thick line) and yaw (thin line) angles versus time (**B**) for common (purple), comet (red), fantail (green) and eggfish (blue).



**Figure 5:** Tailbeat frequency (A), amplitude (B) and stride length (C) versus velocity (common, purple triangle; comet, red square; fantail, green circle; eggfish, blue diamond). Bars represent  $\pm 2\text{S.E.}$



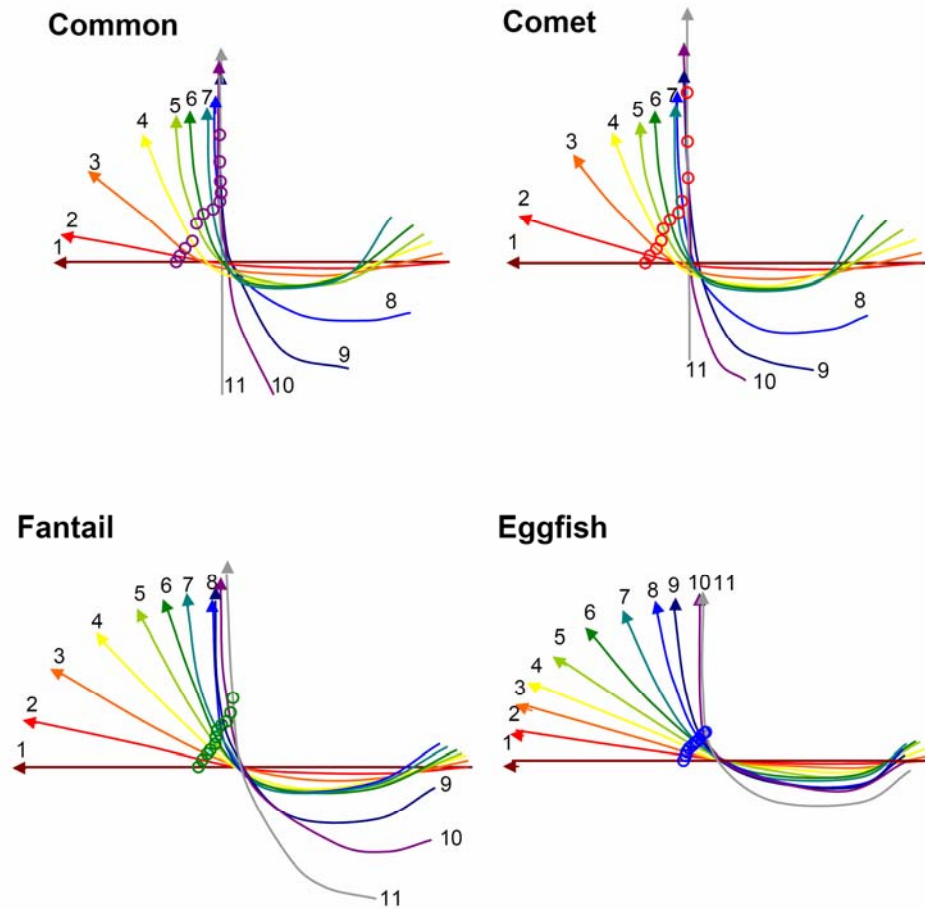
**Figure 6:** Fatigue time (**A**) and total oxygen consumption rate (**B**) versus velocity for common (purple triangle), comet (red square), fantail (green circle) and eggfish (blue diamond).  $V_{crit}$  (+); horizontal bars indicate  $\pm 2S.E.$

### 3.3 Fast-starts

Fast-start responses occurred in the X, Y plane with no discernable vertical movements and consisted of two distinctive stages: stage 1 (S1; unilateral contraction of the axial muscle bending the fish into a C-shape) and stage 2 (S2; strong propulsive stroke of the tail in the opposite direction; Fig. 7). Response latency, turning radius and duration of eggfish fast-starts were significantly higher than those of the other morphotypes ( $P < 0.05$ ; Table 2). Average and maximum velocity and acceleration (S1, S2 and S1+S2) and S1 angular velocity for the common and comet were significantly higher than those of the fantail and eggfish ( $P < 0.05$ ). Eggfish roll angle ( $\gamma \approx 20^\circ$ ) is in the opposite direction of the fast-start trajectory. That of the other morphotypes ( $\gamma < 3^\circ$ ) was in the same direction.

The total thrust force ( $F_M$ ) in the turning direction for the common > comet > fantail > eggfish (Table 3). Fin lifting forces for the common, comet and fantail are similar and an order of magnitude greater than the eggfish (Table 3). The trend of curvature is the same for all morphotypes (Fig. 8). The absolute maximum curvature occurs at  $\approx 0.82 L$ .





**Figure 7:** Centrelines during fast-starts (tip of the snout and centre of mass indicated by arrowheads and circles respectively) for common, comet, fantail and eggfish. The time interval (indicated by successive numbers) is 0.004 s.

**Table 2:** Kinematic data of S1 and S2 fast-starts for four *Carassius auratus* morphotypes.

	Common	Comet	Fantail	Eggfish
<i>N</i>	10	10	10	10
Response latency (s)	0.006 $\pm$ 0.002 <sup>a</sup>	0.008 $\pm$ 0.002 <sup>a</sup>	0.008 $\pm$ 0.003 <sup>a</sup>	0.020 $\pm$ 0.011 <sup>b</sup>
Radius (m)	0.011 $\pm$ 0.006 <sup>a</sup>	0.012 $\pm$ 0.004 <sup>a</sup>	0.018 $\pm$ 0.007 <sup>a</sup>	0.039 $\pm$ 0.013 <sup>b</sup>
(S1+S2) duration (s)	0.058 $\pm$ 0.006 <sup>a</sup>	0.054 $\pm$ 0.007 <sup>a</sup>	0.076 $\pm$ 0.006 <sup>b</sup>	0.128 $\pm$ 0.006 <sup>c</sup>
(S1+S2) distance (m)	0.024 $\pm$ 0.003 <sup>a</sup>	0.024 $\pm$ 0.003 <sup>a</sup>	0.017 $\pm$ 0.01 <sup>b</sup>	0.009 $\pm$ 0.002 <sup>c</sup>
(S1+S2) average velocity (m s <sup>-1</sup> )	0.41 $\pm$ 0.06 <sup>a</sup>	0.45 $\pm$ 0.06 <sup>a</sup>	0.22 $\pm$ 0.02 <sup>b</sup>	0.07 $\pm$ 0.01 <sup>c</sup>
(S1+S2) maximum velocity (m s <sup>-1</sup> )	1.15 $\pm$ 0.13 <sup>a</sup>	1.20 $\pm$ 0.13 <sup>a</sup>	0.80 $\pm$ 0.13 <sup>b</sup>	0.42 $\pm$ 0.12 <sup>c</sup>
(S1+S2) average acceleration (m s <sup>-2</sup> )	7.1 $\pm$ 1.0 <sup>a</sup>	8.3 $\pm$ 1.0 <sup>a</sup>	2.9 $\pm$ 0.2 <sup>b</sup>	0.5 $\pm$ 0.1 <sup>c</sup>
(S1+S2) maximum acceleration (m s <sup>-2</sup> )	33.7 $\pm$ 2.9 <sup>a</sup>	38.2 $\pm$ 3.9 <sup>a</sup>	18.9 $\pm$ 1.6 <sup>b</sup>	6.8 $\pm$ 0.9 <sup>c</sup>
S1 angular velocity (rad s <sup>-1</sup> )	71 $\pm$ 6 <sup>a</sup>	70 $\pm$ 3 <sup>a</sup>	49 $\pm$ 8 <sup>b</sup>	18 $\pm$ 5 <sup>c</sup>
S1 duration (s)	0.022 $\pm$ 0.002 <sup>a</sup>	0.022 $\pm$ 0.001 <sup>a</sup>	0.028 $\pm$ 0.003 <sup>b</sup>	0.038 $\pm$ 0.003 <sup>c</sup>
S2 duration (s)	0.036 $\pm$ 0.006 <sup>a</sup>	0.032 $\pm$ 0.006 <sup>a</sup>	0.048 $\pm$ 0.006 <sup>b</sup>	0.091 $\pm$ 0.006 <sup>c</sup>
S1 distance (m)	0.09 $\pm$ 0.001 <sup>a</sup>	0.010 $\pm$ 0.001 <sup>a</sup>	0.007 $\pm$ 0.001 <sup>b</sup>	0.005 $\pm$ 0.001 <sup>c</sup>
S2 distance (m)	0.021 $\pm$ 0.007 <sup>a</sup>	0.018 $\pm$ 0.008 <sup>a</sup>	0.014 $\pm$ 0.005 <sup>b</sup>	0.034 $\pm$ 0.010 <sup>c</sup>
S1 average velocity (m s <sup>-1</sup> )	0.42 $\pm$ 0.05 <sup>a</sup>	0.43 $\pm$ 0.05 <sup>a</sup>	0.26 $\pm$ 0.02 <sup>b</sup>	0.13 $\pm$ 0.03 <sup>c</sup>
S2 average velocity (m s <sup>-1</sup> )	0.41 $\pm$ 0.07 <sup>a</sup>	0.46 $\pm$ 0.08 <sup>a</sup>	0.20 $\pm$ 0.03 <sup>b</sup>	0.05 $\pm$ 0.01 <sup>c</sup>
S1 average acceleration (m s <sup>-2</sup> )	18.7 $\pm$ 2.3 <sup>a</sup>	19.2 $\pm$ 2.3 <sup>a</sup>	9.4 $\pm$ 0.8 <sup>b</sup>	3.4 $\pm$ 0.8 <sup>c</sup>
S1 maximum acceleration (m s <sup>-2</sup> )	29.0 $\pm$ 3.4 <sup>a</sup>	27.9 $\pm$ 3.4 <sup>a</sup>	17.6 $\pm$ 1.4 <sup>b</sup>	6.6 $\pm$ 0.9 <sup>c</sup>

Means were compared using ANOVA with *post hoc* sequential Tukey-HSD test. Significant differences ( $P < 0.05$ ) among the four groups are indicated by different superscript letters. Values are mean  $\pm$  2. S.E.

**Table 3:** Average segmental (0 - 0.3  $L$ , 0.3 - 0.7  $L$  and 0.7 - 1.0  $L$ ) and total inertial added mass and lifting forces and the resultant turning moment for S1 and S2.

	Force type	Stage (frames)	$\overline{F}_M$ (mN)		$\overline{F}_M$ (mN)		$\overline{F}_M$ (mN)		$\overline{F}_{M(Total)}$ (mN)		Resultant moment (N·m 10 <sup>-3</sup> )
			(0 - 0.3 $L$ )	(0.3 - 0.7 $L$ )	(0.3 - 0.7 $L$ )	(0.3 - 0.7 $L$ )	(0.7 - 1 $L$ )	(0.7 - 1 $L$ )	$\overline{F}_{M(Total)}$ (mN)	$\overline{F}_{M(Total)}$ (mN)	
			$x$	$y$	$x$	$y$	$x$	$y$	$x$	$y$	
Common	<i>Inertial</i>	S1 (1-6)	3	4	5	-28	2	4	14	-30	-2.8
	<i>Lift</i>		-	-	1	-13	3	3			
	<i>Inertial</i>	S2 (6-14)	1	-11	3	12	3	-6	13	-5	3.0
	<i>Lift</i>		-	-	2	10	4	-10			
Comet	<i>Inertial</i>	S1 (1-6)	3.8	4	4.6	-27	1.6	5	12	-26	-3.1
	<i>Lift</i>		-	-	1	-12	1	4			
	<i>Inertial</i>	S2 (6-15)	0.6	-11	3.4	12	3	-6	12	-5	2.9
	<i>Lift</i>		-	-	2	10	3	-10			
Fantail	<i>Inertial</i>	S1 (1-8)	3	4	3	-20	1	4	9	-20	-2.5
	<i>Lift</i>		-	-	1	-14	1	6			
	<i>Inertial</i>	S2 (8-20)	1	-6	3	12	2	-5	9	2	3.0
	<i>Lift</i>		-	-	1	11	2	-10			
Eggfish	<i>Inertial</i>	S1 (1-11)	1.9	2.5	2	-10	1	3	6	-2.5	-2.7
	<i>Lift</i>		-	-	0.5	-1	0.6	3			
	<i>Inertial</i>	S2 (11-33)	0.5	-10	1	11	0.5	-4	2.5	1	2.9
	<i>Lift</i>		-	-	0	10	0.5	-6			

$x$  is in the forward swimming direction and  $-y$  is in the turning direction perpendicular to the midline. Forces and moments were calculated from velocity changes of fish cross-sections between successive 4ms frames.

Negative moments are in the direction of the turn.

### **3.4 Musculature and vertebral column**

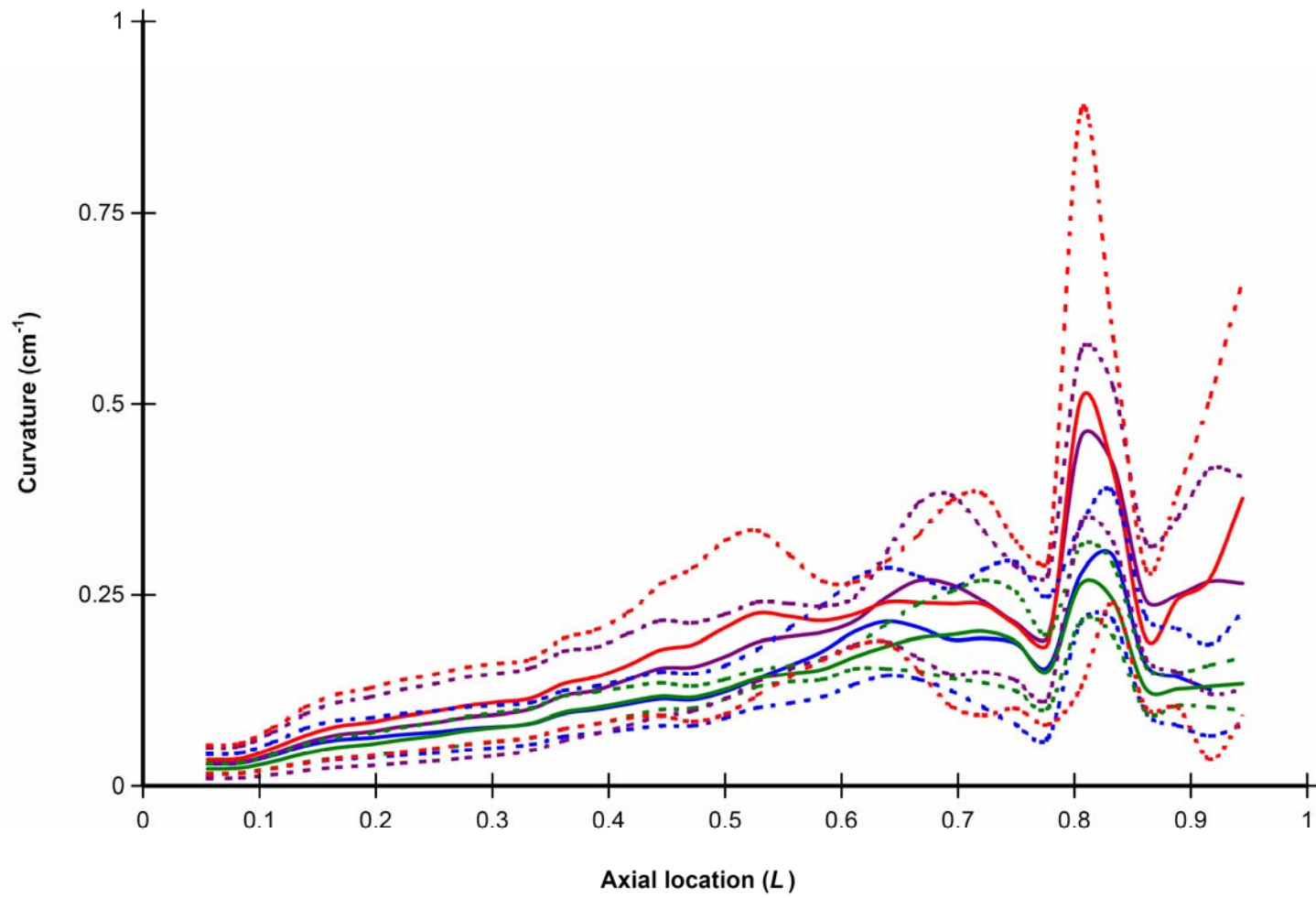
Red and white muscle proportions for the fantail and eggfish were significantly lower than those of common and comet ( $P < 0.05$ ). Red myotomal muscle fibers of the common and comet had a higher mitochondrial volume density and surface density and lower mitochondrial spacing than those in the eggfish and fantail ( $P < 0.05$ ; Table 4; Fig. 9). Eggfish white fibers had a lower mitochondrial density and higher mitochondrial spacing and myofibril diameter than those of the fantail, common and comet ( $P < 0.05$ ). Lipids were present in the red fibres of common and comet but not in the eggfish and fantail.

The backbone had 30 vertebral segments in all morphotypes. Segments lengths were  $0.87 \pm 0.04$ ,  $0.87 \pm 0.04$ ,  $0.84 \pm 0.05$  and  $0.85 \pm 0.05$  mm (mean  $\pm$  2S.E.) for common, comet, fantail and eggfish respectively and were not significantly different ( $P > 0.05$ ).

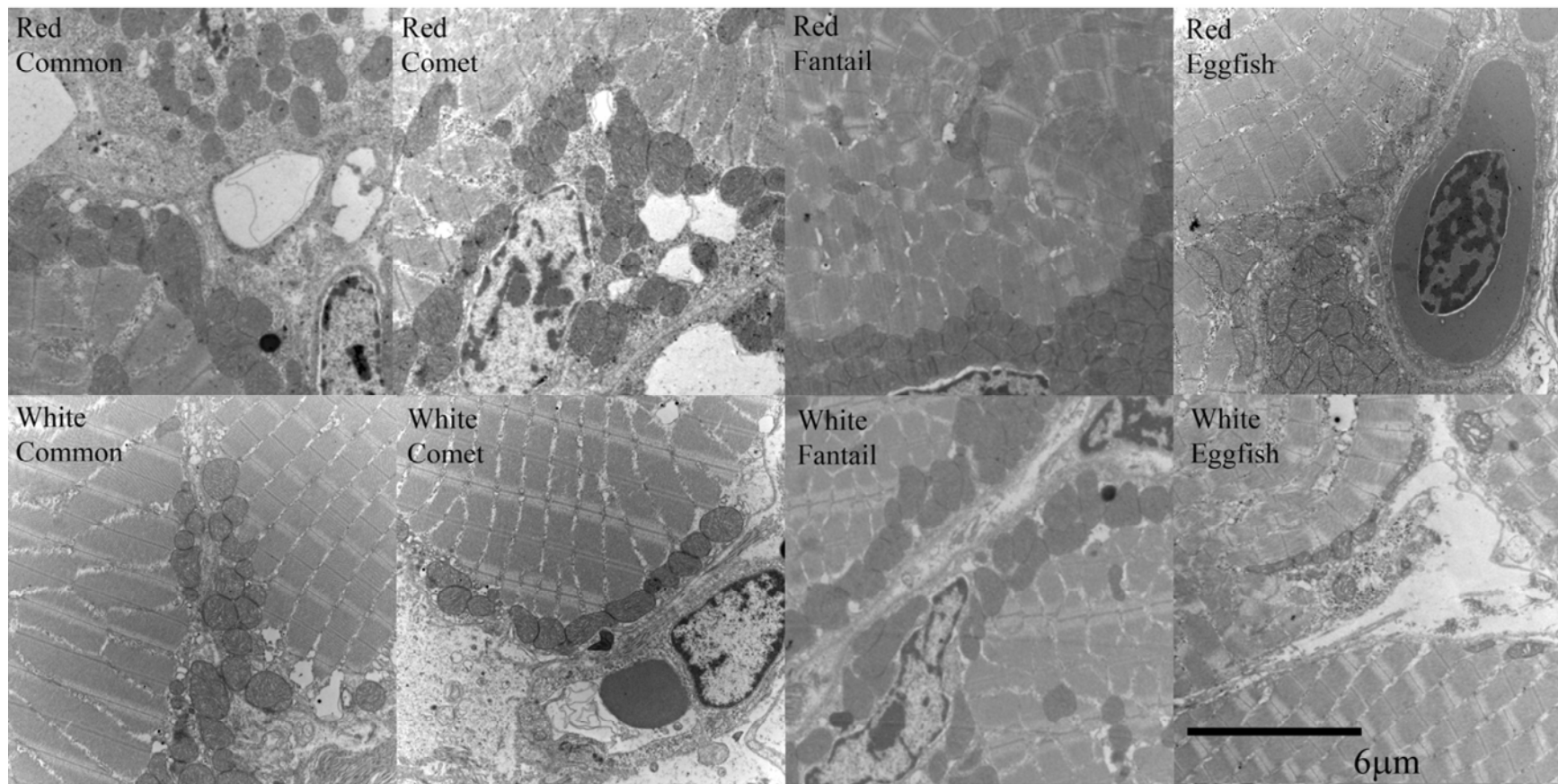
**Table 4:** Mitochondrial volume density ( $V_V$ ), surface density ( $S_V$ ), mitochondrial spacing ( $\lambda_a$ ), myofibril diameter ( $M_d$ ) and capillary to fiber ratio ( $C:F$ ) in goldfish red and white muscle.

	Common	Comet	Fantail	Eggfish
Red muscle				
% of fish mass ( $N=5$ )	$5.6 \pm 0.2^a$	$5.8 \pm 0.2^a$	$2.8 \pm 0.1^b$	$2.7 \pm 0.1^b$
$V_V$ ( $N=75$ )	$0.35 \pm 0.06^a$	$0.35 \pm 0.03^a$	$0.26 \pm 0.02^b$	$0.25 \pm 0.03^b$
$S_V$ ( $N=75$ )	$0.54 \pm 0.02^a$	$0.66 \pm 0.06^b$	$0.22 \pm 0.03^c$	$0.19 \pm 0.04^c$
$\lambda_a$ ( $N=75$ )	$4.8 \pm 0.5^a$	$3.9 \pm 0.4^a$	$13.5 \pm 2.0^b$	$16.3 \pm 2.9^b$
$M_d$ ( $N=75$ )	$9.2 \pm 0.9^a$	$10.0 \pm 1.1^a$	$10.7 \pm 1.8^a$	$10.5 \pm 2.0^a$
$C:F$ ( $N=75$ )	$1.10 \pm 0.37^a$	$0.90 \pm 0.37^a$	$1.00 \pm 0.32^a$	$0.46 \pm 0.25^a$
White muscle				
% of fish mass ( $N=5$ )	$34.7 \pm 1.4^a$	$34.4 \pm 1.2^a$	$23.5 \pm 1.5^b$	$24.7 \pm 0.9^b$
$V_V$ ( $N=75$ )	$0.17 \pm 0.04^a$	$0.17 \pm 0.04^a$	$0.20 \pm 0.04^a$	$0.05 \pm 0.01^b$
$S_V$ ( $N=75$ )	$0.35 \pm 0.04^a$	$0.34 \pm 0.02^a$	$0.34 \pm 0.02^a$	$0.26 \pm 0.04^b$
$\lambda_a$ ( $N=75$ )	$9.8 \pm 1.3^a$	$9.7 \pm 1.0^a$	$9.5 \pm 0.8^a$	$15.1 \pm 2.5^b$
$M_d$ ( $N=75$ )	$10.00 \pm 0.50^a$	$10.20 \pm 0.51^a$	$10.25 \pm 0.50^a$	$12.75 \pm 0.65^b$
$C:F$ ( $N=75$ )	$1.40 \pm 0.49^a$	$1.40 \pm 0.49^a$	$1.20 \pm 0.40^a$	$0.90 \pm 0.20^a$

Means were compared using ANOVA with *post hoc* sequential Tukey-HSD test. Significant differences ( $P < 0.05$ ) among the four groups are indicated by different superscript letters. Values are mean  $\pm$  2 S.E.



**Figure 8:** Fast-start curvature versus axial location (common, purple; comet, red; fantail, green; eggfish, blue). Mean is represented by solid lines and  $\pm 2$ S.E. by dotted lines.



**Figure 9:** Transmission electron micrographs of propulsive red and white muscles from the four goldfish morphotypes.

## 4 DISCUSSION

The hypothesis that swimming decrements would be a function of the extent of domestication is supported. Swimming performance and the functional characteristics of the propulsive musculature (whether significantly different or not) descend in the order: common, comet, fantail and eggfish. For most performance parameters, the morphotypes show a “pairing”: common and comet, fantail and eggfish. For fish of comparable length, drag and drag coefficients, tail-beat frequency and total oxygen consumption rate for the common and comet were lower than those of the fantail and eggfish (Figs. 3, 5 and 6). Stride length, fatigue time,  $V_{crit}$  and fast-start performance (average and maximum velocity and acceleration) (Figs. 5C, 6 and Table 2) for the common and comet were higher than those of the fantail and eggfish. The proportion of propulsive red and white muscle for the common and comet were higher and lower respectively than those of the fantail and eggfish (Table 4). The most derived morphotype (eggfish) shows the greatest performance decrement. In particular, fast-start response latency, turning radius and turning duration were higher than in the other morphotypes (Table 2). There are no significant differences between the four morphotypes for standard metabolic rate (both extrapolated and directly measured), vertebral number and segment lengths. Presumably, these “conservative” ancestral characters are not sensitive to artificial selection.

### 4.1 Drag

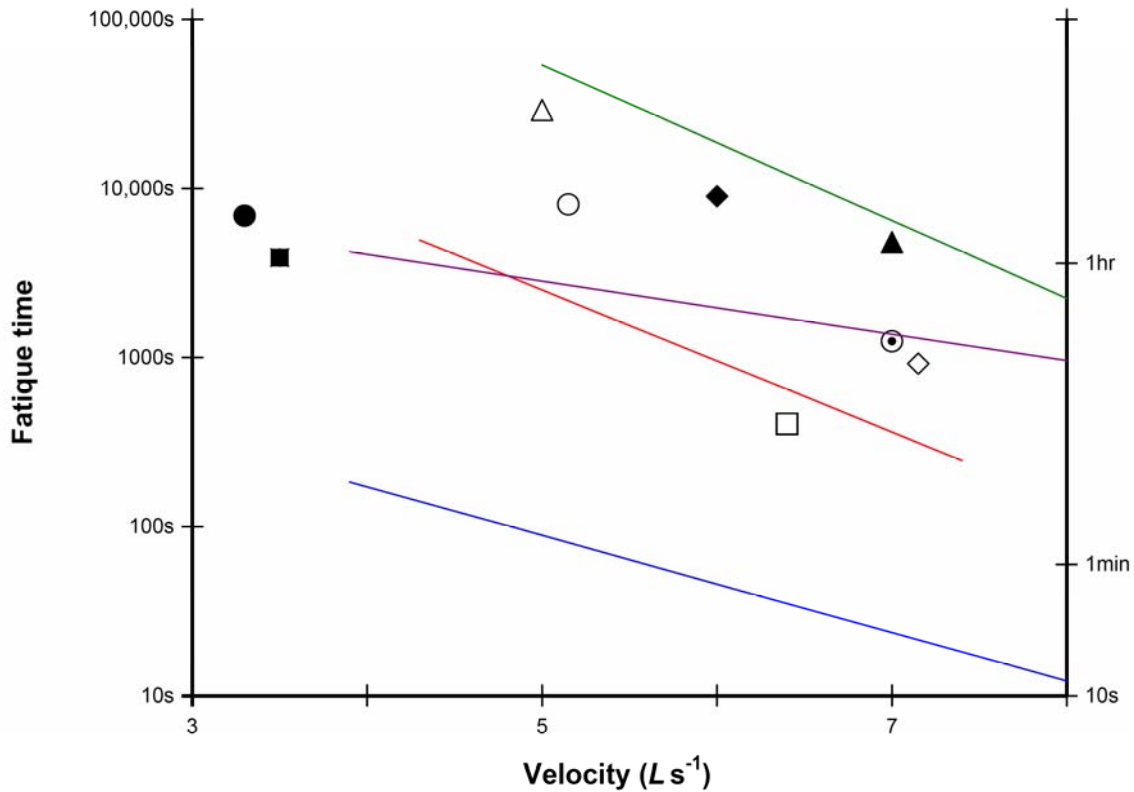
Dead-drag measurements do not reflect the drag of a swimming fish performing undulatory motions where drag is augmented due to boundary layer thinning (Bone in



Lighthill, 1971). However, rigid body values are a useful benchmark for assessing relative drag. Swimming endurance is a function of body form (which is a determinant of drag magnitude; e.g., Webb, 1984; Blake, 2004). For fish of comparable length, drag and drag coefficients for the fantail and eggfish are significantly higher than that for the common and comet ( $P < 0.05$ ; Fig. 3), which are more streamlined (fineness ratio closer to the optimum value of about 4.5 (e.g., Blake, 1983) Table 1;) and should require higher thrust production at any given velocity. This is reflected kinematically; tailbeat frequency and stride length for the common and comet were lower and higher respectively relative to the fantail and eggfish at any given velocity (Fig. 5).

## **4.2 Steady swimming**

Swimming endurance (fatigue time; Fig. 6) for the common and comet is comparable to that of other small fishes (3 - 10 cm; Fig. 10) and the fantail and eggfish perform relatively poorly. The fatigue time of the ancestral form, the Crucian carp (Tsukamoto et al., 1975), is not significantly different from that of the common and comet ( $P > 0.05$ , Fig. 10). Fatigue time is dependent on the proportion and mass specific power output of red muscle (Blake, 1983; McLaughlin and Kramer, 1991). Relative to body mass the proportion of red muscle (Boddeke et al., 1959; Greer-Walker and Pull, 1975) is higher in the common and comet than in the fantail and eggfish (Table 4). Mitochondrial volume density and spacing in red muscle fibres of the common and comet were higher and lower respectively than those of the fantail and eggfish (Table 4). A high mitochondrial volume density enhances ATP supply capacity to the red propulsive musculature through aerobic metabolic pathways and a small mitochondrial spacing



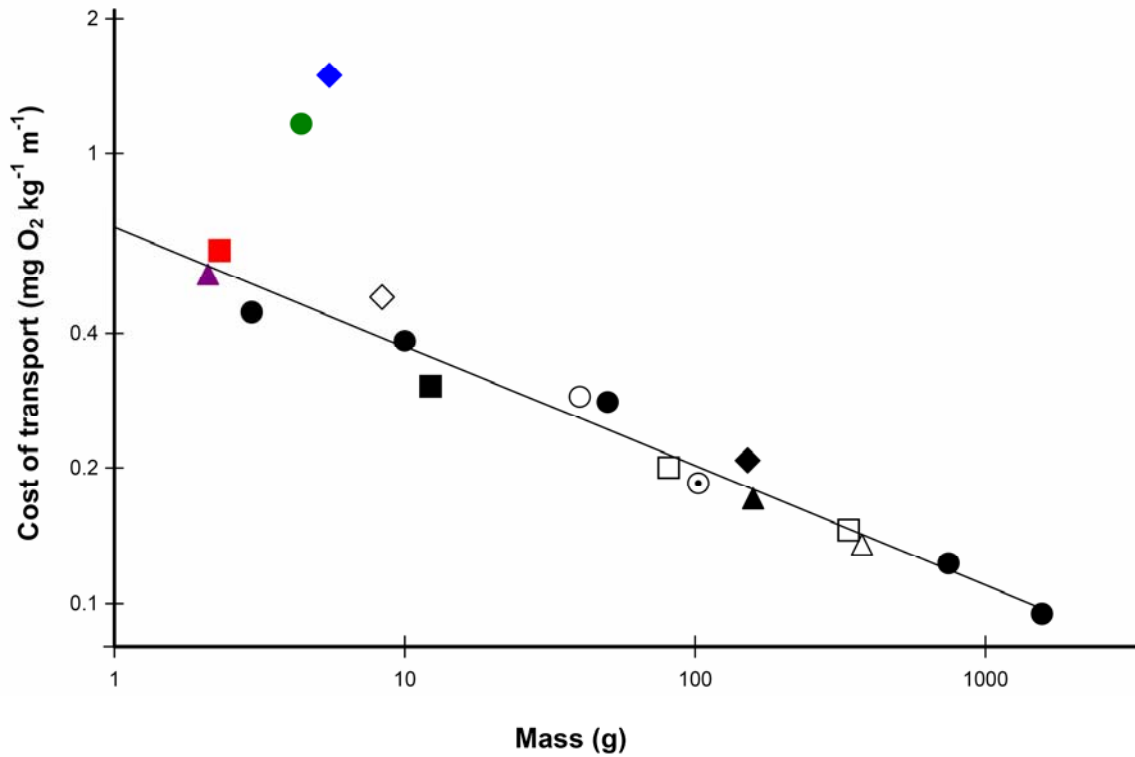
**Figure 10:** Fatigue time for the common and comet (purple line) and fantail and eggfish (blue line) and a variety of small fishes (3 - 10 cm) that include body and caudal fin (*Sardinops sagax* (solid circle; Beamish, 1984), *Carassius carassius* (solid square; Tsukamoto et al., 1975), *Oncorhynchus mykiss* (solid diamond; Tsuyuki and Wiliscroft, 1977), *Oncorhynchus kisutch* (solid triangle; coastal streams; Taylor and McPhail, 1985) and *Oncorhynchus kisutch* (concentric circle; interior streams; Taylor and McPhail, 1985)) and pectoral fin swimmers (three-spined sticklebacks (empty triangle; stream; Whoriskey and Wootton, 1987), three-spined sticklebacks (empty circle; anadromous; Taylor and McPhail, 1986), three-spined sticklebacks (diagonal cross; stream; Taylor and McPhail, 1986), three-spined sticklebacks (empty square; stream; Stahlberg and Peckman, 1987), *Chromis punctipinnis* (empty diamond; Dorn et al., 1979), *Lepomis gibbosus* (orthogonal cross; Brett and Sutherland, 1964)). Limnetic and benthic sticklebacks are given by green and red line respectively (Blake et al., 2005).

reduces the distance over which metabolites diffuse before reaching a mitochondrion (Tyler and Sidell, 1984).

The directly measured SMR's of the four morphotypes ( $\approx 140 \text{ mg O}_2 \text{ kg}^{-1} \text{ hr}^{-1}$ ) were not significantly different ( $P > 0.05$ ) and the same as those measured by Sollid et al. (2005) for common goldfish at the same temperature. Extrapolated values for all morphotypes are about 25 % less than the directly measured values. The difference is likely due to spontaneous activity during the direct measurements (Beamish and Mookherjee, 1964). Values for *C. carassius* ( $200 \text{ mg O}_2 \text{ kg}^{-1} \text{ hr}^{-1}$  at  $25^\circ\text{C}$ ; Sollid et al., 2005) are significantly higher than all four morphotypes ( $P < 0.05$ ) suggesting that the divergence of *C. auratus* from its immediate ancestor, *C. carassius*, was associated with a decrease in SMR. However, SMR for *Cyprinus carpio* ( $\approx 90 \text{ mg O}_2 \text{ kg}^{-1} \text{ hr}^{-1}$  at  $22.5^\circ\text{C}$ ; Zhou et al., 2000) is lower than both.

Fish cost of transport (COT) scales with body mass to the -0.3 power (Schmidt-Nielsen, 1972; Beamish, 1978). For goldfish  $\approx 100 \text{ g}$  (Smit et al., 1971), COT ( $0.65 \text{ mg O}_2 \text{ kg}^{-1} \text{ m}^{-1}$ ) is comparable to a similarly sized trout (Rao, 1971) and COT for the common and comet are consistent with predicted values ( $P > 0.05$ ; Fig. 11). However, those for the fantail and eggfish are significantly higher than the regression ( $P < 0.05$ ) likely due to their relatively high drag (Fig. 3), energy losses due to larger rolling and yawing motions (Fig. 4), relatively low proportion of red muscle, low mitochondrial density (Table 4) and low propulsive and muscle efficiency (Table 5).

Knowing the mean total swimming power and the mechanical equivalent of the active metabolic rate (AMR) allows muscle efficiency to be inferred. The energy equivalent of the consumed oxygen (Fig. 6B) corresponding to AMR at  $V_{crit}$  gives the



**Figure 11:** Cost of transport versus body mass for the common (purple triangle), comet (red square), fantail (green circle) and eggfish (blue diamond) and a variety of other fishes: *Oncorhynchus nerka* (solid circle; Brett, 1964), *Lepomis gibbosus* (solid square; Brett and Sutherland, 1965), *Coregonus* (empty triangle; Wohlschlag *et al.*, 1968), *Tilapia nilotica* (concentric squares; Farmer and Beamish, 1969), *Melanogrammus aeglefinus* (solid triangle; Tytler, 1969), *Liza macrolepis* (empty diamond; Kutty, 1969), *Micropterus salmoides* (solid diamond; Beamish, 1970), *Salmo gairdneri* and *Carassius auratus* (concentric circle; Rao, 1971; Smit *et al.*, 1971 respectively), *Lagodon rhomboids* (empty circle; Schmidt-Nielsen, 1972) and *Thymallus* spp. (empty square, Schmidt-Nielsen, 1972).

**Table 5:** The mean total swimming power output ( $P=m_a w_x W V$ , where  $m_a$  is the added mass,  $w_x$  is the lateral velocity of pushing on a water slice,  $W$  is the lateral velocity of the fin tip (all at the trailing edge of the caudal fin) and  $V$  is forward velocity). The rate of loss of kinetic energy associated with accelerating the water to  $w_x$  ( $P_k=V(0.5m_a w_x^2)$ ) and thrust power ( $P_T=P-P_k$ ). The mechanical power equivalent of the active metabolic rate ( $P_{AMR}$ ) (calculated using an oxy-calorific equivalent of 14.7 J/mg O<sub>2</sub>; Gnaiger and Kemp, 1990) and the muscle, propulsive and aerobic efficiency ( $e_m=P/P_{AMR}$ ,  $e_p=P_T/P$  and  $e_a=P_T/P_{AMR}$  respectively) are shown.

	Common	Comet	Fantail	Eggfish
$P$ ( $\times 10^{-3}$ W)	1.4	1.4	1.7	1.5
$m_a$ (g)	0.9	1.1	1.4	1.2
$w$ ( $s^{-1}$ )	0.05	0.05	0.08	0.10
$W$ ( $ms^{-1}$ )	0.09	0.08	0.10	0.12
$V$ ( $ms^{-1}$ )	0.35	0.34	0.14	0.11
$P_k$ ( $\times 10^{-3}$ W)	0.35	0.41	0.66	0.64
$P_T$ ( $\times 10^{-3}$ W)	1.00	1.01	0.99	0.88
$P_{AMR}$ ( $\times 10^{-3}$ W)	7	7	10	11
$e_m$	0.20	0.20	0.17	0.14
$e_p$	0.74	0.71	0.60	0.58
$e_a$	0.15	0.14	0.10	0.08

overall aerobic swimming power ( $P_{AMR}$ ; Table 5). The mean total swimming power output ( $P$ ; calculated from Lighthill's (1969) simplified bulk momentum model) at  $V_{crit}$  minus the rate of kinetic energy losses ( $P_k$ ) gives the thrust power ( $P_T$ ). The efficiency of the propulsive musculature ( $P/P_{AMR}$ ) for the common and comet is similar to the common expectation of 0.2 - 0.25 (Hill, 1950). At  $V_{crit}$ , values of the propulsive Froude efficiency ( $e_p=P_T/P$ ) and aerobic efficiency ( $e_a=P_T/P_{AMR}$ ) for the common and comet (Table 5) are comparable to rainbow trout (locomotor generalist, subcarangiform swimmer;  $e_p \approx 0.75$  and  $e_a \approx 0.15$ ; Webb, 1971).

### 4.3 Fast-starts

Performance of common and comet C-starts in all categories was superior to that of the fantail and eggfish (Table 2). The former have a lower overall body mass relative to their length (Table 1), and it is likely that the entrained longitudinal added fluid mass force (Webb, 1982) relative to fish mass is higher in the fantail and eggfish due to their unstreamlined form. Although the percentage of white muscle relative to the total muscle mass is comparable for all morphotypes, the ratio of the overall white muscle mass to fish mass is higher than that for the fantail and eggfish (Table 4). In addition, the common and comet have a higher degree of body flexibility than the fantail and eggfish and a more flexible posterior region imparts large reactive forces to the fluid (Fig. 8). Therefore, for a given body length, the common and comet can be expected to generate a higher propulsive force relative to the overall mass to be propelled. This is supported by calculated C-start S1 turning radii based on average values of mass, velocities and centripetal forces ( $R = mV^2F^{-1}$ ; Table 2 and 3), which compare well to the actual performance of all morphotypes. Measured and computed values of  $R$  for the common ( $\approx 0.25 L$ ) and comet ( $\approx 0.20 L$ ) are comparable to measured values for other locomotor generalists (e.g. smallmouth bass,  $0.11 L$ ; rainbow trout,  $0.18 L$ ; Webb, 1983). Fantail ( $\approx 0.30 L$ ) and eggfish ( $\approx 0.75 L$ ) values are comparable to forms highly specialized for efficiency steady swimming that show serious performance compromise in transient turning manoeuvres (Blake et al., 1995).

High acceleration performance is associated with a deep body section, posteriorly placed median fins, large caudal fin area, body flexibility (allowing for large amplitude propulsive movements) and a high percentage of propulsive white muscle all of which

enhance thrust (Weihs, 1973; Webb, 1976, 1977; Rome et al., 1988; Wakeling, 2006). However, performance depends primarily on a compromise between white muscle mass as a percentage of body mass and lateral body and fin profile (Webb, 1977, 1978a; Wakeling, 2006). Webb (1984, 1998) identified three specialist classes of fish swimming: body and caudal fin periodic (sustained steady swimming), body and caudal fin transient (fast-starts) and median and paired fin (manoeuvre specialists) swimmers, and proposed that specialization in any given category would limit performance in any other. He points out that most fish are locomotor generalists with “adequate” performance in all three categories. Blake (2004) amends Webb’s construct by suggesting that design and performance trade-offs primarily occur when the same propulsor is employed for more than one task (“coupled”, e.g. trout and pike which use the same propulsor for routine swimming and fast-starts). Fish employing different propulsors for different tasks (“decoupled”) do not show serious performance trade-offs. The ancestors of the four morphotypes, *C. carpio* and *C. carassius*, are locomotor generalists with a coupled system. Maximum acceleration for the common and comet ( $\approx 40 \text{ m s}^{-2}$ ) was similar to that of other locomotor generalists such as trout (e.g. Weihs, 1973; Webb, 1976, 1977, 1978b), and the contributions of the inertial and lift forces to the total force are about equal (Table 3). Eggfish maximum acceleration ( $\approx 5 \text{ m s}^{-1}$ ; Table 2) is poor, due to the absence of inertial and lifting thrust contributions from the dorsal fin. For all four morphotypes, curvature was maximal at  $\approx 0.8 L$  and similar to the common carp (maximum curvatures at  $0.5 - 0.8 L$ ; Spierts and van Leeuwen, 1999; Wakeling et al., 1999).

#### **4.4 Dynamic stability in yaw and roll**

Assessments of the stability and control of fish steady swimming are based on submarine and airship motions (see Weihs, 2002; Webb, 2006 for reviews). Detailed experimental studies point to the complexities of the processes involved in fish (Drucker and Lauder, 2003, 2005; Lauder and Drucker, 2004; Standen and Lauder, 2007). For locomotor generalists (*sensu* Webb, 1984) such as rainbow trout and goldfish, the dorsal and anal fins produce equal and opposite moments minimizing roll during steady swimming. The lateral forces generated by the dorsal fin are transmitted along the fin base above the centre of mass producing a roll moment. The anal fins produce an equal and opposite lateral moment (Drucker and Lauder, 2003, 2005; Standen and Lauder, 2007). Because much of the dorsal fin is located posterior to the centre of mass, a yaw moment is also created (Drucker and Lauder, 2003, 2005). Yawing moments generated by the caudal fin are dampened by the mass and added mass (mass of fluid entrained during the unsteady motions) at the maximum depth of section, which is enhanced by the dorsal fin (Lighthill, 1970, 1971, 1977). The eggfish (no dorsal fin) rolled and yawed to a greater extent than the other morphotypes (Fig. 4). The pectoral fins may also play a role in countering yaw (Drucker and Lauder, 2003).

Lighthill (1977) developed a reactive-resistive recoil theory (i.e. passive yawing motions of the anterior part of the body generated by the caudal fin) focused at relating the amplitude of yawing motions to any associated energy losses. The principle result was that for a circumstance when the ratio of the reactive response to one in which lateral displacements at the posterior end (caudal fin) have an amplitude equal to the maximum depth of section ( $\xi = F_l / (k\omega\rho d_m^2 L)$ ), where  $F_l$ ,  $k$  and  $\omega$  are tail side force, a constant and



tail-beat frequency respectively; Lighthill, 1977) that is small compared to one ( $\xi < 0.2$ ) energy losses due to recoil are negligible. This condition is met for the common, comet and fantail ( $\xi \approx 0.2$ ). However, for the eggfish,  $\xi \approx 0.4$  implying significant energy losses due to recoil.

Fast-starts are unstable relative to steady rectilinear swimming, and consequently yawing and rolling motions are greater. Yawing instability is advantageous in initiating C-starts in body and caudal fin swimmers (Weihs, 2002) and determines the turning angle (angle between the initial and final orientation) (e.g. Hertel, 1966; Weihs, 1973; Domenici and Blake, 1991). Median fins contribute to fast-start thrust and provide stability in roll and yaw. Overall performance and stability decrease with their progressive removal in rainbow trout (Webb, 1977). Eggfish fast-start roll angles are six times greater than those of the common, comet and fantail, and unlike the other morphotypes, eggfish rolled in the opposite direction of the turn. Both are attributable to the absence of the dorsal fin.

## 5 CONCLUSIONS

Artificially selected fish can bear upon fitness related adaptations associated with form and movement. Results of such studies can complement those focused at understanding the mechanisms of divergent ecological speciation of incipient species in natural systems. Fitness and divergent selection depend on the nature of predator-prey interactions and the intensity of predation pressure (Vamosi and Schluter, 2001; Rundle et al., 2003). Understanding the role of functional design and movement principles employing artificially selected forms could provide insights into the “performance envelope” of natural systems subject to ecological speciation.

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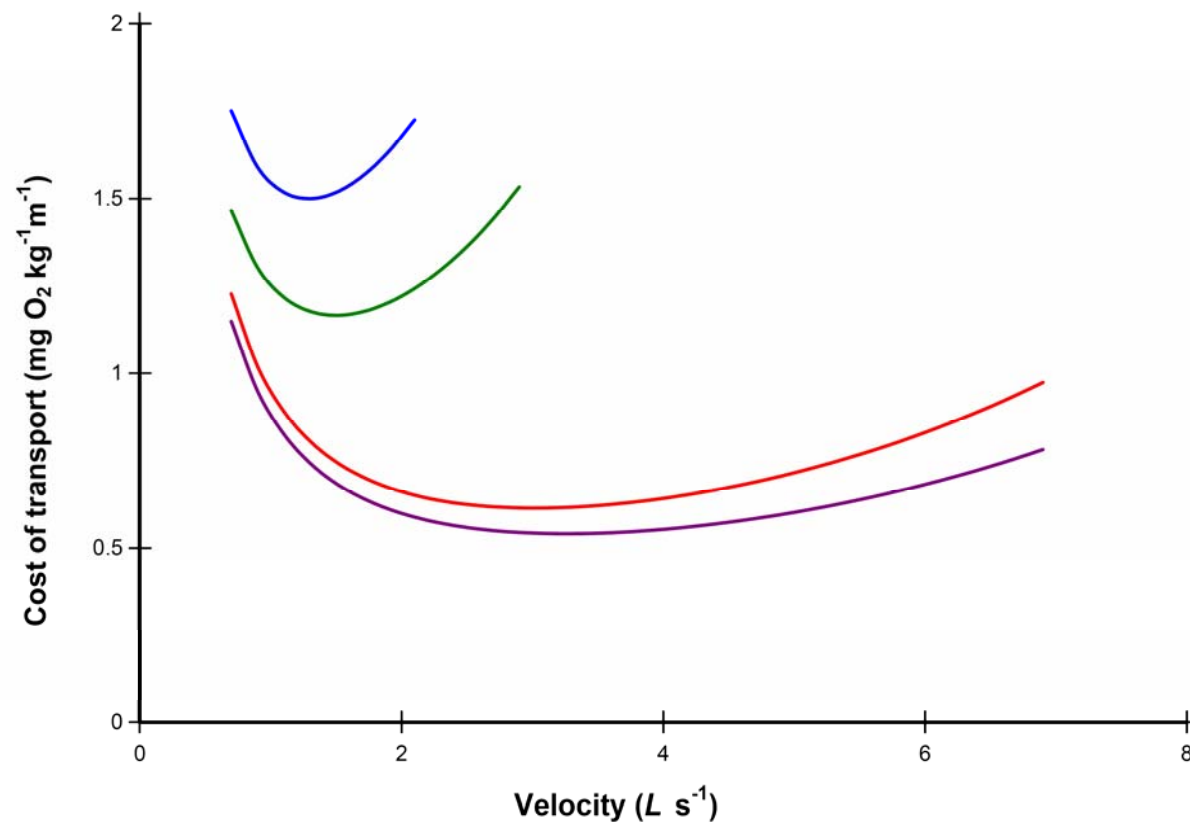
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## APPENDIX 1.

Cost of transport versus velocity for common (purple), comet (red), fantail (green) and eggfish (blue).



## APPENDIX 2.

Conservative ancestral characters of *Carassius auratus* not sensitive to artificial selection.

	Common	Comet	Fantail	Eggfish	Crucian carp	Common carp
Vertebral number ( <i>N</i> =5)	30	30	30	30	32 <sup>1</sup>	38 <sup>2</sup>
Vertebral segment lengthn ( <i>N</i> =5) (mm)	0.87±0.04	0.87±0.04	0.84±0.05	0.85±0.05	NA	NA
Measure standard metabolic rate (mg O <sub>2</sub> kg <sup>-1</sup> hr <sup>-1</sup> )	135±12	138±9	145±15	148±13	200 <sup>3</sup>	90 <sup>4</sup>
Extrapolated standard metabolic rate (mg O <sub>2</sub> kg <sup>-1</sup> hr <sup>-1</sup> )	119	125	132	136	NA	NA
<sup>1</sup> Froese and Pauly (2007), <sup>2</sup> Gerlach (1983), <sup>3</sup> Sollid et al. (2005), <sup>4</sup> Zhou et al. (2000).						

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