1. INTRODUCTION

Body shape in fishes evolved with their adaptations to different environmental conditions (Langerhans et al. 2004) and, because natural flow velocities vary widely, fish adapted to different flow regimes. Generally, fish that have adapted to high flow velocities are strong swimmers and have a streamlined body shape (Langerhans et al. 2007, Yan et al. 2013).

In the laboratory, swimming capability is frequently measured using a stepped velocity test (Brett 1964). Among the stepped velocity tests, the critical swimming speed (Ucrit) protocol is used to evaluate prolonged swimming capability. Although this approach may introduce bias as fatigue accumulates through the time steps, it is useful for comparing the relative influence of factors that affect fish swimming capability. Fish use burst swimming when they pursue prey, flee from predators or encounter high-velocity currents. Although endurance is low at burst speed (Uburs), burst swimming is important for survival. The lowest flow velocity that induces continuous fish motion is termed the induced flow velocity (Uind). This parameter is useful for fish passage design because fish maintain their orientation more easily when flow velocity is higher than Uind (Cai et al. 2018).

Effect of tail fin loss on swimming capability and tail beat frequency of juvenile black carp *Mylopharyngodon piceus*

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ABSTRACT: Fin clipping is a common practice in fisheries management, and hatchery fish are often marked this way. In the wild, the tail (caudal) fin may be damaged or lost to predation or disease. Because the tail fin is important to fish swimming behavior and ability, this study was designed to examine the effects of partial and complete loss of the tail fin on the swimming ability of juvenile black carp *Mylopharyngodon piceus*. Swimming speed and tail beat frequency were measured for 3 groups (intact tail fin, partial tail fin, no tail fin) using a stepped velocity test conducted in a fish respirometer. We found that critical swimming speed (Ucrit) and burst speed (Uburs) decreased slightly in the partial fin group and significantly in the no fin group. In the group with no tail fin, Uburs decreased more than Ucrit, clearly reducing the ability to avoid predators. Moreover, mean tail beat frequency (TBFmean), Ucrit and Uburs all decreased slightly in the partial fin group and significantly in the no fin group. A decrease in tail beat force and TBF both reduce swimming capability. These findings contribute to developing our understanding of the relationship between fish tail fins and swimming.

KEY WORDS: Swimming performance · Tail fin loss · Critical swimming speed · Burst speed · Tail beat frequency
Fin clipping is a common practice in fisheries management, and hatchery fish are often marked by clipping adipose fins and, less frequently, pelvic fins (Hansen 1988, Vander Haegen et al. 2005). The tail (caudal) fin is important, both for locomotion and changing direction (Ohlberger et al. 2007, Handegard et al. 2009), and the sizes and shapes of tail fins vary across species. Tail beat frequency (TBF) is an important index of fish swimming behavior and its correlation with swimming speed is near linear (Hunter & Zweifel 1971, Webb 1975, Beamish 1978). Fish species differ in tail fin type (size and hardness), which affects swimming capability (Plaut 2001). The tail fin may be damaged or lost to predation or disease, and it would thus be useful to investigate the effect of such damage or loss on swimming performance.

The black carp Mylopharyngodon piceus is a cyprinid species native to China and eastern Russia. Preying on snails, shellfish, shrimp and insects, black carp provide biological control of aquatic pests (Ben-Ami & Heller 2001) and survive well in freshwaters if predators, such as yellowcheek Elopichthys bambusa, do not find them. Black carp have been transported, accidentally and/or intentionally, to many countries and are considered an invasive species in certain countries where they threaten native fish. Here, we tested the swimming performance of black carp by measuring \( U_{\text{crit}} \), \( U_{\text{burst}} \), \( U_{\text{ind}} \) and TBF. The effect of tail fin loss on swimming capability was also investigated. The results add to our knowledge of the relationship between fish swimming speed and tail beat.

2. MATERIALS AND METHODS

2.1. Ethics statement

This study was conducted in strict accordance with the laws governing animal experimentation in China. The protocol was approved by the China Three Gorges University. All efforts were made to minimize suffering.

2.2. Test fish

Juvenile black carp (standard length = 11.4 ± 1.0 cm, mass = 23.9 ± 6.1 g; SD, \( n = 60 \)), were obtained from an aquaculture farm in Tongren, China (27°94’N, 108°23’E). The test fish were maintained in tanks of river water (20.2–23.4°C) and fed to satiation daily at 07:00 and 16:00 h with a compound feed (crude protein ≥ 45%, fat ≥ 10%, crude fiber ≥ 3% and ash ≥ 17%).

2.3. Equipment

Based on a study on fish swimming and coasting distance by Müller et al. (2000), Peake & Farrell (2006) suggested that the swim chamber length should be >2.1 body lengths (bl) to avoid the effects of respirometer confinement. Cai et al. (2018) suggested the minimum swim chamber length should be >5 bl, based on measurements of swimming speeds of fish with different body lengths. In the present study, the swim chamber length was 70 cm (4.9–7.7 bl). Fish were tested in a modified Brett-type swimming respirometer with a volume of 95 l and a 28 l rectangular swim chamber (70 cm × 20 cm × 20 cm). A flow rectifier (honeycomb shape) maintained nearly uniform flow in the chamber, and a grid at the end of the chamber prevented fish from being swept away (Cai et al. 2018). Test fish had a maximum cross-sectional area <10% of the chamber cross-section, and it was assumed that fish swimming speed equaled flow velocity (Bell & Terhune 1970). Flow velocity was measured by a propeller-type flow velocity meter (LGY-II). In the respirometer, dissolved oxygen ranged from 7.61 to 8.35 mg l−1 and water temperature ranged from 20.2 to 23.4°C, as measured with a multi-sensor probe (Hach HQ30d). A video camera (Hikvision CS-C6TC-32WFR) was placed over the respirometer to record tail beat.

2.4. Test protocol

Stepped velocity tests were carried out to measure \( U_{\text{crit}} \), \( U_{\text{burst}} \), \( U_{\text{ind}} \) and TBF. Sixty healthy fish with intact fins and squamae were selected randomly for testing and were randomly placed into 3 groups of 20 individuals. Group 1 was not treated (intact fin). In Group 2, the tail fin was partially removed (fin clipped posterior to fork), and in Group 3, the tail fin was completely removed (Fig. 1). Thirty fish (10 from each group) were tested for \( U_{\text{crit}} \) and TBF (Expt 1) and the other thirty fish were tested for \( U_{\text{burst}} \) and \( U_{\text{ind}} \) (Expt 2).

2.4.1. Expt 1

Thirty fish were tested individually. Fish body length and mass were measured, and each fish was allowed to acclimate to experimental conditions at 0.05 m s−1 (0.35–0.50 bl s−1) for 2 h. Flow velocity, initially at 1.0 bl s−1, was increased by 1.0 bl s−1 at 20 min intervals (Brett 1964, Tierney 2011). When the
fish ceased swimming, the flow velocity was decreased, the swim chamber was rapped to encourage swimming, and the test was resumed if the fish continued swimming. A fish was regarded as exhausted when it did not resume swimming and rested against the wire grid for 10 s. The \( U_{\text{crit}} \) was calculated using Eq. (1) in Section 2.5. Tail beat frequency was measured using the digital recordings to obtain \( TBF_{\text{max}} \) and \( TBF_{\text{mean}} \) (beats s\(^{-1}\)).

### 2.4.2. Expt 2

Thirty fish were tested individually. Fish body length and mass were measured, and each fish was allowed to acclimate to experimental conditions at 0.05 m s\(^{-1}\) for 2 h. At that velocity, the fish remained nearly motionless along the flow direction. The flow velocity was then increased by 0.01 m s\(^{-1}\) at 5 s intervals and, when the fish began actively swimming, the flow velocity was reported as \( U_{\text{ind}} \) (Cai et al. 2018). Flow velocity was then adjusted to 1.0 bl s\(^{-1}\) and increased by 1.0 bl s\(^{-1}\) at 1 min intervals (Tierney 2011, Wang et al. 2017). When the fish ceased swimming, the flow velocity was decreased, the swim chamber was rapped to encourage swimming, and the test was resumed if the fish continued swimming. A fish was regarded as exhausted when it did not resume swimming and rested against the wire grid for 10 s. \( U_{\text{burst}} \) was calculated using Eq. (1).

### 2.5. Data analyses

\( U_{\text{crit}} \) (and \( U_{\text{burst}} \)) were calculated using Eq. (1) (Brett 1964, Dai & Suski 2019):

\[
U_{\text{crit}} = U_{i-1} + \left( \frac{t_i}{\Delta t} \right) \times \Delta U \tag{1}
\]

where \( i \) is the increment number in stepped velocity tests, \( U_{i-1} \) (bl s\(^{-1}\)) is the velocity during the last complete time increment, \( \Delta U \) (bl s\(^{-1}\)) is the velocity step, \( \Delta t \) (s) is the time step, and \( t_i \) (s) is the time elapsed at fatigue during the last (incomplete) time step.

The data were analyzed using Origin 9.0 (Origin-Lab), and parameter values are reported as mean ± SD. Data on fish body length, mass, \( U_{\text{crit}} \), \( U_{\text{burst}} \), \( U_{\text{ind}}, \) \( TBF_{\text{max}} \) and \( TBF_{\text{mean}} \) did not significantly deviate from normality, according to a Lilliefors test (\( p > 0.05 \)). Homogeneity of variance among parameters was tested using Levene’s test and differences in variance were not significant (\( p > 0.05 \)). ANOVA was used to test differences among mean values, and \( a \) posteriori pairwise comparisons were made using a Tukey test.

### 3. RESULTS

In Expts 1 and 2, there were no significant differences between the 3 treatment groups with respect to body length and mass (all \( p > 0.05 \)). The results for \( U_{\text{crit}}, U_{\text{burst}}, U_{\text{ind}}, TBF_{\text{max}} \) and \( TBF_{\text{mean}} \) are presented in Figs. 2–5. Based on 1-way ANOVA, there were significant effects of experimental treatments on \( U_{\text{crit}} \) (bl s\(^{-1}\) and m s\(^{-1}\), both \( p < 0.001 \)) and \( TBF_{\text{mean}} \) (beats s\(^{-1}\), \( p < \) 0.001).
0.001), but effect was not significant on $U_{\text{ind}}$ (bl s$^{-1}$ and m s$^{-1}$, $p = 0.179$ and 0.229) or $TBF_{\text{max}}$ (beats s$^{-1}$, $p = 0.130$). Based on comparison of means (Tukey test), $U_{\text{crit}}$, $U_{\text{burst}}$ and $TBF_{\text{mean}}$ were significantly lower in the no fin groups than in the intact fin groups (all $p < 0.05$), but $U_{\text{crit}}$, $U_{\text{burst}}$ and $TBF_{\text{mean}}$ in the partial fin groups were not significantly lower than in the intact fin groups (all $p > 0.05$). Thus, complete loss of the tail fin had considerably more effect on swimming performance than partial loss, and the effect of tail fin loss was significant on $U_{\text{crit}}$, $U_{\text{burst}}$ and $TBF_{\text{mean}}$, but not on $U_{\text{ind}}$ and $TBF_{\text{max}}$.

4. DISCUSSION

4.1. Critical swimming speed, $U_{\text{crit}}$

The tail fin is important to fish swimming capability (Hunter & Zweifel 1971, Webb 1975, Beamish 1978). Fin loss reduces swimming capability (Plaut 2001), but the reduction varies significantly among species (Fu et al. 2013). $U_{\text{crit}}$, a measure of prolonged swimming capability, can be attained primarily by aerobic metabolism (Brett 1964, Milligan 1996). In this study, the decrease in $U_{\text{crit}}$ was not significant for the partial fin group but was significant for the no fin group (Fig. 2). It appears likely that the decrease in $U_{\text{crit}}$ would also be significant in the partial fin group if the sample size was larger.

The black carp *Mylopharyngodon piceus* is 1 of 4 common domestic fishes of China; the other 3 species are grass carp *Ctenopharyngodon idella*, silver carp *Hypophthalmichthys molitrix* and bighead carp *Aristichthys (Hypophthalmichthys) nobilis*. In China, all 4 species inhabit the same rivers and lakes and all are important commercially. $U_{\text{crit}}$ values for juveniles of the other 3 species are shown in Table 1. The $U_{\text{crit}}$ of *M. piceus* is higher than that of *H. molitrix*, but lower than that of *C. idellus* and *A. nobilis*. Black carp primarily inhabit the middle to bottom waters and forage for snails, shellfish, shrimp and insects. They are not considered to be very active fish, consistent with the relatively low swimming capability found in this study.

4.2. Burst speed, $U_{\text{burst}}$

$U_{\text{burst}}$ is an estimate of the speed that can be attained with the contribution of anaerobic metabolism, which leads to lactic acid accumulation (Brett 1964, Dominy 1971). Compared with the intact fin group, $U_{\text{burst}}$ decreased slightly in the partial fin
group and significantly in the no fin group (Fig. 3), similar to the results for prolonged swimming capability (U\text{crit}). It has been speculated that swimming propulsion by the caudal fin is mainly provided by the front half of the tail because the soft, flexible back half can generate only a weak propulsive force (Tangorra et al. 2010). It is also possible that swimming behavior can be altered to partially offset the loss of the caudal fin, and the degree of compensation depends on the amount of tail that is missing.

The U\text{crit} decreased by ~25% from the intact fin group to the no fin group (Fig. 2), and U\text{burst} decreased by ~40% (Fig. 3). The large decrease in burst speed has serious consequences for avoiding predators such as Elopichthys bambusa. Fish missing the tail fin are also less able to pass obstructions and control structures, such as road crossings, that generate high-velocity flows, which also negatively affects dispersal and migration.

### 4.3. Induced flow velocity, U\text{ind}

Holding their position in a current is innate behavior for fish. Fish sense water motion by means of the lateral line organ and adjust swimming as needed to counter the current (Arnold 1974, Montgomery & Macdonald 1987). The U\text{ind} (m s\(^{-1}\)) increases with body length (Cai et al. 2018). In Fig. 4, the differences in U\text{ind} among the 3 treatment groups was not significant, indicating that the tail fin has little effect on U\text{ind}.

### 4.4. Tail beat frequency, TBF

TBF is integral to the kinematics of swimming and is closely related to swimming capability (Webb 1975). The linear correlation between TBF and U has been verified repeatedly (Videler & Wardle 1991, Ohlberger et al. 2007, Cai et al. 2013). In the present study, tail fin loss had little effect on the TBF\text{max} of black carp (Fig. 5), consistent with the findings for the cyprinid Spinibarbus sinensis (Fu et al. 2013) and contrary to the results for common carp Cyprinus carpio and goldfish Carassius auratus, for which TBF\text{max} increased significantly with tail fin loss (Fu et al. 2013).

TBF\text{mean} was slightly lower in the partial fin group and significantly lower in the no fin group (Fig. 5), similar to results for U\text{crit} and U\text{burst}. Loss of the tail fin lowers thrust (tail beat force) and, when tail beating is ineffective, the lower TBF could be an instinctive response evolved from the need to conserve energy. A large tail fin and small tail fin aspect ratio are advantageous for fish swimming capability (Langerhans et al. 2004, Domenici et al. 2008). With loss of tail fin area, the thrust per tail beat is lower and the kinematics are less efficient. However, thrust is not generated from the tail fin alone, as other fins and the body also generate thrust.

The tail fin has the potential for decreasing muscle activity and conserving energy by exploiting the vortices created by the beating tail (Liao et al. 2003). Fish use a burst-and-coast gait in the U\text{burst} test and in the higher-velocity steps of the U\text{crit} test. Burst and coast phases generate different vortices, and the drag coefficient is lower during the coast phase (Wu et al. 2007), conserving energy. While partial fin loss does not significantly reduce swimming capability, total loss does significantly decrease swimming capability and increases the energy cost of transport.

The difference between swimming capability between the intact fin and partial fin groups was small (Figs. 2 & 3). Hence, we speculate that partial fin loss does not significantly affect thrust and vortices. The
rear half of the tail fin is soft, and thus the beat force is lower and may not have a large effect on the vortices. This speculation could be verified by future studies on particle image velocimetry.

5. CONCLUSION

This study provides data on $U_{\text{crit}}$, $U_{\text{burst}}$, $U_{\text{ind}}$, TBF$_{\text{max}}$ and TBF$_{\text{mean}}$ of black carp, and the effect of partial and complete tail fin loss on TBF and swimming capability. Differences among $U_{\text{ind}}$ and TBF$_{\text{max}}$ in the 3 treatment groups were not significant. $U_{\text{crit}}$ and $U_{\text{burst}}$ decreased slightly with partial loss of fin, but decreased significantly with complete loss. Partial, and especially complete loss, of the tail fin resulted in lower beat force and TBF$_{\text{mean}}$. Further, tail fin loss interrupts the vortices produced by tail beats, lowering the potential for energy conservation during burst-and-coast swimming and decreasing $U_{\text{crit}}$ and $U_{\text{burst}}$.

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