RESEARCH ARTICLE

The effects of caudal fin loss and regeneration on the swimming performance of three cyprinid fish species with different swimming capacities

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SUMMARY

In nature, the caudal fins of fish species are frequently lost to some extent by aggressive behaviour, predation and diseases. To test whether the swimming performance of fish with different swimming capacities would be differentially affected due to caudal fin loss and regeneration, we investigated the critical swimming speed (U_{crit}), swimming metabolic rate ($\dot{M}_{O_2}$), tail beat frequency (f_{TB}) and tail beat amplitude (A_{TB}) after caudal fin loss and regeneration (20 days) in juveniles of three cyprinid fish species: the qingbo (*Spinibarbus sinensis*; strong swimmer), the common carp (*Cyprinus carpio*; intermediate swimmer) and the goldfish (*Carassius auratus*; poor swimmer). The U_{crit} values of the caudal-fin-lost qingbo, common carp and goldfish were 49, 32 and 35% significantly lower than those of the control groups, respectively. The maximum tail beat amplitude (A_{TBmax}) (all three fishes), the maximum tail beat frequency (f_{TBmax}) (only the common carp and the goldfish) and/or the active metabolic rate ($\dot{M}_{O_2active}$) (only the common carp) of the caudal-fin-lost fish were significantly higher than those of the control groups. After 20 days of recovery, the caudal fins recovered to 41, 47 and 24% of those of the control groups for the qingbo, the common carp and the goldfish, respectively. However, the U_{crit} values of the fin-regenerated qingbo, common carp and goldfish recovered to 86, 91 and 95% of those of the control group, respectively. The caudal-fin-regenerated qingbo and common carp showed a significantly higher A_{TBmax} and f_{TBmax}, respectively, compared with those of the control groups. The qingbo had a higher f_{TBmax} but a lower A_{TBmax} than the common carp and the goldfish, which suggested that a strong swimmer may maintain swimming speed primarily by maintaining a greater f_{TBmax}, for which the caudal fin plays a more important role during swimming, than a poor swimmer. The $\dot{M}_{O_2active}$ of fish (common carp) with a redundant respiratory capacity could increase due to caudal fin loss to meet the increase in energy expenditure required by an increase in f_{TBmax}. In addition, the sustained swimming performance may not be the only selective pressure acting on caudal fin size in these three species, and the present caudal fin size may be a trade-off between sustain swimming performance and other factors (e.g. sexual selection, escape responses).

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INTRODUCTION

Swimming performance is important for fish because it is closely related to the ability to gain food, to avoid predators and to perform other daily activities (Plaut, 2001; Zeng et al., 2009; Kieffer, 2010; Fu et al., 2012). As an important locomotive organ for most fish species, the caudal fin plays a crucial role in propelling and guiding fish during swimming (Lauder, 2000; Motani, 2002; Handegard et al., 2009). The shape, size and stiffness of the caudal fin are all expected to strongly affect swimming performance (Plaut, 2000). In nature, the caudal fin is frequently observed to be partly lost due to aggressive behaviour, predation and diseases (Winemiller, 1990; Ziskowski et al., 2008; Sinclair et al., 2011). Thus, fish must physiologically and behaviourally adjust to the probable negative effects on swimming performance caused by caudal fin loss and avoid the decline of Darwinian fitness. The relationship between the caudal fin and swimming performance has attracted broad attention for a long time, and caudal fin amputation has been widely used in previous studies (Webb, 1973; Webb, 1977; Champagne et al., 2008; Yang et al., 2013). It has been found that caudal fin amputation profoundly alters the swimming behaviour and/or speed

in sockeye salmon (*Oncorhynchus nerka*) (Webb, 1973), rainbow trout (*Salmo gairdneri*) (Webb, 1977) and Chinese bream (*Parabramis pekinensis*) (Yang et al., 2013), while it showed no effect on swimming performance of brown darters (*Etheostoma edwini*) (Champagne et al., 2008). Thus, the caudal fin may be a different size and present a different level of importance for fish with different swimming capacities; therefore, the regeneration of the caudal fin in these fish may be different to meet those different swimming-capacity needs. The overall change in swimming capacity during caudal fin loss and regeneration has become an important question, but little investigation into this issue has been reported.

Under sustainable speeds, most fish species that utilise body and caudal fin propulsion increase their swimming speed primarily by increasing their tail beat frequency (f_{TB}) and/or their tail beat amplitude (A_{TB}) (Hunter and Zweifel, 1971; Hunter, 1972; Dickson et al., 2002). Variation in f_{TB} and A_{TB} could therefore be used as an indicator of mechanical power output (Ellerby, 2010). When fish with caudal fin loss or partial caudal fin regeneration swim at the same speed as fish with intact caudal fins, f_{TB} and/or A_{TB} may increase due to the decreased effective area for thrust, to generate a similar thrust to that

Fig. 1. Photographs of the left side of intact, caudal-fin-lost and partly regenerated fish (qingbo, common carp and goldfish).

of fish with intact caudal fins, which may increase the energy expenditure of fin-damaged fish when swimming at a given speed (Plaut, 2000). Thus, caudal fin damage may result in a decline in swimming performance. However, the decreased caudal fin area will also result in a decrease in drag during swimming (Webb, 1973; Sinclair et al., 2011), making it easier for fish with damaged caudal fins to finish each tail beat. In addition, fin shape and size in many fish species is subject to sexual selection, either because females choose to mate with males that have larger fins or because males with larger fins gain access to more females through male-to-male competition (Warner and Schultz, 1992; Jordan et al., 2006; Wilson et al., 2010). Thus, for many fish species, the existing size of the caudal fin may not be best suited to sustainable swimming performance, but instead may be a response to sexual selection or a compromise with unsteady swimming performance, which come from the selective pressure of reproduction and escape, respectively (Sinclair et al., 2011). If that is the case, it will be interesting to investigate the changes in swimming capacity for caudal-fin-damaged fish, especially changes in f_{TB}, A_{TB} and the metabolic rate ($\dot{M}_{O_2}$) during swimming. In addition, changes in f_{TB}, A_{TB} and $\dot{M}_{O_2}$ during swimming caused by decreased fin area may be different in fish with different swimming capacities and different caudal fin shapes and sizes.

The maximum sustainable swimming speed, or critical swimming speed (U_{crit}), has long been a widely used parameter for the evaluation of aerobic swimming ability (Plaut, 2001; MacNutt et al., 2004; Li et al., 2010). The maximum oxygen consumption (active oxygen consumption rate, $\dot{M}_{O_2active}$) during the U_{crit} test was assumed to be the maximum aerobic metabolic capacity (Alsop and Wood, 1997; Lee et al., 2003; Fu et al., 2011). However, recent studies found that

the locomotion activity alone cannot elicit the maximum metabolic rate in fish species such as the common carp (Dupont-Prinet et al., 2009; Pang et al., 2011; Zhang et al., 2012). Thus, for those fishes, the high respiratory capacity may allow a greater increase in f_{TB} and A_{TB} after fin loss. Thus, we hypothesise that fish with different swimming and respiratory capacities may have different changes in swimming capacity, swimming behaviour (f_{TB} and A_{TB}) and metabolic rates due to caudal fin loss and regeneration.

To test our hypothesis, we selected three Cyprinidae fish species: the qingbo [*Spinibarbus sinensis* (Bleeker 1871)], the common carp (*Cyprinus carpio* Linnaeus 1758) and the goldfish [*Carassius auratus* (Linnaeus 1758)] (Fig. 1, Table 1). The qingbo shows superior swimming performance and has the smallest caudal fin (Table 1) (Zhang et al., 2012). The goldfish is a poor swimmer but with a large, long caudal fin. The swimming capacity and caudal fin size of the common carp is moderate, and it has a redundant respiratory capacity that is greater than necessary for locomotion (Pang et al., 2011; Zhang et al., 2012). These three cyprinid species are all active, omnivorous fishes, and they have a close phylogenetic relationship to the Barbinae subfamily (Kong et al., 2007). Thus, any possible noise from genetic and ecological factors during statistical analysis was minimised in the present study. We first measured the change in swimming performance after caudal fin loss in the qingbo, the common carp and the goldfish. Then, following 20 days of recovery, we repeated the measurement of swimming performance. The aims of this study were (1) to test whether caudal fin loss and regeneration had different effects on swimming performance among fishes with different swimming capacities, and (2) to test whether the fish could compensate for caudal fin loss

Table 1. Body mass, body length and body and caudal fin morphology in juvenile qingbo, common carp and goldfish

Group	N	Body mass (g)	Body length (cm)	Fitness ratio	Caudal fin index (%)	Caudal fin aspect ratio (%)
Qingbo						
0 days – Control	10	7.32±0.25	7.21±0.12	3.57±0.04	3.43±0.10	3.56±0.09
Fin loss	10	7.30±0.32	7.26±0.10	3.67±0.04	–	–
20 days – Control	10	7.95±0.44	7.48±0.16	3.74±0.02	3.65±0.12	3.37±0.10
20 days – Recovery	10	7.40±0.33	7.30±0.11	3.76±0.02	1.44±0.06	2.77±0.12
Common carp						
0 days – Control	10	8.04±0.30	6.87±0.14	3.04±0.04	5.2±0.19	3.33±0.10
Fin loss	10	8.26±0.21	6.87±0.07	3.04±0.03	–	–
20 days – Control	10	8.28±0.32	6.86±0.09	3.10±0.05	5.14±0.20	3.33±0.09
20 days – Recovery	10	8.49±0.37	6.99±0.13	3.04±0.03	2.22±0.16	3.12±0.10
Goldfish						
0 days – Control	8	9.73±0.37	6.48±0.11	2.65±0.02	17.24±0.84	3.98±0.30
Fin loss	10	9.23±0.29	6.35±0.10	2.64±0.05	–	–
20 days – Control	8	9.76±0.34	6.40±0.07	2.59±0.03	16.17±1.12	3.89±0.16
20 days – Recovery	10	9.01±0.20	6.43±0.07	2.63±0.02	3.67±0.26	2.95±0.10

through kinematics (f_{TB} and A_{TB}) and whether these compensations were related to swimming capacity and caudal fin size.

MATERIALS AND METHODS
Experimental animals and holding
Experimental juvenile qingbo (5–11 g, N=100), common carp (6–12 g, N=100) and goldfish (6–13 g, N=100) were obtained from local farmers and kept in dechlorinated tanks for 1 month before the experiments were performed (Table 1). All of the fish were kept in the same type of tanks (length×width×height, 1.5×0.6×0.5 m) and assessed over the same season and time frame. The fish were fed to satiation with a commercial diet once daily at 09:00 h. The uneaten food and faeces were cleared using a siphon 1 h after feeding. The water temperature was maintained at 25.0±0.5°C, and the water oxygen content was maintained above 7.0 mg l^{-1}. The ammonia-N ranged from 0.005 to 0.025 mg l^{-1}. Fish were maintained on a 12 h:12 h light:dark photoperiod cycle.

We declare that the experiments comply with the current laws of the country in which the experiments were performed.

Experimental protocol
All tests were performed at a water temperature of 25°C. At the beginning of the experiment, 20 fish of each fish species (18 fish for goldfish) were chosen from the holding tanks and randomly divided into two groups, i.e. half of the fish were placed into the control groups (with no treatment to the caudal fin) and the other half were placed into the caudal fin treatment groups (caudal fin amputation). For fish in the treatment groups, each individual fish was transferred to a bucket with 2 l of clean and dechlorinated water and was anaesthetised with eugenol (30 mg l^{-1}) (Velíšek et al., 2005). Then, both the epaxial and hypaxial caudal fin lobes of the fish in the treatment groups were amputated with a pair of sharp scissors, ~2 mm from the tail muscular peduncle (Webb, 1973). After amputation, the fish were returned back to the holding tanks and allowed a 48 h recovery period before any experimental measurement. No fish died during the whole manipulation process. A pilot experiment revealed that the anaesthesia had no significant effects on swimming locomotion after 48 h of recovery (supplementary material Figs S1, S2, Table S1). The fish in the control group remained in the holding tanks.

After 48 h, the swimming performance of fish in both the control and treatment groups was measured. During the 48 h, the fish of both control and treatment groups were kept unfed. The fish were individually introduced into a Brett-type swimming tunnel respirometer (Brett, 1964) and held for 1 h at a slow water velocity (~3 cm s^{-1}) for recovery (Jain et al., 1997). First, we conducted a pilot experiment to determined the approximate U_{crit} and found that there was no significant difference in U_{crit} measured by different initial swimming speed (supplementary material Figs S3, S4, Table S1). Then the individual fish were tested in a ramp-U_{crit} test for the measurement of U_{crit} and $\dot{M}_{O_2}$ during swimming. The ramp-U_{crit} tests involved increasing water speed to ~50% of U_{crit} over a 5 min period, after which water speed was increased by 6 cm s^{-1} increments every 20 min until the fish became exhausted. Simultaneously, the swimming behaviour of each individual fish was recorded using a digital camera in video mode (model IXUS 105, Canon, Tokyo, Japan; 30 frames s^{-1}) positioned above the respirometer to obtain a dorsal view of the fish during each swimming speed. The videos were used for the measurement of f_{TB} and A_{TB}. After the U_{crit} test, the fish were individually anaesthetised with eugenol (30 mg l^{-1}) (Velíšek et al., 2005) to measure body mass and length, and then photographs of the right side of each individual fish were taken for morphometric measurements of the body and the caudal fin. The starting swimming

speeds of caudal-fin-lost fish during the U_{crit} test among the three different species were different from those of caudal-fin-intact fish; thus, both fin-lost and fin-intact fish swam for a similar duration in the U_{crit} test (Fig. 3). All the fish were then transferred to their previous tanks and allowed to recover for 20 days, i.e. the treatment of 20 days recovery; the treatment of fin-loss is referred to as 0 days for comparison. The housing conditions for this recovery period were the same as those in the holding period. Following recovery, the measurements of U_{crit}, $\dot{M}_{O_2}$, f_{TB} and A_{TB} of the fish of both treatment and control groups were repeated, following the same procedures as the first time.

Parameter measurements
Measurement of U_{crit} and swimming $\dot{M}_{O_2}$
A Brett-type swimming tunnel respirometer (Brett, 1964) was used to measure U_{crit} and $\dot{M}_{O_2}$ during swimming as a function of swimming speed (for details, see Pang et al., 2010). The respirometer was constructed from clear plastic poly-methyl-methacrylate. A circulating water flow was generated in the tunnel (total volume 3.4 l) by an acrylic propeller attached to a variable speed pump. The speed pump was controlled by a variable voltage power source. A digital camera in video mode was used to calibrate the water velocity from the pump controller by tracking small black agar balls (with a density the same as water) in current. Then the relationship between water velocity and voltage output could be built to an indicial equation. The water velocity could be achieved by tuning the voltage output. A honeycomb screen was secured at both ends of the swimming chamber to reduce turbulence and to ensure uniform water velocity across the swimming chamber. Each individual fish was placed downstream of the propeller in a swimming chamber with a 19.9 cm^2 cross-sectional area. The water temperature in the swimming chamber was controlled to within ±0.2°C using a water bath connected to a stainless steel heat exchanger. U_{crit} was calculated for each individual fish using Brett's equation (Brett, 1964):

$$U_{crit} = V + (t / T) \, \Delta V, \qquad (1)$$

where V is the highest speed at which the fish swam during the full time period of the experiment (cm s^{-1}); ΔV is the velocity increment [approximately 1 body length (BL) s^{-1}; 6 cm s^{-1}]; T is the prescribed period of swimming per speed (20 min); and t is the time that the fish swam at the final speed (min). The criterion for determining whether an individual fish failed to swim was when the fish failed to move off the rear honeycomb screen of the swimming chamber for 20 s (Lee et al., 2003).

The O$_2$ concentration was measured continuously throughout the ramp-U_{crit} test as a function of swimming speed. The respirometer could switch between an open mode and a closed mode to replenish the oxygen and to measure the $\dot{M}_{O_2}$, respectively. In the open mode (~2 min), the respirometer was supplied with fully aerated and thermo-regulated water. In the closed mode (20 min), the tunnel was isolated from the reservoir tank and the water was recirculated within the system. A small volume of water was drawn from the sealed respirometer by a small pump, forced past a dissolved oxygen probe housed in a sealed temperature-controlled chamber (5 ml), and then returned to the respirometer. The oxygen concentration (mg l^{-1}) was recorded once every 2 min. The $\dot{M}_{O_2}$ (mg kg^{-1} h^{-1}) of each individual fish during swimming was calculated from the depletion of oxygen, according to the equation:

$$\dot{M}_{O_2} = 60Sv / m \, , \qquad (2)$$

where S (mg l^{-1} min^{-1}) is the decrease in the water's dissolved oxygen content per minute (slope); v is the total volume of the respirometer

(3.4 l) minus the volume of the fish; and m is the body mass (kg) of the fish. The slope was obtained from a linear regression between time (min) and the dissolved oxygen content (mg l^{-1}). Only slopes with an $r^2>0.95$ were considered in the analysis. The maximum $\dot{M}_{O_2}$ during the U_{crit} test was defined as the active $\dot{M}_{O_2}$ ($\dot{M}_{O_2active}$). The water oxygen content in the respirometer was never allowed to fall below 85% oxygen saturation by switching between the open and closed mode of the respirometer (Claireaux et al., 2006).

Measurement of f_{TB} and A_{TB} during swimming

A 10-min video recording was made at each speed at which a fish swam during its $\dot{M}_{O_2}$ measurements. A 10 cm ruler of a similar height to the fish swimming in the chamber was used to calculate a scaling factor from each video.

The f_{TB} was calculated from the two-dimensional display of the progression of the tip of the tail over time by dividing the number of consecutive tail beat cycles by the time. Each 2-min video recording (when the fish was positioned in the centre of the chamber and swam steadily) that was selected from the former 10-min recording for each swimming speed of each individual fish was used to count the number of tail beats, which was then transformed into tail beats per minute. One tail beat cycle was defined as the excursion of the tail from one side of the body to the other and back again. Using the same two-dimensional display, the A_{TB}, the distance between the lateral-most positions of the tip of the caudal peduncle during one complete tail beat cycle and the middle axis of the body, was calculated by measuring the distance of each symmetrical tail beat in pixels. These values were then converted into centimetres by dividing by the scaling factor (pixels cm^{-1}) calculated prior to digitising. Video segments in which the fish was swimming steadily for eight tail beats and was positioned in the centre of the chamber, away from the walls and the bottom of the chamber, were selected for A_{TB} analysis. Five points along the dorsal midline of each fish that could be identified consistently were digitised in sequential video fields for eight tail beats at each speed: the tip of the snout, the points along the dorsal midline between both the anterior and the posterior insertion points of the eyes, the midpoint between the anterior insertions of the pectoral fins, and the tip of caudal peduncle (Donley and Dickson, 2000). The A_{TB}

(cm) was transformed into a percentage of the fish body length (%BL) to reduce the influence of body length (Donley and Dickson, 2000; Dickson et al., 2002).

Measurement of morphology

Geometric morphometric methods were used to quantify the body and caudal fin shapes. Photographs of the right side of each fish, viewed together with a ruler, were taken with a digital camera and then analysed with tps software (http://life.bio.sunysb.edu/morph). We measured body length, body height, caudal fin area and caudal fin height, and calculated the values of the following morphological traits: (1) fitness ratio (FR)=body length/body height; (2) caudal fin aspect ratio (AR)=caudal fin height^2/caudal fin area; and (3) caudal fin index (FI)=caudal fin area/body length^2.

Data handling and analysis

Statistics17 (SPSS, Chicago, IL, USA) was used for data analysis. All values are presented as means ± s.e.m., and $P<0.05$ was used as the level of statistical significance. The effects of species, caudal fin treatment and recovery period on U_{crit}, $\dot{M}_{O_2active}$, f_{TBmax} and A_{TBmax} were determined using a mixed-model three-way ANOVA in three fish species. The effects of swimming speed and caudal fin treatment on swimming $\dot{M}_{O_2}$, f_{TB} and A_{TB} were determined using a one-way analysis of covariance (ANCOVA), i.e. we performed a regression for each treatment group and then made a comparison of their coefficients. The ANOVA was followed by a Duncan test or a t-test if it was necessary to determine the difference of the value of different treatment groups. A t-test was used to determine the difference between the control and the treatment groups.

RESULTS
Effects of caudal fin loss and regeneration on U_{crit}
Species effect
Species had significant effects on U_{crit} ($F_{2,52}=72.20$, $P<0.001$; Fig. 2A, Table 2). The U_{crit} of goldfish was significantly lower than that of common carp while the latter was significantly lower than that of the qingbo in both the control and recovery groups ($P<0.05$).
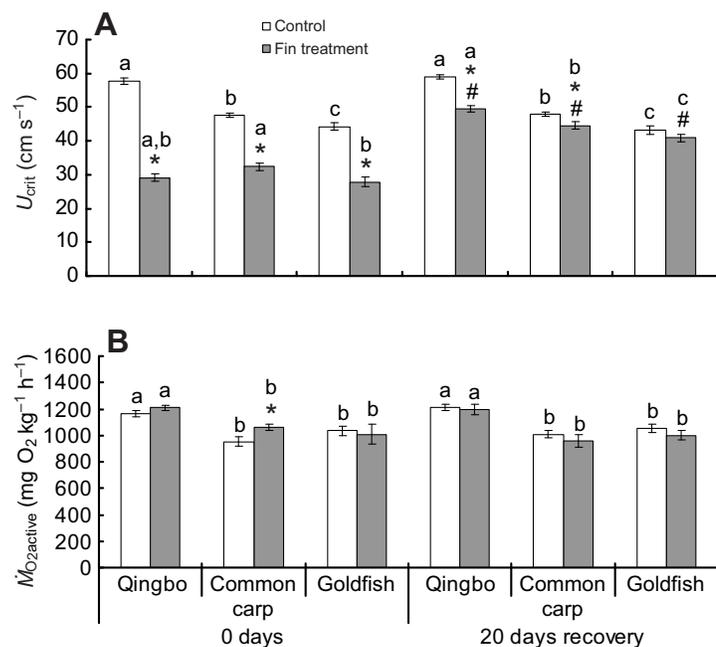

Fig. 2. Critical swimming speed (U_{crit}) (A) and active metabolic rate ($\dot{M}_{O_2active}$) (B) of control (open bars) and treatment (filled bars; caudal-fin-lost fish at 0 days and caudal-fin-regenerated fish at 20 days recovery) groups of juvenile qingbo, common carp and goldfish. Different lowercase letters indicate statistically significant differences between fish species in both control and treatment groups. *Significant difference in variables between control and treatment groups. #Significant difference in variables between 0 days and 20 days (recovery) groups ($P<0.05$). Data are means ± s.e.m.

Table 2. The effect of species (between-subject factor), caudal fin amputation (between-subject factor) and 20 days recovery (within-subject factor) on swimming parameters, based on a mixed-model three-way ANOVA

	d.f.	U_{crit}	$\dot{M}_{O2active}$	f_{TBmax}	A_{TBmax}
Species effect (S)	2	$F=72.20$ $P<0.001*$	$F=37.23$ $P<0.001*$	$F=71.58$ $P<0.001*$	$F=125.02$ $P<0.001*$
Treatment effect (T)	1	$F=345.85$ $P<0.001*$	$F=0.00$ $P=0.990$	$F=0.03$ $P=0.862$	$F=27.19$ $P<0.001*$
Recovery effect (R)	1	$F=206.90$ $P<0.001*$	$F=0.00$ $P=0.994$	$F=14.95$ $P<0.001*$	$F=63.13$ $P<0.001*$
S × T	2	$F=23.85$ $P<0.001*$	$F=0.98$ $P=0.391$	$F=5.12$ $P=0.010*$	$F=0.13$ $P=0.883$
S × R	2	$F=9.37$ $P<0.001*$	$F=0.222$ $P=0.804$	$F=10.24$ $P<0.001*$	$F=0.94$ $P=0.398$
T × R	1	$F=196.25$ $P<0.001*$	$F=3.21$ $P=0.079$	$F=2.47$ $P=0.123$	$F=37.89$ $P<0.001*$
S × T × R	2	$F=3.79$ $P=0.029*$	$F=0.60$ $P=0.553$	$F=1.84$ $P=0.169$	$F=3.82$ $P=0.029*$

*Significantly different ($P<0.05$).

Treatment effect

Caudal fin treatment also had significant effects on U_{crit} (caudal fin loss, $F_{1,52}=345.85$, $P<0.001$; Fig. 2A, Table 2). The qingbo, the common carp and the goldfish showed a significantly different 49, 32 and 35% decrease in U_{crit}, respectively, following caudal fin loss (interaction effect: $F_{2,52}=23.85$, $P<0.001$).

Recovery effect

After 20 days of recovery, the caudal fin index of caudal-fin-regenerated fish recovered to 41, 47 and 24% of those of the control group for the qingbo, the common carp and the goldfish, respectively (Fig. 1, Table 1). The U_{crit} of the caudal-fin-regenerated qingbo, common carp and goldfish was significantly increased ($F_{1,52}=206.90$, $P<0.001$) and recovered to 86, 91 and 95% of those of the control group, respectively (interaction effect: $F_{1,52}=196.25$, $P<0.001$), and there was no significant difference in U_{crit} between goldfish in the caudal-fin-regenerated and the control group ($P=0.16$).

Effects of caudal fin loss and regeneration on $\dot{M}_{O_2}$ during swimming

Among fish in the 0 days groups, $\dot{M}_{O_2}$ increased significantly with an increase in the swimming speed for all experimental groups ($P<0.001$), but it increased more sharply in the treatment groups for all three fish species compared with those of the control groups within each species ($P<0.05$; Fig. 3A,C,E, Table 3).

After 20 days of recovery, there was no significant difference between the $\dot{M}_{O_2}$–speed curves of the caudal-fin-regenerated and the control groups in all three species (Fig. 3B,D,F).

Effects of caudal fin loss and regeneration on $\dot{M}_{O2active}$
Species effect

Species had a significant effect on $\dot{M}_{O2active}$ ($F_{2,52}=37.23$, $P<0.001$; Fig. 2B, Table 2). The $\dot{M}_{O2active}$ values of the qingbo were significantly higher than those of the common carp and the goldfish in both the control and the recovery groups ($P<0.05$; Fig. 2B).

Treatment effect

Treatment had no effect on $\dot{M}_{O2active}$ ($F_{1,52}=0.00$, $P=0.990$; Fig. 2B, Table 2). However, the $\dot{M}_{O2active}$ of the common carp increased significantly after caudal fin loss in the control group by t-test ($P=0.027$).

Recovery effect

Recovery had no effect on $\dot{M}_{O2active}$ ($F_{1,52}=0.00$, $P=0.994$; Fig. 2B, Table 2).

Effects of caudal fin loss and regeneration on f_{TB} during swimming

The f_{TB} increased significantly with an increase in the swimming speed for all experimental groups, but it increased more sharply in the treatment groups for all three fish species compared with those of the control group within each species ($P<0.05$; Table 3, Fig. 4A, Fig. 5A, Fig. 6A). After 20 days of recovery, only caudal-fin-regenerated goldfish showed a sharper curve compared with those of the control group (Fig. 4C, Fig. 5C, Fig. 6C).

Effects of caudal fin loss and regeneration on f_{TBmax}
Species effect

Species had significant effects on f_{TBmax} ($F_{2,52}=71.58$, $P<0.001$; Fig. 7A, Table 2). The f_{TBmax} values of the qingbo were significantly higher than those of both the common carp and the goldfish in both the control and recovery groups ($P<0.001$).

Treatment effect

The f_{TBmax} of the common carp ($P=0.001$) and the goldfish ($P=0.013$) increased significantly by 13 and 11%, respectively, after caudal fin loss, while there was no significant difference in the qingbo (interaction effect: $F_{1,52}=5.12$, $P<0.010$).

Recovery effect

After 20 days of recovery, the f_{TBmax} of common carp decreased significantly ($P<0.001$). Thus, there was no significant difference between caudal-fin-regenerated and control groups in the common carp ($P=0.36$) while the caudal-fin-regenerated goldfish still showed a significantly higher f_{TBmax} than that of the control fish ($P=0.014$; Fig. 7A).

Effects of caudal fin loss and regeneration on A_{TB} during swimming

The A_{TB} increased significantly with increased swimming speeds for all experimental groups, but it increased more sharply in the treatment groups in all three fish species compared with those of the control group within each species ($P<0.001$; Table 3, Fig. 4B, Fig. 5B, Fig. 6B). There was no significant difference in slope of
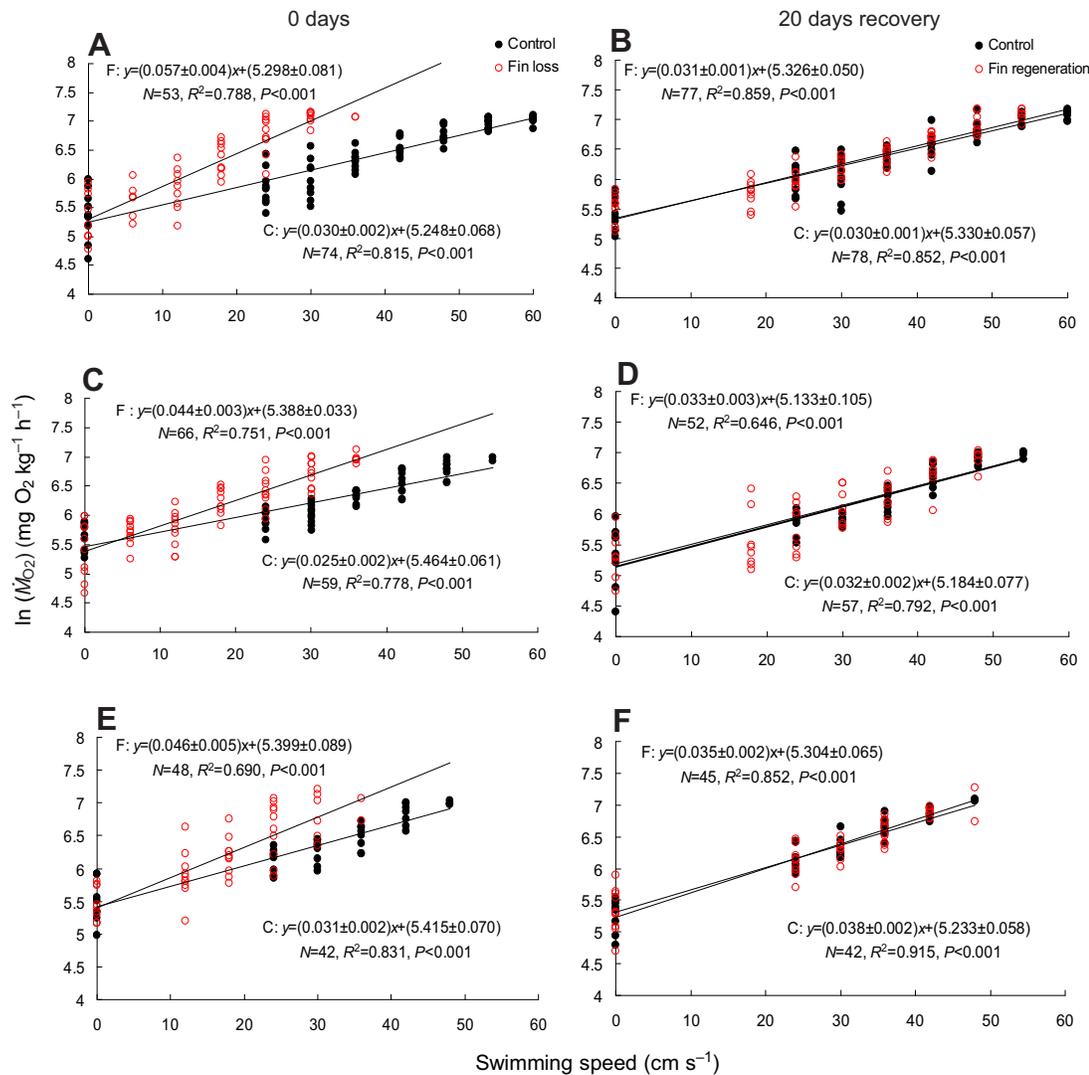
Fig. 3. Oxygen consumption rate of control (caudal-fin-intact fish; filled circles) and treatment (open circles; caudal-fin-lost fish at 0 days and caudal-fin-regenerated fish at 20 days recovery) groups of qingbo (A,B), common carp (C,D) and goldfish (E,F).

A_{TB}–swimming speed curve between control and fin-regenerated fish. However, both qingbo and common carp still showed significantly higher A_{TB} than those of the control groups due to the significantly higher intercept ($P<0.05$), while there was no significant difference between the caudal-fin-regenerated and control groups in goldfish.

Effects of caudal fin loss and regeneration on A_{TBmax}
Species effect
Species had significant effects on A_{TBmax} ($F_{2,52}=125.02$, $P<0.001$; Fig. 7B, Table 2). The A_{TBmax} of the qingbo was significantly lower than those of the common carp and the goldfish in both the control and recovery groups ($P<0.001$).

Treatment effect
Caudal fin treatment had significant effects on the A_{TBmax} ($F_{1,52}=27.19$, $P<0.001$; Fig. 7B, Table 2). Among the control groups, the A_{TBmax} values of the qingbo, the common carp and the goldfish increased significantly by 16, 25 and 17%, respectively, after caudal fin loss ($P<0.001$).

Recovery effect
After 20 days of recovery, the A_{TBmax} of all three fish species decreased significantly ($F_{1,52}=63.13$, $P<0.001$; Fig. 7B, Table 2).

Only caudal-fin-regenerated qingbo showed a significantly higher A_{TBmax} than the control groups ($P=0.011$; Fig. 7B) while the A_{TBmax} of both the caudal-fin-regenerated common carp ($P=0.69$) and the caudal-fin-regenerated goldfish ($P=0.91$) did not change compared with those of the control groups.

DISCUSSION
The present study aimed to investigate the effects of caudal fin loss and regeneration on swimming locomotive performance in juveniles of three cyprinid fish with different swimming capacities, morphologies and metabolic capacities. We found that caudal fin loss had pronounced negative effects on swimming performance, but the effects were different among different fish species. To cope with the decline in the effective area for thrust following caudal fin loss, all three fish species showed significant increases in A_{TBmax}, f_{TBmax} and/or $\dot{M}_{O2active}$. After 20 days of recovery, the caudal fins of the fish in the treatment groups recovered to approximately 20–40% while U_{crit} values recovered to 86–95%. We found that a strong swimmer may maintain swimming speed primarily by maintaining a greater f_{TBmax} and a smaller A_{TBmax}, for which the caudal fin plays a more important role during swimming than for a poor swimmer. Another interesting finding was the asymmetry of recovery between caudal fin and swimming performance, which suggested that these three fish species may not have the best equipped caudal fin size

Table 3. The difference in variable–swimming speed curves between control and fin-loss (or fin-regeneration) groups within each fish species according to the results of one-way ANCOVA

		Qingbo		Common carp		Goldfish	
		0 days	20 days	0 days	20 days	0 days	20 days
d.f.		1, 127	1, 155	1, 125	1, 109	1, 90	1, 91
$\dot{M}_{O_2}$	Intercept	$F=0.230$	$F=0.004$	$F=0.678$	$F=0.155$	$F=0.018$	$F=0.645$
		$P=0.633$	$P=0.948$	$P=0.412$	$P=0.695$	$P=0.893$	$P=0.424$
	Slope	$F=41.79$	$F=0.376$	$F=28.98$	$F=0.089$	$F=9.47$	$F=1.074$
		$P<0.001$	$P=0.541$	$P<0.001$	$P=0.766$	$P=0.003$	$P=0.303$
f_{TB}	Intercept	$F=1.628$	$F=0.062$	$F=0.678$	$F=0.276$	$F=1.835$	$F=2.013$
		$P=0.205$	$P=0.804$	$P=0.412$	$P=0.600$	$P=0.177$	$P=0.160$
	Slope	$F=82.85$	$F=1.622$	$F=34.65$	$F=3.595$	$F=11.99$	$F=5.815$
		$P<0.001$	$P=0.205$	$P<0.001$	$P=0.060$	$P=0.001$	$P=0.018$
A_{TB}	Intercept	$F=28.26$	$F=3.94$	$F=30.58$	$F=9.336$	$F=18.03$	$F=2.060$
		$P<0.001$	$P<0.001$	$P<0.001$	$P=0.003$	$P<0.001$	$P=0.154$
	Slope	$F=67.24$	$F=0.160$	$F=14.17$	$F=0.024$	$F=19.11$	$F=0.307$
		$P<0.001$	$P=0.690$	$P<0.001$	$P=0.876$	$P<0.001$	$P=0.581$

See Figs 3–6 for the regression equations, and hence the intercept and slope coefficient values of each fish group.

needed to sustain swimming performance, and some other factors (e.g. sexual selection, escape responses) may also be involved in the size and shape of the caudal fin.

f_{TB} and A_{TB} as a function of swimming performance
Swimming locomotive performance has attracted much attention for a long time because of its importance for survival (Plaut, 2001; Zeng et al., 2009; Kieffer, 2010). It is generally believed that the body morphology necessary to maximise steady swimming efficiency involves a streamlined body shape and a high AR (Fisher and Hogan, 2007; Langerhans, 2009). There may be a morphological reason that the U_{crit} of the qingbo is higher than that of the common carp and the goldfish; and while the large, long caudal fin of the goldfish is less stiff and has a higher drag, it had the lowest U_{crit} of the three fish species, though it had a high AR.

At sustainable swimming speeds, most fishes utilise body and caudal fin propulsion to drive them forward. The increased propulsion, along with swimming speed, is governed by an increase in f_{TB} and A_{TB} (Anderson and Johnston, 1992; Ellerby, 2010). Bainbridge (Bainbridge, 1958) and Hunter and Zweifel (Hunter and Zweifel, 1971) showed that speed during steady swimming is determined by f_{TB} and that A_{TB} is essentially constant when f_{TB} is greater than 5 Hz (Fuiman and Batty, 1997); in contrast, previous studies showed that the chub mackerel (*Scomber japonicus*) (Gibb et al., 1999; Donley and Dickson, 2000) and cod (*Gadus morhua*) (Webber et al., 2001) increased their A_{TB} with swimming speeds during the entire swimming process (including when f_{TB} was greater than 5 Hz). In the present study, both f_{TB} and A_{TB} in all three fish species showed significant increases with an increase in swimming speed during the entire swimming process. There is a
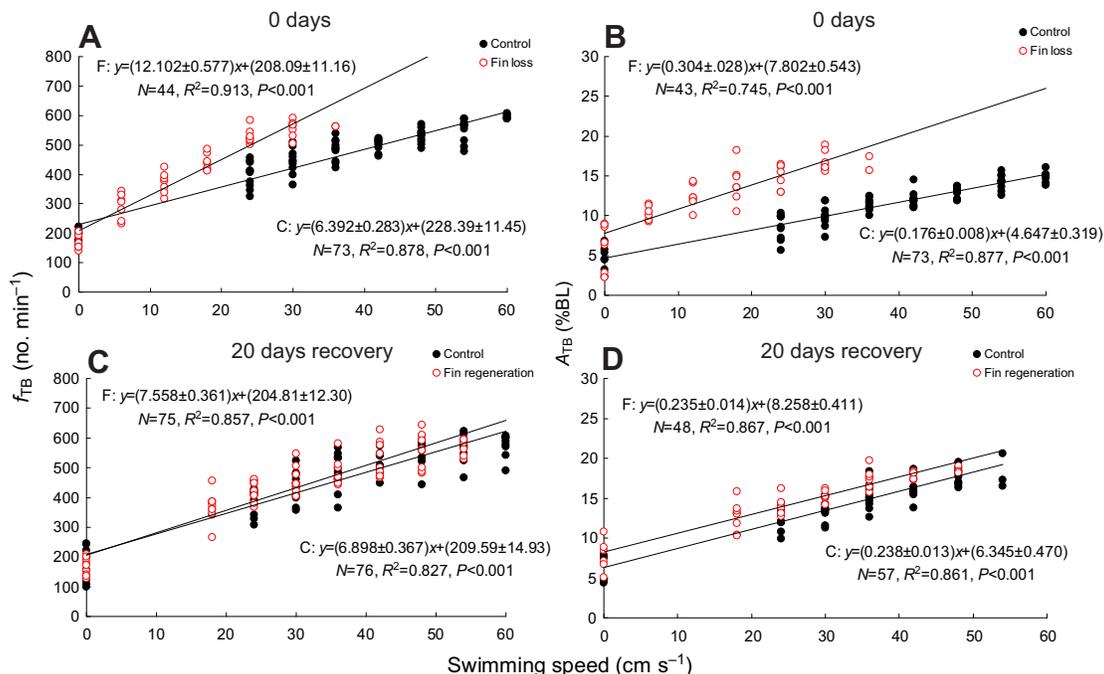

Fig. 4. Tail beat frequency (f_{TB}; A,C) and tail beat amplitude (A_{TB}; B,D) of control (caudal-fin-intact fish; filled circles) and treatment (open circles; caudal-fin-lost fish at 0 days and caudal-fin-regenerated fish at 20 days recovery) groups of qingbo.
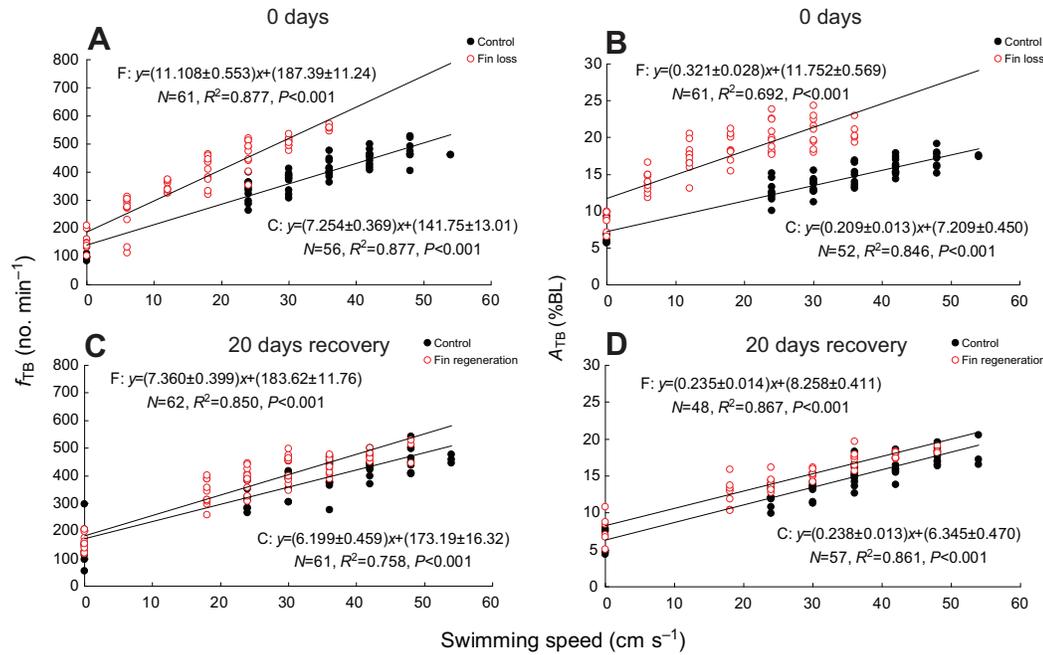
Fig. 5. As Fig. 4, but for common carp.

great deal of variability in the present and published data, possibly because of the different species and sizes of the fish; for instance, large herring (*Clupea harengus*) larvae modulated swimming speed without making significant changes to their A_{TB}, but the small larvae varied their A_{TB} with swimming speed, despite the fact that their f_{TB} values were greater than 5 Hz (Fuiman and Batty, 1997).

The qingbo, which is a strong swimmer, showed a higher f_{TBmax} but a lower A_{TBmax} than the common carp and the goldfish. These data suggest that strong swimmers may primarily rely on their higher f_{TBmax} to achieve their greater swimming capacity because the laterally moving portions of their body experience an augmented drag (Lighthill, 1971). However, a higher f_{TBmax} will lead to a higher energy expenditure because f_{TB} has a strong, positive correlation with $\dot{M}_{O_2}$ (Herskin and Steffensen, 1998; Lowe, 2001; Steinhausen

et al., 2005); thus, the strong-swimmers (qingbo) have a higher $\dot{M}_{O2active}$ than the common carp and the goldfish to satisfy the higher energy expenditure caused by a higher f_{TBmax}. The kawakawa tuna (*Euthynnus affinis*) had a greater f_{TB} and a lower A_{TB} than the chub mackerel and also had higher energy expenditure (Donley and Dickson, 2000). Thus, good swimmers may keep their high swimming capacity at the cost of high energy expenditure because of the importance of swimming capacity for those fish.

The effects of caudal fin loss on the swimming performance of three fish species

The caudal fins are the main transmitters of momentum from the muscles to the water. Without caudal fins, the effective area for thrust is substantially reduced, and the obvious result is a reduction
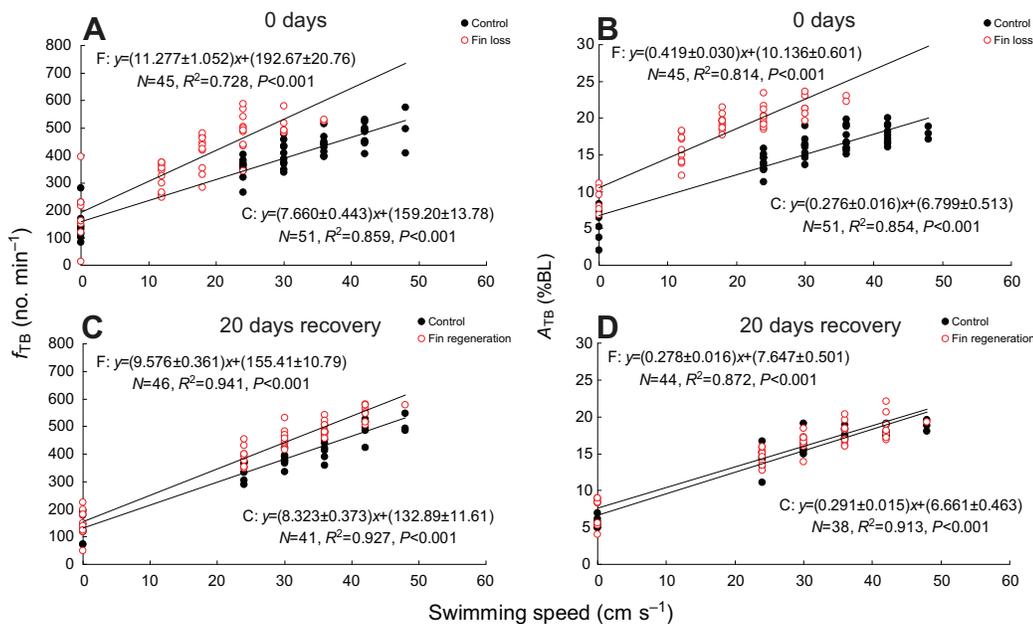

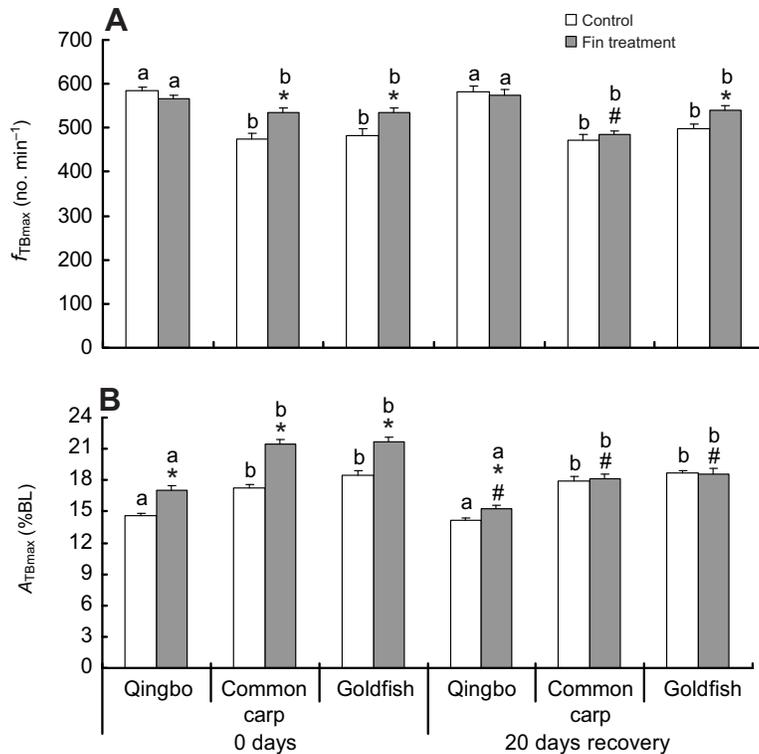
Fig. 6. As Fig. 4, but for goldfish.

Fig. 7. Maximum tail beat frequency (f_{TBmax}; A) and maximum tail beat amplitude (A_{TBmax}; B) of control (open bars) and treatment (filled bars; caudal-fin-lost fish at 0 days and caudal-fin-regenerated fish at 20 days recovery) groups of qingbo, common carp and goldfish. Different lowercase letters indicate statistically significant differences between fish species in both control and treatment groups. *Significant difference in variables between control and treatment groups. #Significant difference in variables between 0 days and 20 days (recovery) groups (*P*<0.05). Data are means ± s.e.m.

in swimming performance (Plaut, 2000). The U_{crit} of no-tail or caudal-fin-lost zebrafish (*Danio rerio*), Chinese bream (*Parabramis pekinensis*) and sockeye salmon (*Oncorhynchus nerka*) significantly decreased by 65% (15.5–6.9 BL s^{-1}) (Plaut, 2000), 40% (7.83–4.66 BL s^{-1}) (Yang et al., 2013) and 16% (3.02–2.53 BL s^{-1}) (Webb, 1973), respectively, compared with those of caudal-fin-intact fish. In the present study, the strong-swimming qingbo also showed the greatest decrease (49%, 8.26–4.17 BL s^{-1}) in U_{crit} after caudal fin loss among the three selected fish species. These data suggested that the caudal fins of strong-swimming fish played a more important role in swimming performance than those of poor-swimming fish.

Animals often take some measures to compensate for a decrease in locomotive capacity because of its importance for survival. Loaded green anoles took off at steeper angles compared with unloaded anoles to compensate for a reduction in take-off speed caused by loading (Kuo et al., 2011). Bluegill sunfish (*Lepomis macrochirus*) with partially impaired pectoral fins (35% original fin area) protracted their pectoral fins significantly more to compensate for a decrease in deceleration ability during braking (Higham et al., 2005). The caudal-fin-lost Chinese bream showed a higher f_{TB}, A_{TB} and $\dot{M}_{O_2}$ at higher swimming speed (Yang et al., 2013). In the present study, to cope with a decline in swimming capacity as a consequence of caudal fin loss, three cyprinid fish species all showed swimming behavioural and metabolic changes. Like the Chinese bream, the f_{TB}, A_{TB} and $\dot{M}_{O_2}$ of the caudal-fin-lost qingbo, common carp and goldfish were significantly higher than those of intact fish within each species at any given swimming speed. These increases may occur because the caudal-fin-lost fish require a thrust similar to that of intact fish at the same swimming speeds. The generation of a similar thrust for caudal-fin-lost fish would require a greater tail beat frequency, a greater tail beat amplitude and a greater energy input because proportionally more energy is lost in cross-flows around the relatively larger circumference (Webb, 1973).

In addition, all three cyprinid fish showed significant increases in their A_{TBmax}, which might partly compensate for the substantial decline in propulsion caused by fin loss, to a certain degree because an increased body curvature produces a larger thrust and a greater energy output (McHenry et al., 1995; Azizi and Landberg, 2002; Porter et al., 2009). However, the improved A_{TBmax} of caudal-fin-lost fish may mainly be caused by a loss of drag as a consequence of a decreased propeller area (Bainbridge, 1963; Webb, 1973). Moreover, both the common carp and the goldfish showed significant increases in their f_{TBmax}, while only the common carp showed a significant increase in $\dot{M}_{O2active}$. It used to be assumed that the $\dot{M}_{O2active}$ was the maximum metabolic rate, limited by the oxygen-absorption capacity of the cardio-branchial system. However, recent studies found that, at least for some fish species, such as the common carp and the sea bass (*Dicentrarchus labrax*), $\dot{M}_{O2active}$ was not the maximum metabolic rate because fed fish showed a higher $\dot{M}_{O2active}$ than that of fasting fish (Thorarensen and Farrell, 2006; Pang et al., 2011). Therefore, the common carp showed a higher $\dot{M}_{O2active}$ due to increased energy expenditure as a result of the swimming behavioural compensation in f_{TBmax}. It is interesting that the caudal-fin-lost goldfish also showed a significantly higher f_{TBmax} but an unchanged $\dot{M}_{O2active}$ compared with those of intact fish. This result may be due to the large and long, but soft and less effective, caudal fin of the goldfish. The caudal fins in the goldfish were 4.6 and 3.1 times larger than those of the qingbo and the common carp, respectively. Thus, large-long-finned goldfish are likely to be more affected by drag forces and, therefore, less efficient swimmers (Plaut, 2000). A substantial decline in drag on the caudal-fin-lost goldfish made it easier to complete each tail beat. Thus, the caudal-fin-lost goldfish showed significant increase in the f_{TBmax} but not in the $\dot{M}_{O2active}$ compared with those of intact fish. Furthermore, some other reasons, for example, the possible increased Ca^{2+} handling capacity when facing intensified oxygen and energy demand during swimming after caudal fin loss, may

also contribute to the increases in A_{TBmax} and f_{TBmax}, as suggested by a recent study in common carp (Seebacher et al., 2012).

The effects of caudal fin regeneration on the swimming performance of three fish species

Caudal fin loss must have a serious negative impact on the growth and survival of fish (Winemiller, 1990). For example, the damaged fins of captive fish are more susceptible to bacterial and fungal infection (Böckelmann et al., 2010). Fin damage adversely affects swimming performance, which, in turn, hinders feeding and escape efficiency (Sinclair et al., 2011; Sazima and Pombal, 1988). Therefore, fish require rapid caudal fin regeneration to decrease all of these negative effects. The epidermis has a fundamental role in the regenerative process of fish fins (Akimenko et al., 1995; Böckelmann et al., 2010), and this complex process starts only 12 h following loss in adult zebrafish (Andreasen et al., 2006). Brown darters (*Etheostoma edwini*) completely regenerated their fins during 67 days at 21°C (Champagne et al., 2008). After 20 days of recovery for three fish species, the caudal fin index of the caudal-fin-regenerated fish recovered to 41, 47 and 24% of the caudal-fin-intact fish in the qingbo, the common carp and the goldfish, respectively. The caudal fins of the goldfish regenerated the slowest of the three fish species, which may be due to the larger caudal fin area of intact goldfish. However, it is amazing that the U_{crit} of the qingbo, the common carp and the goldfish (which showed no significant differences between caudal-regenerated and caudal-intact fish) recovered to 86, 91 and 95% of control groups, respectively. The qingbo and the goldfish still had the swimming behavioural compensations of a higher A_{TBmax} and a higher f_{TBmax}, respectively, but it is still difficult to understand the substantial increase in U_{crit} in all three fish species because the caudal fins recovered to less than 50% of the control groups. Thus, the caudal fin size of the three selected fish species may not be the optimal fin area to sustain swimming. Fin size in many fish species is subject to sexual selection because fish with larger fins have greater success during reproduction (Warner and Schultz, 1992; Jordan et al., 2006; Wilson et al., 2010). Furthermore, the stronger unsustained swimming performance is expected to support a larger caudal fin (Langerhans, 2009). Thus, caudal fin size may be a trade-off between sustained swimming performance, unsustained swimming performance, sexual selection and other factors. In fish with intact caudal fins, large fins can hinder sustained swimming capacity. One disadvantage of long fins is that they can increase the wet surface area of the fish, creating more frictional drag and resulting in greater power requirements for swimming (Barrett et al., 1999; Plaut, 2000; Sinclair et al., 2011). Thus, both the drag and the thrust decreased for the caudal-fin-regenerated fish. If the reduction in thrust were of a similar order as the reduction in drag, then small areas of caudal fin regeneration could result in a large recovery in U_{crit} (Webb, 1973). However, caudal-fin-regenerated fish may still have other compensatory mechanisms. For example, the caudal-fin-regenerated fish could possibly adapt to caudal fin deficiency, and those fish may swim with more coordination after 20 days of recovery. These issues require further research. The other interesting finding was that the shapes of the regenerated caudal fins were different from those of the intact caudal fins in all three fish species, and the ARs of the regenerated caudal fins were lower than those of the intact caudal fins. A lower AR was expected to be beneficial to enhancing fast-start swimming performance, which is a rapid, high-energy swimming burst elicited by threatening stimuli and is important for escape from predation (Langerhans, 2009), by improving the capacity of acceleration (Langerhans and Reznick, 2009). These results demonstrate that escape from predation may be the most important issue for caudal-fin-lost fish, causing the recovery of fast-start swimming performance to be prioritised.

AUTHOR CONTRIBUTIONS

S.-J.F. conceived and designed the experiments. C.F., Z.-D.C. and S.-J.F. performed the experiments. C.F., Z.-D.C. and S.-J.F. analyzed the data. C.F. and S.-J.F. wrote the paper.

COMPETING INTERESTS

No competing interests declared.

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