



FEATURE ARTICLE

# Flow and stress acclimation both enhance predator avoidance in a common cyprinid fish

Shi-Jian Fu\*

Laboratory of Evolutionary Physiology and Behaviour, Chongqing Key Laboratory of Animal Biology, Chongqing Normal University, Chongqing 401331, PR China

**ABSTRACT:** I investigated the impact of flow and predator stress acclimation on the swimming performance and predator avoidance ability of juvenile qingbo *Spinibarbus sinensis*. The experimental subjects were acclimatized for 20 d to nearly still water (control), flowing water, or nearly still water in the presence of their natural predators. Fish housed in flowing water showed a significantly greater capacity for prolonged swimming, as suggested by their critical swimming speeds compared to those of the other 2 groups. The group acclimatized to predators reacted more quickly to a predator stimulus, but did not exhibit faster burst (indicated by fast-start escape response) or prolonged swimming speeds. However, both the group housed in flowing water and the group exposed to predators demonstrated significantly greater predator avoidance capabilities than the control group. Therefore, both treatments substantially improved predator avoidance capabilities, although, apparently, via different mechanisms. This result may have considerable importance in the development of optimal rearing conditions in hatcheries for fish that are destined to be released into the wild.

**KEY WORDS:** Swimming performance · Flow regime · Predator stress · Flexibility

## INTRODUCTION

Swimming performance variables, such as critical swimming speed ( $U_{crit}$ ) and fast-start escape response, are often used as indicators of fitness (Plaut 2001, Kieffer 2010, Gotanda et al. 2012). In fish,  $U_{crit}$  is the swimming speed a fish can maintain over a prolonged period of time and is often used as a relative indicator of prolonged swimming performance



A qingbo fleeing from an attack by a southern catfish.

(Photo: Cheng Fu, Qingyi Wu)

(i.e. aerobic swimming capacity), though it is recognized that there is an anaerobic contribution to  $U_{crit}$  (Brett 1964, Plaut 2001, Lee et al. 2003). Prolonged swimming has been documented in the field against a current, searching for food, patrolling for predators, chasing mates, seeking favorable abiotic conditions and migrating (Plaut 2001, Kieffer 2010). Fast-start swimming is characterized by rapid acceleration and is fuelled anaerobically (Domenici & Blake 1997). It is one kind of burst swimming that is commonly used by fishes as a component of antipredator behavior, i.e. to evade attack by a potential predator (Webb 1986, Law & Blake 1996, Walker et al. 2005); thus, maximum speed during predator-elicited fast-start responses ( $V_{max}$ ) can be used in the evaluation of predator avoidance capacity. Some studies show an intraspecific tradeoff

\*Corresponding author: shijianfu9@cqu.edu.cn

between  $V_{\max}$  and  $U_{\text{crit}}$  that might reflect the relative costs and benefits of both behaviors in the environment (Fu et al. 2013).

Fish live in environments that vary significantly in water velocity and in the abundance of predators. Natural selection is predicted to favor different locomotor strategies in habitats with different water velocities and levels of predator stress (Langerhans 2008, 2009, Fu et al. 2012, 2013). Selection is expected to favor prolonged swimming in high-flow environments, where fish must often swim to maintain position and perform routine tasks. In contrast, burst swimming is favored in low-velocity and/or high-predation-stress environments, where fish are largely freed from severe demands on endurance and can instead exploit strategies requiring high acceleration or maneuverability (Langerhans 2008). Both inter- and intra-specific variation in swimming performance among different habitats has been documented in cyprinids (Yan et al. 2013, Fu et al. 2014) and other fish species (Fulton et al. 2005, Yavno & Fox 2013, Binning et al. 2014, Binning & Roche 2015). Furthermore, even short-term acclimation to high flow-rate conditions can elicit higher  $U_{\text{crit}}$  in fish species such as common carp *Cyprinus carpio* (He et al. 2013) and qingbo *Spinibarbus sinensis* (Zhao et al. 2012). A previous study found that crucian carp *Carassius carassius* showed improved burst swimming performance after short-term exposure to predators via adaptive morphological change (Domenici et al. 2008). Whether short-term exposure to predators can induce profound change in swimming performance without morphological change is unknown. I hypothesized that fish acclimated to the presence of predators can develop fast-start performance capabilities and, hence, improved predator avoidance capabilities. Furthermore, fish acclimated to flowing water (vs. nearly still water) may develop high  $U_{\text{crit}}$  but low  $V_{\max}$  values as a functional trade-off and, hence, a low predator avoidance capacity. Thus, the aim of this study was to test whether prolonged swimming performance, fast-start swimming performance and, hence, predator avoidance capacity changed after acclimation to either changes in flow conditions or predator stress.

To achieve these goals, qingbo, a cyprinid fish species widely distributed in the Three-Gorges Reservoir and its tributary rivers was selected as the experimental animal. The fish shows both high prolonged and burst swimming performance and prefers a riptide flow regime as habitat (Yan et al. 2013), suggesting that performance in both types of

swimming conditions confers fitness benefits in different contexts. Flow regime and predator stress vary profoundly in its natural habitat. Southern catfish *Silurus meridionalis*, an ambush predator preferring calm-flowing water, is one of its primary predators throughout its life history. I measured the swimming performance (both  $U_{\text{crit}}$  and fast-start swimming) and predator avoidance capacity (directly by looking at mortality rates when exposed with a predator) of qingbo in 3 groups: acclimated to flowing water (flow group), to predators (predator group, in nearly still water with caged southern catfish and to nearly still water (control group). Due to the functional trade-off between prolonged and burst swimming performance, I predicted that the flow group would show high prolonged swimming performance, low burst swimming performance and a decreased predator avoidance capacity, whereas the predator group would show high burst swimming performance, low prolonged swimming performance and increased predator avoidance capacity, relative to the control group.

## MATERIALS AND METHODS

### Experimental animals and holding conditions

Experimental juvenile qingbo (body mass: 7.80 to 10.29 g, body length: 6.90 to 8.00 cm, N = 160) were obtained from local farmers in order to guarantee their naïvety to predators. Fish were kept in dechlorinated tanks (length  $\times$  width  $\times$  height, 1.5  $\times$  0.6  $\times$  0.5 m, with 0.3 m depth of water) at 25°C water temperature for 1 mo before the experiments were performed. The fish were fed to satiation with a commercial diet (Tongwei Company; dietary composition: 41.2  $\pm$  0.9% protein; 8.5  $\pm$  0.5% lipid; 25.7  $\pm$  1.2% carbohydrate and 12.3  $\pm$  0.4% ash) 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  $\pm$  0.5°C, and the water oxygen content was maintained at >7.0 mg l<sup>-1</sup>. Fish were maintained on a 12 h light:12 h dark photoperiod cycle. All fish were tagged intraperitoneally with passive integrated transponders (PIT; Guangzhou Hongteng Barcode Technology Company) under anaesthesia with neutralized tricaine methane sulfonate (MS222, 50 mg l<sup>-1</sup>). All of the experiments were conducted according to the Guidelines on the Humane Treatment of Laboratory Animals established by the Ministry of Science and Technology of the People's Republic of China.

## Experimental protocol

Forty fish were randomly selected for each group and then transferred to training tanks (450 l water, 1 tank treatment<sup>-1</sup>, 3 training tanks in total) with different water velocities (see diagram in Li et al. 2010). The fish in the flow group were placed in tanks with a water flow of 28 cm s<sup>-1</sup> (i.e. 4 body lengths [BL] s<sup>-1</sup>, about 50%  $U_{crit}$ ), whereas fish in both control and predator groups were maintained in tanks with a flow of 3 cm s<sup>-1</sup> (a speed which ensures full water exchange but does not elicit apparent swimming activities). Fish in the predator group were housed together with 1 caged southern catfish (a pilot experiment found that a caged predator elicits a similar effect on routine activities as does direct predation). Since the experimental fish from each group were held in separate tanks, during the acclimation period, all physical conditions such as temperature and dissolved oxygen level were maintained similarly, thus ensuring that the differences among different experimental groups are a reflection of the treatment rather than tank variations. After 20 d of acclimation, 8 fish from each group underwent  $U_{crit}$  measurements while another 8 fish from each group underwent fast-start measurements. The remaining 24 fish were used for predator avoidance trials (3 trails, 8 fish trail<sup>-1</sup>) using southern catfish as the predator. Fish were fasted for 2 d prior to all experimental measurements.

### Measurement of the success rate of predator avoidance

To measure the success rate of predator avoidance, 8 fish from each group were selected and placed together in a tank (1.5 × 0.6 × 0.5 m, filled with 300 l water) with 1 southern catfish (ca. 250 to 350 g). The number of prey was monitored every 6 h. If fish were eaten at the end of a 6 h span, the southern catfish was scanned by PIT to identify the prey and the predator was replaced with another southern catfish. The experiment ended when half of the prey were eaten. The experiment was repeated 3 times. It lasted for 6 d for each measurement (i.e. half of the prey were eaten), and there was never >1 fish eaten in each tank (i.e. either 1 or no fish were consumed) during each 6 h span.

### Measurement of $U_{crit}$

A Brett-type swim tank (Brett 1964) was used to measure  $U_{crit}$ . The instrument was constructed from

clear plastic poly-methyl-methacrylate (PMMA). Circulating water flow was generated in the tank (total volume: 3.5 l) by an acrylic propeller attached to a variable speed pump (for details see Penghan et al. 2014). The speed pump was controlled by a variable voltage power source. A video camera 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 the 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. The swim tank was designed to switch between a closed mode and an open mode—the latter to replenish oxygen levels (water was flushed for 2 min every 20 min). Two honeycomb screens were secured at both ends of the swimming tank to reduce turbulence and to ensure uniform water velocity across the swimming tank. Each individual fish was placed downstream of the propeller in a swimming chamber with a 20 cm<sup>2</sup> cross-sectional area. Fish were introduced into the swim tank and held for 4 h (which was sufficient for recovery according to the pilot experiment) at a water speed of 3 cm s<sup>-1</sup> for acclimation (which ensures full water exchange but does not elicit apparent swimming activity). Then, individual fish were tested using an  $U_{crit}$  test, i.e. the water speed was increased in 7 cm s<sup>-1</sup> (1 BL s<sup>-1</sup>) increments every 20 min until the fish became exhausted (Yan et al. 2013). Testing was terminated when the fish failed to move off the rear honeycomb screen of the swimming tank for 20 s (Yan et al. 2013). 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):

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

where  $V$  is the highest speed at which the fish swam during the entire experiment (cm s<sup>-1</sup>),  $\Delta V$  is the velocity increment (7 cm s<sup>-1</sup>, 1 BL s<sup>-1</sup>),  $T$  is the prescribed period of swimming per speed (20 min) and  $t$  is the time that the fish swam at the final speed (min).  $U_{crit}$  was not corrected for the solid blocking effect because the cross-sectional area of the fish did not exceed 10% of that of the swim tank. The water oxygen content in the tank was never allowed to fall below 85% oxygen saturation.

### Measurement of fast-start escape response

Fast-start escape performance was measured with a device developed by the Laboratory of Evolutionary

Physiology and Behavior, Chongqing Normal University (for details see Yan et al. 2012). The device includes a high-speed camera (500 frames  $s^{-1}$ , Basler A504K) and an LED matrix light source and sink ( $40 \times 40 \times 15$  cm engraved with  $1 \text{ cm}^{-1}$  grid lines on the bottom). The fish were anesthetized with neutralized MS-222 (50 mg  $l^{-1}$ ) and dorsally marked at the center of the mass position with titanium oxide. The duration of the whole process was  $< 30$  s, and fish were allowed to recover for 4 h following the procedure. Fish were then gently herded toward the acclimation zone of the experimental system and allowed to rest for another hour (Yan et al. 2013). Then, fish were introduced individually into the filming zone through an alleyway. Escape responses were elicited by an electrical impulse (0.75 V  $cm^{-1}$ ; 50 ms) administered when the fish maintained a position at the center of the filming zone. The recording was initiated as soon as the LED (synchronized with the electrical stimulus) was illuminated. The high-speed camera was used to record the entire escape process (time span: 3 s) (for examples of fast-start escape process in qingbo taken by the high speed camera see Wang et al. [2012]). The resulting images were analyzed using image processing software (ACDsee 10, ACD Systems International) and digitized by TpsUnil and TpsDig software (<http://life.bio.sunysb.edu/morph>) to define the track of the centroid of the locomotion performed by the fish during its escape response. The following parameters were calculated: response latency (ms), maximum linear velocity ( $V_{max}$ ,  $m \text{ s}^{-1}$ ),  $S_{120ms}$  and maximum acceleration velocity ( $A_{max}$ ,  $m \text{ s}^{-2}$ ) (Domenici & Blake 1997). Response latency was defined as the time elapsed between the initiation of the stimulus (LED light) and the time when escape behavior was observed.  $S_{120 \text{ ms}}$  (cm) was defined as the total escape distance travelled by the centroid locomotion during the first 120 ms after the stimulus.  $V_{max}$  was calculated from the maximum distance moved by the centre of mass in 2 ms (2 consecutive video frames), and  $A_{max}$  was further calculated by the change in  $V_{max}$ . Both  $V_{max}$  and  $A_{max}$  appeared in Stage 2 of the fast-start response.  $V_{max}$ ,  $A_{max}$  and  $S_{120 \text{ ms}}$  were computed using a 5-point smoothing regression to smooth the center of mass displacement data (Lanczos 1956).

### Data analysis

SPSS Statistics17 was used for data analysis. All values are presented as means ( $\pm$ SE), and a  $p < 0.05$  was used as the level of statistical significance. The effects of acclimation on swimming performance

( $U_{crit}$ ,  $V_{max}$ ,  $A_{max}$ ,  $S_{120ms}$  and response latency) were determined using 1-way ANCOVA (with body length as a covariate). The effects of time and experimental treatments on number of prey that were eaten during a 6 d predation trail were determined using 2-way ANOVA. The effects of acclimation on the success rate of predator avoidance (indicated by the percent number of fish left from each group at the end of 6 d of predation, repeated 3 times) were determined using 1-way ANOVA. One-sample Kolmogorov-Smirnov test and Levene's test were used to check whether the data met ANOVA assumptions of normality and heteroscedasticity, respectively; no data transformations were needed to meet the assumptions. The ANCOVA or ANOVA were followed by a Duncan multiple-comparison post hoc test if it was necessary to determine within-group differences.

## RESULTS

### Effect of acclimation on swimming performance

Body length showed no significant effect on  $U_{crit}$  ( $F_{1,20} = 1.404$ ,  $p = 0.250$ ), whereas experimental treatments showed significant effects on  $U_{crit}$  ( $F_{2,20} = 11.153$ ,  $p = 0.001$ ). After 20 d of acclimation, fish in the flow group showed significantly higher  $U_{crit}$  than those in the control group (Fig. 1) ( $p < 0.001$ ). However, there was no significant difference in  $U_{crit}$  between the control and predator groups ( $p = 0.177$ ).

Body length showed no significant effect on response latency ( $F_{1,20} = 0.125$ ,  $p = 0.728$ ), whereas experimental treatments showed significant effects on response latency ( $F_{2,20} = 7.447$ ,  $p = 0.004$ ). After 20 d of acclimation, fish in the predator group showed significantly shorter response latency periods than those of the control group, i.e. fish in the predator group took less time to respond to a threat stimulus than did the control group (Fig. 2) ( $p < 0.05$ ). However, there was no significant difference in response latency between the control and flow groups ( $p = 0.088$ ).

Body length showed no significant effect on  $V_{max}$ ,  $A_{max}$  or  $S_{120ms}$ . Furthermore, there was no significant difference in  $V_{max}$ ,  $A_{max}$  or  $S_{120ms}$  among different acclimation groups (Table 1).

### Effect of acclimation on success rate of predator avoidance

Five out of 24 gingbo were eaten on Day 1 of the predator avoidance experiment. It took 6 d until 50%

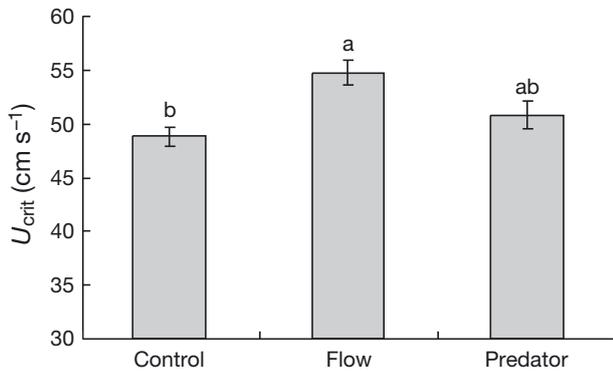


Fig. 1. *Spinibarbus sinensis*. Critical swimming speed ( $U_{crit}$ ) of qingbo after 20 d of different experimental acclimation conditions (mean  $\pm$  SE, N = 8). Groups with different lower case letters are significantly different (Duncan,  $p < 0.05$ ). Control group: nearly still water; flow group: 28 cm s<sup>-1</sup> (4 body lengths s<sup>-1</sup>) water flow; predator group: nearly still water with predator

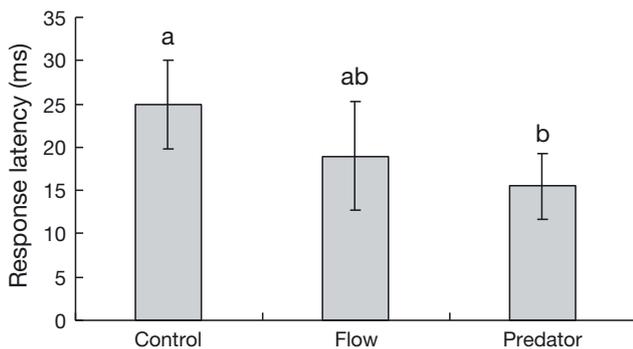


Fig. 2. *Spinibarbus sinensis*. The response latency (i.e. time taken to respond to a threat stimulus) of qingbo after 20 d of different experimental acclimation conditions (mean  $\pm$  SE, N = 8). Groups with different lower case letters are significantly different (Duncan,  $p < 0.05$ ). See Fig. 1 for further information

(12 individuals) of the qingbo were finally consumed (Fig. 3). Experimental treatment showed a significant effect on prey consumed by predators ( $F_{2,36} = 12.12$ ,  $p < 0.001$ ). More qingbo were eaten in the control group than in the other 2 groups after Day 3 ( $p < 0.05$ ).

Thus, after 6 d of predation, both the flow group and the predator group showed a significantly higher success rate of predator avoidance ( $F_{2,20} = 60.50$ ,  $p < 0.001$ ) (Fig. 4).

## DISCUSSION

### Effect of flow condition and predator stress acclimation on swimming performance

Improved prolonged swimming performance after flow condition acclimation as indicated by  $U_{crit}$  has been demonstrated in several fish species such as striped bass *Morone saxatilis* (Young & Cech 1993, 1994), zebrafish *Danio rerio* (McClelland et al. 2006), common carp *Cyprinus carpio* (He et al. 2013) and qingbo (Zhao et al. 2012). A previous study in qingbo found that fish acclimated to fast-flowing water showed improved growth performance and better body condition in comparison to those acclimated to still water (Li et al. 2013). This may be one important reason why fish in the flow group exhibited enhanced swimming performance. The underlying mechanisms for enhanced swimming performance may involve improved cardio-respiratory capacity (Li et al. 2010, Brauner et al. 2011), altered muscle enzyme activity (Johnston & Moon 1980, Farrell et al. 1991, McClelland et al. 2006), increased energy store (Johnston & Moon 1980, Pearson et al. 1990), enhanced clearance rate of metabolic products (Zhao et al. 2012), increased muscle fiber size (Martin & Johnston 2006) and/or increased numbers of mitochondria (Davison & Goldspink 1977, Davie et al. 1986). It has been shown that fish in good condition display both higher prolonged swimming performance and quicker evasion during predator attacks (Chick & Van den Avyle 2000), suggesting the flow group may exhibit improved fast-start performance as a consequence of better condition compared to the control group. On the other hand, it has also been suggested that individuals with fast prolonged swimming performance might show poor burst swim-

Table 1. *Spinibarbus sinensis*. Effects of different experimental acclimation conditions on maximum linear velocity ( $V_{max}$ ), maximum acceleration velocity ( $A_{max}$ ) and total escape distance travelled by centroid locomotion during the first 120 ms ( $S_{120ms}$ ) after stimulus during a predator-elicited fast-start response (mean  $\pm$  SE, N = 8)

Parameters	Control	Flow	Predator	Covariate effect		Main effect	
				$F_{1,20}$	p	$F_{2,20}$	p
$V_{max}$ (m s <sup>-1</sup> )	1.32 $\pm$ 0.19	1.30 $\pm$ 0.25	1.31 $\pm$ 0.16	0.002	0.969	0.025	0.976
$A_{max}$ (m s <sup>-2</sup> )	126.01 $\pm$ 43.47	116.26 $\pm$ 36.74	155.72 $\pm$ 96.47	1.418	0.248	0.822	0.454
$S_{120ms}$ (mm)	69.01 $\pm$ 10.12	73.92 $\pm$ 26.56	70.31 $\pm$ 7.10	2.079	0.165	0.392	0.681

Unit corrected  
after publication

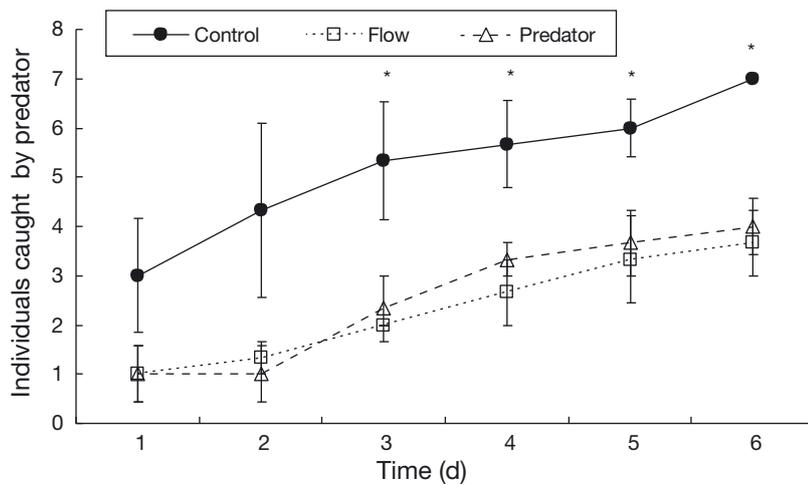


Fig. 3. *Spinibarbus sinensis*. Number of qingbos consumed by predators after different periods of predator exposure (mean  $\pm$  SE, N = 3). Asterisks indicate significant differences among different experimental acclimation groups (Duncan,  $p < 0.05$ ). See Fig. 1 for further information

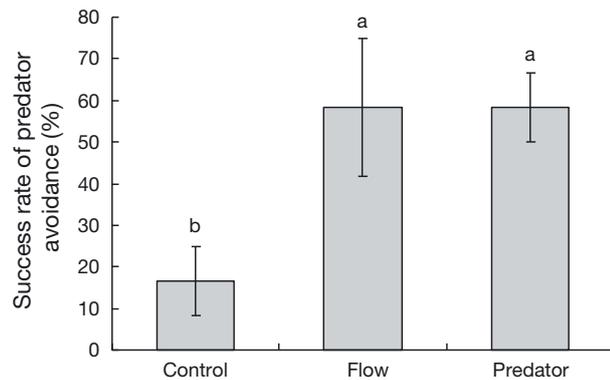


Fig. 4. *Spinibarbus sinensis*. The success rate of predator avoidance by qingbos after 20 d of different experimental acclimation conditions (mean  $\pm$  SE, N = 3). Groups with different lower case letters are significantly different (Duncan,  $p < 0.05$ ). See Fig. 1 for further information

ming performance as a functional trade-off (Langerhans et al. 2004, Domenici et al. 2008). However, none of the variables involved in the fast-start escape response differed among qingbos in the flow and control groups in the present study. This may be an outcome of the combined effects of morphological, physiological and biochemical changes under different acclimation conditions.

$V_{\max}$ ,  $A_{\max}$  and  $S_{120\text{ms}}$  all showed no change after predator acclimation. This substantiates studies on Chinese hook snout carp *Opsariichthys bidens* and pale chub *Zacco platypus*, which found that  $V_{\max}$  was irrelevant to predator stress in both species (Fu et al. 2012, 2013). However, it is noteworthy that response

latency decreased significantly in the predator group, which may be the main reason for the improved predator avoidance capacity (see below). This may be related to a higher concentration of adrenaline and cortisone (Barton 2002) and up-regulation of metabolic status (Brown et al. 2005) in the presence of a predator. The present study demonstrates that the sublethal effects of predator presence during the juvenile stage may have physiological and behavioral repercussions and, hence, possibly long-term consequences for fish population recruitment. Preisser et al. (2005) showed that in aquatic systems, the mere presence of a predator has a similar or greater effect on prey population density than predation itself.

#### Effect of flow condition and predator stress acclimation on predator avoidance capacity

Interestingly, both acclimation groups showed a profoundly improved predator avoidance capacity, as suggested by the 3- to 4-fold increase in the success rate of predator avoidance in both groups. The improved predator avoidance capacity in the predator group is easy to understand, although the mechanism was not what was expected (i.e. fast response rather than improved  $V_{\max}$ ). Fish exposed to predators often have stronger anti-predator responses than predator-naïve prey (Magurran & Pitcher 1987, Brown & Warburton 1999, Huntingford 2004, El Balaa & Blouin-Demers 2011, Meager et al. 2011). The underlying mechanisms of improved anti-predator capacity include alterations in behavior, morphology and physiology after predator experience (Sih et al. 1985, Brönmark & Miner 1992, Creel & Christianson 2008). Besides a shorter response and improved  $V_{\max}$  (which was not found in the present study), some behavioral changes, such as increased spontaneous movements and higher vigilance, might also be involved in the improved predator avoidance capacity in predator-acclimated fish (Magnhagen et al. 2012). For example, a previous study of poeciliids (*Brachyrhaphis episcopi*) found that individuals from a highly predated population were more explorative and more active than those from a low-predation population (Archard & Braithwaite 2011).

The flow group also showed a higher predator avoidance capacity, suggesting that improved prolonged swimming performance might also be correlated with predator avoidance capacity since only  $U_{crit}$  increased in the flow group. The observations of Grorud-Colvert & Sponaugle (2006, p. 286) were substantiated; they suggested that

critical swimming speed, evasion speed, and other evasive behaviors can influence the outcome of a predator encounter by predicting how quickly a fish can respond as well as how fast and how long a recruit can outswim a predator.

Furthermore, the higher predator avoidance capacity of fish in the flow group may be due to the decreased foraging activities in the presence of a predator threat as a consequence of good body condition (Floyd & Anderson 2010). Nevertheless, the outcome of predator-prey interactions changed profoundly after either flow or predator acclimation of juvenile qingbos. The possible mechanisms include improved swimming abilities (and thus enhanced predator avoidance) and/or a decrease in the risk-prone behavior of fish. Flow or predator acclimation in early life stages may have a profound effect on physiological and behavioral traits and, hence, long-term consequences for ecology. Furthermore, rearing fish in optimal flow conditions and/or under sublethal predator stress may facilitate their survival after subsequent release in the wild.

In conclusion, acclimation to faster-flowing water only improved prolonged swimming performance, while acclimation to predator stress only shortened the response latency of escape responses. However, both types of acclimation resulted in an improved anti-predator capability, while the underlying mechanisms require further investigation. These results may be important in developing guidelines for providing optimal rearing conditions for fish destined to be released into the wild.

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