

# Predator-induced morphology enhances escape locomotion in crucian carp

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Fishes show a remarkable diversity of shapes which have been associated with their swimming abilities and anti-predator adaptations. The crucian carp (*Carassius carassius*) provides an extreme example of phenotypic plasticity in body shape which makes it a unique model organism for evaluating the relationship between body form and function in fishes. In crucian carp, a deep body is induced by the presence of pike (*Esox lucius*), and this results in lower vulnerability to gape-limited predators, such as pike itself. Here, we demonstrate that deep-bodied crucian carp attain higher speed, acceleration and turning rate during anti-predator responses than shallow-bodied crucian carp. Therefore, a predator-induced morphology in crucian carp enhances their escape locomotor performance. The deep-bodied carp also show higher percentage of muscle mass. Therefore, their superior performance in escape swimming may be due to a combination of higher muscle power and higher thrust.

**Keywords:** crucian carp; escape response; swimming performance; fish shape; induced morphology; predator–prey interactions

## 1. INTRODUCTION

Fishes show a remarkable diversity of morphologies and each aspect of fish design may have several implications (Alexander 1974; Lauder 1996). In particular, the body morphology of fishes has been associated with their swimming abilities (Alexander 1974; Blake 1983, 2004; Webb 1984a; Videler 1993; Domenici 2003), but the morphology may also affect the risk of becoming a victim to predation. For example, some fish species possess spines and others have a large body depth that decreases vulnerability to gape-limited predators (Alexander 1974; Nilsson *et al.* 1995; Godin 1997). The most common way of avoiding predation, however, is the escape response, a burst swimming movement shown by most fishes when attacked by a predator (Domenici & Blake 1997). Various characteristics of this response were shown to be fundamental for avoiding predation, such as reaction distance, escape path, distance-derived variables (such as velocity and acceleration) and turning rates (Walker *et al.* 2005). Previous work has shown that certain morphological defences, such as changes in body shape, can be induced by the presence of predators (Brönmark & Miner 1992). However, it is not known whether these inducible morphological defences can, in turn, also affect the escape locomotion abilities of fishes.

Earlier studies on the relationship between body shape and swimming ability have been based on a comparison among different species (Webb 1978; Blake 1983; Harper & Blake 1990; Videler 1993). Trade-offs were identified in body morphology, since enhancing specific aspects of locomotor performance often results in reducing performance in other types of locomotion

(Alexander 1974; Webb 1984a). For example, specialization in unsteady motions, implying accelerations or turning manoeuvres, trades off with specialization in cruising swimming (Webb 1984a; Domenici 2003; Blake 2004). Generally, the body of cruising specialists is streamlined to minimize drag, while acceleration specialists have a large body depth and area, especially posteriorly, and a large proportion of muscle mass to maximize thrust (Webb 1984a). However, past interspecific comparisons of one trait were naturally constrained by potential differences in other traits. The problems arising from interspecific comparisons have been partially overcome by studies at the intraspecific level, which showed that genetically distinct morphs of a given species have different swimming performances (Taylor & McPhail 1985, 1986; Ghalambor *et al.* 2004; Langerhans *et al.* 2004). However, differences in morphology among fish populations can also occur as a result of phenotypic plasticity (Brönmark & Miner 1992; Stauffer & Van Snik Gray 2004).

An extreme example of phenotypic plasticity in body shape is found in crucian carp (figure 1), which makes it a unique model organism for evaluating the relationship between body form and function in fishes (Brönmark & Miner 1992; Holopainen *et al.* 1997; Vøllestad *et al.* 2004; Andersson *et al.* 2006). Crucian carp respond to chemical cues from piscivorous fishes by increasing their body depth (Brönmark & Pettersson 1994). The increased body depth in crucian carp decreases its risk of predation by gape-limited piscivores like pike (Nilsson *et al.* 1995). As in other examples of inducible defence, there is a cost associated with this morphological change, i.e. deep-bodied crucian carp experience higher drag, and therefore an energetic disadvantage during cruising compared with shallow-bodied crucian carp (Pettersson & Brönmark 1997, 1999). However, given the

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Figure 1. Crucian carp (*Carassius carassius*) from ponds with and without predators (pike, *Esox lucius*) show different body shapes. (a) Shallow-bodied morph from a predator-free pond and (b) deep-bodied morph from a pond with predators. Scale bars, 10 mm.

trade-offs existing between different body shapes and various swimming functions (Webb 1984a), an induced morphological change may not necessarily imply a cost for all locomotor activities. A large body depth may enhance the acceleration performance during escape locomotion, which is considered crucial for avoiding predation in most fish species (Weihs 1973; Webb 1984a; Domenici & Blake 1997; Godin 1997; Walker *et al.* 2005). Based on the idea of a trade-off between a deep and a shallow body as linked to accelerator versus cruiser characteristics (Webb 1984a), we used two morphs of crucian carp to test the prediction that predator-induced deep-bodied fishes have higher locomotor performance in escape manoeuvres than shallow-bodied fishes. In addition, we tested whether a large body depth is accompanied by a large proportion of muscle mass, and therefore high muscle power, since this could also increase acceleration performance (Webb 1984a).

## 2. MATERIAL AND METHODS

### (a) Fish care and maintenance

Deep-bodied and shallow-bodied crucian carp (figure 1) were obtained by electrofishing from six local ponds (near Lund, southern Sweden). The deep-bodied individuals were collected from three ponds in which piscivorous pike were present while the shallow-bodied fishes were collected from three ponds without piscivorous pike. They were kept in 200 l aerated aquaria at  $15.5 \pm 0.5^\circ\text{C}$  (range) and a 12 L : 12 D cycle for three to four weeks prior to the experiments. Before the experiments, body lengths (total length, TL), depths (just anterior to the dorsal fin, to the nearest millimetre) and weights (to the nearest 0.1 g) were measured. At least 1 hour before the experiment, fishes were marked dorsally, on the midline of the fish, in the position of the centre of mass (CM) of the fish when stretched straight, with a  $3 \times 3$  mm square retroreflective tape glued onto the skin. Their CM was determined to be at 0.35 body length from the snout, based on measurements carried out on fishes from different morphs (range 0.349–0.358 body length, measured on five specimens from each morph).

Fishes of a similar size were used for each morph (tables 1 and 2). Fish body morphology was expressed as the ratio of body length to body depth (L : D). The relationship between length and weight (log-transformed) of each morph yielded regressions (deep-bodied morph:  $\log \text{ weight} = 2.99 \log \text{ length} - 4.46$ ;  $R^2 = 0.98$ ;  $p < 0.0001$ ,  $N = 40$ ; shallow-bodied morph:  $\log \text{ weight} = 2.92 \log \text{ length} - 4.68$ ;  $R^2 = 0.98$ ;  $p < 0.0001$ ;  $N = 41$ ) with no significant differences in slopes ( $F = 0.45$ ; d.f. = 77;  $p = 0.5$ ) but different elevations ( $F = 77.44$ ; d.f. = 78;  $p < 0.0001$ ). Drag coefficients were calculated according to Pettersson & Brönmark (1999), using a given speed of  $0.1 \text{ m s}^{-1}$ . The proportion of muscle mass/total body mass was also measured in individual fishes ( $n = 5$  for each pond). Total wet mass (to the nearest 0.1 g) was determined for each fish, after which muscles were dissected out and weighed.

### (b) Experimental protocol

For the experiments, 19, 11 and 10 individuals were used from each of the three ponds with predators (i.e. deep-bodied morph), and 19, 10 and 12 individuals were used from each of the three ponds without predators (i.e. shallow-bodied morph). Single fishes were introduced into a circular arena (diameter 1.22 m, water level 18 cm), with oxygenated water at  $16 \pm 1^\circ\text{C}$ . After being released into the experimental tank (mean time from release to startle  $15.8 \pm 1.2$  min (mean  $\pm$  s.e.; no difference between morphs;  $n = 81$ ;  $t = 0.19$ ;  $p = 0.85$ ), fishes were startled by the release of a black plastic cylinder (145 mm long and 28 mm in diameter), from a height of 1.1 m over the water surface. This was accomplished by turning off an electromagnet to which the cylinder was attached via a metal disc (2 cm in diameter) applied to the top end of the cylinder. The plastic cylinder was released so that it hit the water surface and entered the water without hitting the bottom, due to a wire to which it was attached. The cylinder had a tapering point (15 mm long) to minimize surface waves. The escape response of each fish was recorded with a high-speed camera (Redlake PCI 1000S) at  $500 \text{ frames s}^{-1}$ . A grid on the tank bottom allowed us to evaluate surface waves. No image distortion was present in any of the sequences analysed.

### (c) Data handling and statistics

The CM and the snout were digitized on a computer with a tracking software (WINANALYSE, Micromak GmbH). The position of the CM was used to determine the cumulative distance swum, as the sum of the distance between subsequent points, at any given time. The cumulative distance was then derived with respect to time, in order to obtain the speed data, using a five-point differentiation-based smoothing method (Lanczos 1956). Acceleration was determined in a similar manner, by differentiating the speed data with respect to time using the Lanczos method (Lanczos 1956). Cumulative distance and speed were evaluated within a fixed time (60 ms; Webb 1976; Domenici & Blake 1993), which approximately corresponds to the average duration of the first two tail flips of the tail (the first two axial bends, i.e. stages 1 and 2) of all fishes considered ( $64.5 \pm 1.7$  ms,  $n = 81$ ). These two stages are considered crucial for avoiding ambush predator attacks (Webb 1976, 1978). Maximum acceleration was measured as the peak acceleration at any point in time during the escape response. The angle achieved by the fish during

Table 1. Morphological and performance variables for deep-bodied and shallow-bodied crucian carps. (Numbers refer to group average  $\pm$  s.e.)

	variable	deep-bodied	shallow-bodied
morphology	length (mm)	97.8 $\pm$ 2.8	102.0 $\pm$ 2.1
	weight (g)	17.2 $\pm$ 1.7	16.3 $\pm$ 1.0
	length/depth	2.85 $\pm$ 0.03	3.50 $\pm$ 0.02
	drag coefficient	0.047 $\pm$ 0.0005	0.040 $\pm$ 0.0003
performance	muscle mass (%)	31.0 $\pm$ 2.3	25.6 $\pm$ 1.6
	latency (ms)	13.1 $\pm$ 0.6	13.7 $\pm$ 0.7
	cumulative distance (cm)	4.36 $\pm$ 0.12	3.58 $\pm$ 0.09
	velocity (m s <sup>-1</sup> )	1.18 $\pm$ 0.03	0.97 $\pm$ 0.03
	acceleration (m s <sup>-2</sup> )	44.8 $\pm$ 1.7	36.6 $\pm$ 1.1
	turning rate ( $^{\circ}$ s <sup>-1</sup> )	2881 $\pm$ 73	2503 $\pm$ 79
	stage 1 angle ( $^{\circ}$ )	95.8 $\pm$ 5.2	104 $\pm$ 6.3
	stage 1 duration (ms)	33.4 $\pm$ 1.7	40.8 $\pm$ 2.1

Table 2. Predator and pond effects on morphological variables in crucian carp. (Difference between the morphs was tested with a nested MANOVA (see text). Values refer to subsequent univariate tests. Muscle mass was tested separately with a nested ANOVA.)

source	dependent variable	type III sums of squares	d.f.	mean square	F	p
predator	weight	28.9	1	28.9	0.50	0.48
	length	241.4	1	241.4	1.30	0.26
	length/depth	7.67	1	7.67	415.43	<0.001
	drag coefficient	0.0009	1	0.0009	205.40	<0.001
pond (predator)	weight	1697.6	4	424.4	7.32	<0.001
	length	6204.0	4	1551.0	8.36	<0.001
	length/depth	0.35	4	0.088	4.78	0.002
	drag coefficient	0.0003	4	0.00008	16.43	<0.001
predator	percentage muscle	0.027	1	0.027	11.10	0.003
pond (predator)	percentage muscle	0.078	4	0.019	7.90	<0.001

stage 1 (stage 1 angle) was calculated as the angle between the lines joining CM and the snout at the beginning of the response and the end of the turn accomplished during the first body bend (Domenici & Batty 1997; Domenici & Blake 1997). Rotational performance was measured by determining turning rate, defined as the ratio of stage 1 angle and stage 1 duration. Escape latencies were measured as the time from the contact between stimulus and water, to the first visible reaction of the fish. Difference in percentage of muscle mass between morphs was tested with a nested ANOVA (pond nested under the presence or absence of pike) on arcsine-transformed data (Zar 1984). Differences between morphs in morphological (length, weight, fineness ratio (L : D) and drag coefficient) and performance variables (latency, velocity, acceleration, cumulative distance, average turning rate, stage 1 angle and stage 1 duration) were analysed with nested MANOVAs (pond nested under the presence or absence of pike) on log-transformed data. Ponds were treated as fixed effects rather than random. This means that we have selected the ponds because they belonged to two categories of ponds that had specific fixed attributes (the presence of predators), and they were used as a natural experiment. Therefore, the sites were not chosen at random but were expected to differ *a priori* (Bennington & Thayne 1994). We can revisit these ponds year after year and if no major disturbance occurs they should have the same attributes. This is unlike a true random effect nested ANOVA design, e.g. a situation where a large number of ponds were stocked with crucian carp, to be randomly assigned to treatment (predator presence) and analysed with

treatment as fixed and ponds as random effects. Strictly speaking, therefore, our results are applicable only to the sites chosen and caution should be used in generalizing our results. Nevertheless, the use of fixed effect in studies testing the effect of predator presence, using an experimental nested design similar to ours (localities with and without predators, where localities are treated as a fixed effect), is a common procedure in the literature (e.g. Reznick & Endler 1982; Reznick 1989; Leips & Travis 1999; Kelly *et al.* 2000; Jennions & Telford 2002; Langerhans *et al.* 2004). *F*-ratios used type III sums of squares.

### 3. RESULTS

The presence or absence of pike was found to significantly affect the morphological variables (MANOVA (pond nested under the presence or absence of pike); Wilks' lambda = 0.135; *p* < 0.001; mean values listed in table 1). In particular, there were significant differences in length/depth ratio and drag coefficients but not in lengths or weights (table 2). In addition, shallow-bodied individuals had a significantly lower proportion of muscle mass in relation to total mass than deep-bodied ones (ANOVA (pond nested under the presence or absence of pike); *F* = 11.1; *p* = 0.003; table 2).

Performance variables were found to be significantly different between ponds with and without the presence of pike (MANOVA (pond nested under the presence or absence of pike); Wilks' lambda = 0.606; *p* < 0.001; mean values listed in table 1). Subsequent univariate tests

Table 3. Predator and pond effects on performance variables in crucian carp. (Difference between the morphs was tested with a nested MANOVA (see text). Values refer to subsequent univariate tests.)

source	dependent variable	type III sums of squares	d.f.	mean square	<i>F</i>	<i>p</i>
predator	latency	0.003	1	0.003	0.21	0.65
	cumulative distance	0.097	1	0.097	23.9	<0.001
	velocity	0.099	1	0.099	23.6	<0.001
	acceleration	0.131	1	0.131	17.1	<0.001
	turning rate	0.068	1	0.068	10.3	0.002
	stage 1 duration	0.120	1	0.120	6.00	0.017
	stage 1 angle	0.008	1	0.008	0.23	0.63
pond (predator)	latency	0.042	4	0.010	0.66	0.62
	cumulative distance	0.150	4	0.037	9.24	<0.001
	velocity	0.099	4	0.025	5.93	<0.001
	acceleration	0.050	4	0.012	1.61	0.18
	turning rate	0.053	4	0.013	2.03	0.10
	stage 1 duration	0.125	4	0.031	1.55	0.20
	stage 1 angle	0.060	4	0.015	0.46	0.77

(table 3) show that deep-bodied crucian carp had superior performance in all locomotor variables measured (cumulative distance, speed and acceleration). Similarly, the turning rate was higher in deep-bodied than in shallow-bodied fishes (table 3). The angle of turn (stage 1 angle) was not different between the two morphs, while stage 1 duration was, suggesting that differences in turning rates were not due to the extent of the body bend. No difference was found in the escape latencies of the two morphs (table 3). In addition, a pond effect was found on both morphological (MANOVA (pond nested under the presence or absence of pike); Wilks' lambda=0.358;  $p < 0.001$ , table 2) and performance variables (MANOVA (pond nested under the presence or absence of pike); Wilks' lambda=0.420;  $p < 0.001$ ; table 3).

#### 4. DISCUSSION

Our results show that predator presence induces an increase in escape locomotor performance in crucian carp. This increase in performance is accompanied by drastic changes in morphology, such as a deep body and a high percentage of muscle mass. Both of these changes may cause higher performance in fast-start swimming according to functional morphology theories (Webb 1984a; Domenici 2003). These suggest that characteristics such as a large body depth and a relatively high muscle mass:body mass ratio enhance acceleration performance, owing to the high thrust produced by a large area, and high muscle power. Besides having superior acceleration, the predator-induced deep-bodied individuals had a higher turning rate than the shallow-bodied ones. This implies that deep-bodied crucian carp can achieve any given turn away from danger in a shorter time than shallow-bodied individuals. A high proportion of muscle mass, and hence muscle power, may increase turning rate. Here, muscle mass was measured as total muscle, as done in previous fast-start studies (e.g. Webb 1978). While anaerobic (white) fibres are the main source of power at high speeds, red fibres were shown to be active during escape responses (on *Cyprinus carpio*, Kashin *et al.* 1979; on *Lepomis macrochirus*, Jayne & Lauder 1993). The activation of red fibres at high speeds may aid power production or force transmission (Syme 2006). In addition, red muscle is present in a relatively small

proportion of the total muscle mass in most fishes (Greer-Walker & Pull 1975). In particular, Johnston & Lucking (1978) found that the percentage of red muscle/total muscle mass was only 4% in *Carassius auratus*, a similar species to *Carassius carassius*. Since the differences in total muscle mass/body mass found between the two morphs of crucian carp are of the order of 20%, they can reasonably be ascribed to differences in white muscle mass.

Potentially, differences in body mass may affect inertia and therefore acceleration performance. However, while deep-bodied fishes of any given length are heavier than shallow-bodied fishes, there is a considerable overlap between the body mass values of the two morphs, such that differences in body mass are not significant. Therefore, it is unlikely that body mass differences played a major role in determining performance differences. We suggest that performance differences are mainly due to the differences in body shape (length/depth) and proportion of muscle mass, although the possibility that other additional factors (e.g. part of the 'design box' *sensu* Domenici (2003), like muscle properties) may play a role in determining swimming performance differences cannot be ruled out. Further studies are needed in order to investigate the relative contribution of these two factors to enhancing escape locomotion. In addition, despite the different body morphologies, there was very little variation in the position of the CM. Nevertheless, digitizing a fixed point (0.35 body length) along the body in both morphs makes the performance measurements comparable.

Prey fishes do not necessarily escape at their maximum capacity (Webb 1986). Therefore, potentially, performance differences between the two morphs could be due to behavioural differences related to different predation risks, rather than morphological differences, since deep-bodied fishes have been exposed to predator presence, while shallow-bodied individuals are predator naive. However, if differences in escape response were to be due to behavioural rather than morphological differences, then other performance parameters not affected by morphology, like escape latency (i.e. readiness to escape), may be expected to be enhanced (i.e. shorter latency) in the deep-bodied morph. Escape latency, however, did not differ between morphs (tables 1 and 3), suggesting that differences in morphology rather than

behaviour are the most likely causes of locomotor performance differences between the two morphs. In addition, our results show that there is some effect of the pond on performance and morphology. This is not surprising, however, since different ponds may show different nutrient regimes and other physical-chemical characteristics.

While our work found that predator presence increases escape locomotor performance, this is only indirect evidence that predator presence may increase the ability of fishes to escape from predator attacks. Recent work addresses the issue of which variables may affect the escape success of fishes (Walker *et al.* 2005). Walker *et al.* (2005) found that four main variables affect prey vulnerability: (i) reaction distance, (ii) the evasion path, (iii) the ability of the prey to generate rapid tangential acceleration (measured by the net distance travelled, maximum velocity and maximum acceleration), and (iv) turning rates. Here, we found that both (iii) and (iv) were affected, and this suggests that the ability to escape a predator attack was also affected.

The evolution of adaptation to one function often comes at the expense of the performance of another function, i.e. trade-offs between traits can be identified (Reznick & Travis 1996). For example, recent work has shown that burst swimming performance may trade off with male genital size in the mosquitofish *Gambusia affinis* (Langerhans *et al.* 2005). Earlier work on different morphs of fishes, carried out on various species, found trade-offs among different body shapes in relation to swimming performance. In these studies, the deep-bodied form showed superior escape swimming performance and inferior endurance compared with the shallow-bodied form (Taylor & McPhail 1985, 1986, but see Law & Blake 1996, where no differences were found). More recent work shows that enhanced escape swimming performance in specific fish populations may increase escape success and has been linked to exposure to high predation pressure (Ghalambor *et al.* 2004; Langerhans *et al.* 2004). Fishes from populations with high predation pressure have superior locomotor performance during escapes and higher survival when exposed to predation from piscivorous fishes compared with fishes from genetically and morphologically different low-predation populations (O'Steen *et al.* 2002; Ghalambor *et al.* 2004; Langerhans *et al.* 2004). Clearly, different morphologies linked to different predation pressures can give rise to genetically distinct morphs as a process of natural selection. However, the differences between these morphs are inherited, while in the crucian carp, the difference is plastic, such that individuals shift from one morph to the other depending on predator presence (Brönmark & Miner 1992; Brönmark & Pettersson 1994; Holopainen *et al.* 1997; Stabell & Lwin 1997; Vøllestad *et al.* 2004; Andersson *et al.* 2006).

In crucian carp, there appears to be a trade-off between escape swimming performance, which is superior in deep-bodied individuals, and energy expenditure in cruising which increases with body depth due to higher drag during forward swimming (Alexander 1974; Webb 1984a; Brönmark & Miner 1992; Pettersson & Brönmark 1999; table 1). Growth experiments on crucian carp suggest that a deep body may increase energetic costs, since deep-bodied fishes show reduced growth in the absence of predators and at low resource levels, when

compared with shallow-bodied crucian carp (Pettersson & Brönmark 1997). The inducement of a deep body form in the presence of predators suggests that the advantages of low vulnerability presumably outweigh the additional energetic costs associated with a deep body. Among other vertebrates, tadpoles (genus *Hyla*) exhibit predator-induced phenotypic changes in body morphology, which include a longer and wider tail (McCollum & Van Buskirk 1996; Van Buskirk & McCollum 2000). The burst performance of the induced morph is not significantly different from the non-induced morph (Van Buskirk & McCollum 2000). However, the induced morph shows reduced predation rates, possibly as a result of attracting the predator lunge towards the tail where an attack would be less likely to be lethal (McCollum & Van Buskirk 1996; Van Buskirk & McCollum 2000). In addition, McCollum & Van Buskirk (1996) show that, in the absence of predators, the two morphs grew at the same rate, although the induced tadpole morph showed decreased fitness due to higher mortality related to causes other than predation.

The phenotypic plasticity of crucian carp may be related to the variable environment in which they live. In Scandinavian lakes and ponds, pike and crucian carp often coexist (Brönmark & Miner 1992). Predation pressure on crucian carp can vary greatly within one prey generation due to hypoxic events which may kill pike and other predators, but not crucian carp, since they are extremely resistant to hypoxia (Stecyk *et al.* 2004). Phenotypic plasticity allows crucian carp to take advantage of a shallow body form for high cruising ability in the absence of predators, while the deep-bodied morph shows a high escape swimming performance, together with a defence mechanism in the presence of gape-limited predators. Therefore, deep-bodied crucian carp achieve low vulnerability to predation via two routes that are relatively independent since increased escape swimming and morphological defences are not always associated in fishes (Andraso 1997). Indeed, fishes with spines and armours often show reduced escape swimming performance or absence of a startle response (Andraso 1997; Godin 1997). In small crucian carp, deep-bodied morphs may enjoy only one of the two potential anti-predator advantages, as they may benefit from enhanced escape swimming performance although their profile may not be deep enough to deter attacks from gape-limited piscivores. In addition to the predator defence benefits, changes in body morphology may also be advantageous to crucian carp by affecting foraging success when feeding on prey from different microhabitats (benthic versus pelagic; Andersson *et al.* 2006).

While a large body depth, especially caudally, accompanied by a high percentage of muscle mass, has been regarded as a feature for high acceleration performance (Webb 1984a; Domenici & Blake 1991), the design solutions for acceleration specialists may vary depending on their lifestyle and feeding habits. For example, the pike, an acceleration specialist, has a large caudal area but not a large body depth, although it has a large percentage of muscle mass (Webb 1984a). Pike are ambush predators and their reduced body profile minimizes the reaction distance of prey, thereby increasing the predator capture success (Webb 1984b; Domenici 2002). On the other hand, a large body depth extended through most of the

body can decrease vulnerability to gape-limited predators, and it may be regarded as a design solution for non-piscivorous fish subject to high predation risk (Domenici 2003). The phenotypic plasticity of crucian carp represents a unique opportunity to study the functional consequences of different morphologies in fishes. Arguably, the principles driving the morphological variability in crucian carp can provide an important model for understanding the relationship between body form and function in fishes.

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## REFERENCES

- Alexander, R. McN. 1974 *Functional design in fishes*. London, UK: Hutchinson Publishers.
- Andersson, J., Johansson, F. & Söderlund, T. 2006 Interactions between predator- and diet-induced phenotypic changes in body shape of crucian carp. *Proc R. Soc. B* **273**, 431–437. (doi:10.1098/rspb.2005.3343)
- Andraso, G. M. 1997 A comparison of startle response in two morphs of the brook stickleback (*Culaea inconstans*): further evidence for a trade-off between defensive morphology and swimming ability. *Evol. Ecol.* **11**, 83–90. (doi:10.1023/A:1018487529938)
- Bennington, C. C. & Thayne, W. V. 1994 Use and misuse of mixed-model analysis of variance in ecological studies. *Ecology* **75**, 717–722. (doi:10.2307/1941729)
- Blake, R. W. 1983 *Fish locomotion*. Cambridge, UK: Cambridge University Press.
- Blake, R. W. 2004 Fish functional design and swimming performance. *J. Fish Biol.* **65**, 1193–1222. (doi:10.1111/j.0022-1112.2004.00568.x)
- Brönmark, C. & Miner, J. G. 1992 Predator-induced phenotypical change in body morphology in crucian carp. *Science* **258**, 1348–1350. (doi:10.1126/science.258.5086.1348)
- Brönmark, C. & Pettersson, L. B. 1994 Chemical cues from piscivores induce a change in morphology in crucian carp. *Oikos* **70**, 396–402. (doi:10.2307/3545777)
- Domenici, P. 2002 The visually-mediated escape response in fish: predicting prey responsiveness and the locomotor behaviour of predators and prey. *Mar. Freshw. Behav. Physiol.* **35**, 87–110. (doi:10.1080/10236240290025635)
- Domenici, P. 2003 Habitat, body design and the swimming performance of fish. In *Vertebrate biomechanics and evolution* (eds V. L. Bels, J.-P. Gasc & A. Casinos), pp. 137–160. Oxford, UK: BIOS Scientific Publishers Ltd.
- Domenici, P. & Batty, R. S. 1997 The escape behaviour of solitary herring and comparisons with schooling individuals. *Mar. Biol.* **128**, 29–38. (doi:10.1007/s00227050065)
- Domenici, P. & Blake, R. W. 1991 The kinematics and performance of the escape response in the angelfish, *Pterophyllum eimekei*. *J. Exp. Biol.* **156**, 187–205.
- Domenici, P. & Blake, R. W. 1993 The effect of size on the kinematics and performance of angelfish (*Pterophyllum eimekei*) escape responses. *Can. J. Zool.* **71**, 2319–2326.
- Domenici, P. & Blake, R. W. 1997 Fish fast-start kinematics and performance. *J. Exp. Biol.* **200**, 1165–1178.
- Ghalambor, C. K., Reznick, D. N. & Walker, J. A. 2004 Constraints on adaptive evolution: the functional trade-off between reproduction and fast-start swimming performance in Trinidadian guppy (*Poecilia reticulata*). *Am. Nat.* **164**, 38–50. (doi:10.1086/421412)
- Godin, J.-G. J. 1997 Evading predators. In *Behavioural ecology of teleost fishes* (ed. J.-G. J. Godin), pp. 191–236. Oxford, UK: Oxford University Press.
- Greer-Walker, M. & Pull, G. A. 1975 A survey of red and white muscle in marine fish. *J. Fish Biol.* **7**, 295–300. (doi:10.1111/j.1095-8649.1975.tb04602.x)
- Harper, D. G. & Blake, R. W. 1990 Fast-start performance of rainbow trout *Salmo gairdneri* and northern pike *Esox lucius*, during escapes. *J. Exp. Biol.* **150**, 321–342.
- Holopainen, I. J., Tonn, W. M. & Paszkowski, C. A. 1997 Tales of two fish: the dichotomous biology of crucian carp (*Carassius carassius* (L.)) in northern Europe. *Ann. Zool. Fenn.* **34**, 1–22.
- Jayne, B. C. & Lauder, G. V. 1993 Red and white muscle activity and kinematics of the escape response of bluegill sunfish during swimming. *J. comp. Physiol. A* **173**, 495–508. (doi:10.1007/BF00193522)
- Jennions, M. D. & Telford, S. R. 2002 Life-history phenotypes in populations of *Brachyrhaphis episcopi* (Poeciliidae) with different predator communities. *Oecologia* **132**, 44–50. (doi:10.1007/s00442-002-0952-2)
- Johnston, I. A. & Lucking, M. 1978 Temperature induced variation in the distribution of different types of muscle fibre in the goldfish (*Carassius auratus*). *J. Comp. Physiol.* **124**, 111–116.
- Kashin, S. M., Fedman, A. G. & Orlovsky, G. N. 1979 Different modes of swimming in the carp, *Cyprinus carpio*. *J. Fish Biol.* **14**, 403–405. (doi:10.1111/j.1095-8649.1979.tb03535.x)
- Kelly, C. D., Godin, J. G. J. & Abdallah, G. 2000 Geographical variation in the male intromittent organ of the Trinidadian guppy (*Poecilia reticulata*). *Can. J. Zool.* **78**, 1674–1680. (doi:10.1139/cjz-78-9-1674)
- Lanczos, C. 1956 *Applied analysis*. Eaglewood Cliffs, NJ: Prentice Hall.
- Langerhans, R. B., Layman, C. A., Shokrollahi, M. & DeWitt, T. 2004 Predator-driven phenotypic diversification in *Gambusia affinis*. *Evolution* **58**, 2305–2318.
- Langerhans, R. B., Layman, C. A. & DeWitt, T. J. 2005 Male genital size reflects a tradeoff between attracting mates and avoiding predators in two livebearing fish species. *Proc. Natl Acad. Sci. USA* **102**, 7618–7623. (doi:10.1073/pnas.0500935102)
- Lauder, G. V. 1996 The argument from design. In *Adaptation* (eds M. R. Rose & G. V. Lauder), pp. 55–91. San Diego, CA: Academic Press.
- Law, T. C. & Blake, R. W. 1996 Comparison of the fast-start performance of closely related, morphologically distinct threespine sticklebacks (*Gasterosteus* spp.). *J. Exp. Biol.* **199**, 2595–2604.
- Leips, J. & Travis, J. 1999 The comparative expression of lifehistory traits and its relationship to the numerical dynamics of four populations of the least killifish. *J. Anim. Ecol.* **68**, 595–616. (doi:10.1046/j.1365-2656.1999.00311.x)
- McCollum, S. A. & Van Buskirk, J. V. 1996 Costs and benefits of a predator-induced polyphenism in the gray treefrog *Hyla Chrysoscelis*. *Evolution* **50**, 583–593. (doi:10.2307/2410833)
- Nilsson, P. A., Brönmark, C. & Pettersson, L. B. 1995 Benefits of a predator-induced morphology in crucian carp. *Oecologia* **104**, 291–296. (doi:10.1007/BF00328363)

- O'Steen, S., Cullum, A. J. & Bennett, A. F. 2002 Rapid evolution of escape ability in Trinidadian guppies (*Poecilia reticulata*). *Evolution* **56**, 776–784.
- Pettersson, L. B. & Brönmark, C. 1997 Density-dependent costs of an inducible morphological defense in crucian carp. *Ecology* **78**, 1805–1815.
- Pettersson, L. B. & Brönmark, C. 1999 Energetic consequences of an inducible morphological defense in crucian carp. *Oecologia* **121**, 12–18. (doi:10.1007/s004420050901)
- Reznick, D. & Travis, J. 1996 The empirical study of adaptation in natural populations. In *Adaptations* (eds M. R. Rose & G. V. Lauder), pp. 243–289. San Diego, CA: Academic Press.
- Reznick, D. N. 1989 Life-history evolution in guppies: 2. Repeatability of field observations and the effects of season on life histories. *Evolution* **43**, 1285–1297. (doi:10.2307/2409363)
- Reznick, D. N. & Endler, J. A. 1982 The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). *Evolution* **36**, 160–177. (doi:10.2307/2407978)
- Stabell, O. B. & Lwin, M. S. 1997 Predator-induced phenotypic changes in crucian carp are caused by chemical signals for conspecifics. *Environ. Biol. Fish.* **49**, 145–149. (doi:10.1023/A:1007368815511)
- Stauffer Jr, J. R. & Van Snik Gray, E. 2004 Phenotypic plasticity: its role in trophic radiation and explosive speciation in cichlids (Teleostei: Cichlidae). *Anim. Biol.* **54**, 137–158. (doi:10.1163/1570756041445191)
- Stecyk, J. A. W., Stenlücken, K.-O., Farrell, A. P. & Nilsson, G. E. 2004 Maintained cardiac pumping in anoxic crucian carp. *Science* **306**, 77. (doi:10.1126/science.1100763)
- Syme, D. A. 2006 Functional properties of skeletal muscle. In *Fish biomechanics* (eds R. E. Shadwick & G. V. Lauder), pp. 179–240. San Diego, CA: Academic Press.
- Taylor, E. B. & McPhail, J. D. 1985 Variation in burst and prolonged swimming performance among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. *Can. J. Fish. Aquat. Sci.* **42**, 2029–2033.
- Taylor, E. B. & McPhail, J. D. 1986 Prolonged and burst swimming in anadromous and freshwater threespine sticklebacks. *Can. J. Zool.* **64**, 416–420.
- Van Buskirk, J. V. & McCollum, S. A. 2000 Influence of tail shape on tadpole swimming performance. *J. Exp. Biol.* **203**, 2149–2158.
- Videler, J. J. 1993 *Fish swimming*. London, UK: Chapman and Hall.
- Vøllestad, L. A., Varreng, K. & Poléo, A. B. S. 2004 Body depth variation in crucian carp *Carassius carassius*: an experimental individual-based study. *Ecol. Freshw. Fish* **13**, 197–202. (doi:10.1111/j.1600-0633.2004.00048.x)
- Walker, J. A., Ghalambor, C. K., Grist, O. L., Kenney, D. M. & Reznick, D. N. 2005 Do faster starts increase the probability of evading predators? *Funct. Ecol.* **19**, 808–815. (doi:10.1111/j.1365-2435.2005.01033.x)
- Webb, P. W. 1976 The effect of size of the fast-start performance of rainbow trout *Salmo gairdneri*, and a consideration of piscivorous predator–prey interactions. *J. Exp. Biol.* **65**, 157–177.
- Webb, P. W. 1978 Fast-start performance and body form in seven species of teleost fish. *J. Exp. Biol.* **74**, 211–226.
- Webb, P. W. 1984a Body form, locomotion and foraging in aquatic vertebrates. *Amer. Zool.* **24**, 107–120.
- Webb, P. W. 1984b Body and fin form and strike tactics of four teleost predators attacking fathead minnow (*Pimephales promelas*) prey. *Can. J. Fish. Aquat. Sci.* **41**, 157–165.
- Webb, P. W. 1986 Effect of body form and response threshold on the vulnerability of four species of teleost prey attacked by largemouth bass (*Micropterus salmoides*). *Can. J. Fish. Aquat. Sci.* **43**, 763–771.
- Weih, D. 1973 The mechanism of rapid starting of slender fish. *Biorheology* **10**, 343–350.
- Zar, J. H. 1984 *Biostatistical analysis*. Englewood Cliffs, NJ: Prentice Hall.