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Do body and fin form affect the abilities of fish to stabilize swimming during maneuvers through vertical and horizontal tubes?

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Synopsis

Goldfish, *Carassius auratus*, silver dollar, *Metynnis hypsauchen*, and angelfish, *Pterophyllum scalare* were induced to swim through narrow vertical and horizontal tubes ranging in length from 0 to 20 cm (approximately 0 to 3 times total fish length, FL). The ability to stabilize the body while negotiating these confined spaces was quantified as (1) the minimum width of vertical (w_v) and horizontal (w_h) tubes traversed, where width is the smaller cross-sectional dimension of the tube, (2) the ratio w_v/w_h, and (3) transit speed through the tubes. Tube width was expressed as relative width, obtained by dividing tube width by fish length. Minimum relative widths traversed increased from 0.15 to 0.19 in the order silver dollar < angelfish < goldfish for vertical tubes and from 0.17 to 0.18 in the order goldfish = silver dollar < angelfish for horizontal tubes. w_v/w_h increased from 0.91 to 1.10 in the order silver dollar = angelfish < goldfish. Minimum tube widths generally increased with tube length for vertical tubes. Although significant differences in relative minimum widths among species were found, these were small. In contrast, for horizontal tubes, there was no significant effect of tube length on minimum tube width for any species. Large differences were found in transit speed. Transit speed generally decreased as the tube length increased. The slope of the relationship between transit speed and tube length varied among species generally increasing from – 0.41 to – 1.16 for horizontal tubes in the order goldfish < silver dollar < angelfish and from – 0.42 to – 1.07 in the order silver dollar < goldfish < angelfish for vertical tubes. As a result, goldfish usually took longest to traverse tubes of zero length but the shortest time to traverse the longest tubes. In contrast, angelfish traversed short tubes in the least time and long tubes in the greatest time. Deeper bodied angelfish swam slowly and traversed tubes with difficulty because they required experience during each trial to replace median and paired fin with body and caudal fin swimming. According to our data, goldfish were best able to swim in confined spaces.

Introduction

Maneuverability, the ability to move in a small space or volume, and agility, the speed at which an animal performs maneuvers, are essential survival behaviors for the capture of food and avoidance of predators. As such, selection for maneuverability and agility is likely to have been strong, and there is growing interest in the morphological and mechanical factors determining performance (Bandyopadhyay et al. 1997, Fish 1998, Webb 1998a, b). However, it is also well known from human engineering that maneuverability is usually antithetical to stability: maneuverable vehicles are usually unstable,

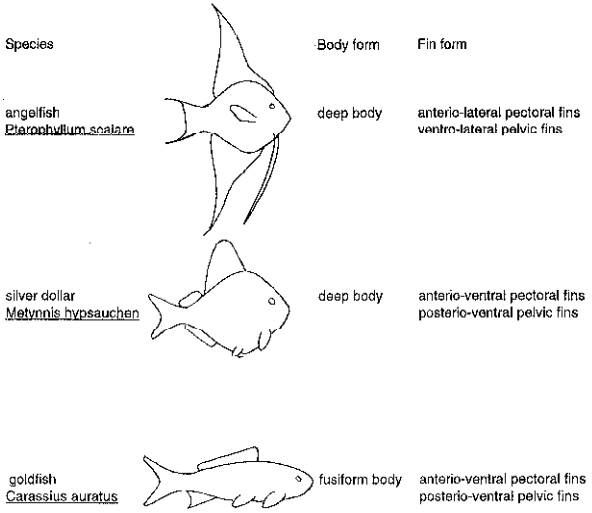

Figure 1. Outline drawing of three species of fish induced to swim through tubes, and the corresponding morphological features of each.

while highly stable vehicles are not very maneuverable. Highly maneuverable bodies invariably require much effort to stabilize their trajectories between maneuvers. In contrast, fishes are considered not only highly maneuverable but also remarkably stable when swimming.

On the basis of natural history observations (Moyle & Cech 1996) and ideas on resistance to maneuvers (Alexander 1967), acanthopterygian fishes with anterio-lateral pectoral fins, ventro-lateral pelvic fins, well developed dorsal and anal fins, and a deep body are considered most maneuverable. If fishes are similar to human-engineered vehicles, these fishes might be expected to be less stable. However, the acanthopterygian body and fin configuration also provides a wide range of control forces to stabilize the body. In contrast, the malacopterygian body and fin bauplan, usually with a more fusiform body, smaller and more anterior median fins, anterio-ventral pectoral fins and posterio-ventral pelvic fins are presumed to be less maneuverable, but might be more stable during swimming. For example, the fin configuration of soft rayed fishes promotes dynamic equilibrium (Weihs 1989, 1993).

In a previous study (Webb et al. 1996), we compared low speed maneuvers of goldfish, silver dollar, and angelfish passing through vertical and horizontal slits. Here we consider the ability of the same three species to stabilize body posture by extending the duration of such maneuvers and inducing fish to pass through vertical and horizontal tubes up to 20 cm (approximately 3 fish lengths) in length. The three species tested represent a range of morphological features believed to affect maneuverability and hence presumably stability. Angelfish, *Pterophyllum scalare*, is representative of acanthopterygians living in highly structured habitats where maneuverability would be at a premium. Goldfish, *Carassius auratus*, is representative of soft-rayed fishes common on beaches as well as among macrophytes. Silver dollar, *Metynnis hypsauchen*, is intermediate, with a gibbose body and well developed dorsal and anal fins similar to angelfish, but with the malacopterygian fin distribution (Figure 1). On the basis of the well-known observations from human engineering experience, we predict angelfish to be less stable than silver dollar, requiring more time to traverse wider tubes, and silver dollar in turn to be less stable than goldfish.

Materials and methods

Goldfish, silver dollar and angelfish were obtained from a local pet store. Eight individuals of each species were held in separate aquaria (50 × 26 × 30 cm) at 25 °C. The water in each aquarium was aerated by a floss-filled, air-lift corner filter. The fishes were fed TetraMin® flake food daily, to excess.

Each tank was divided vertically by a frame supporting a removable opaque partition less than 1 mm thick. There was a rectangular opening 12.7 cm high and 10 cm wide in each partition. These partitions were left in the tank at all times and fishes swam freely through the opening.

Characteristic body and fin dimensions were measured once a week (Table 1). Fishes were anesthetized with 1 ppm 3-aminobenzoic acid ethyl ester (MS-222). Total length was measured to the nearest millimeter, maximum body width (at eyes for silver dollar and angelfish and posterior to the eyes for goldfish) was measured to the nearest 0.1 mm using vernier calipers, and body mass was measured to within 0.01 g with an electric balance.

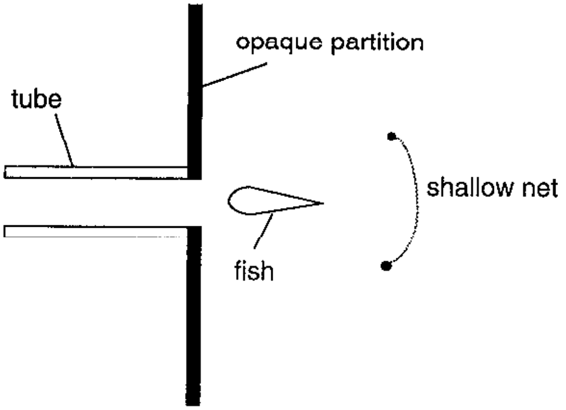

Figure 2. Illustration of the experimental setup for fishes traversing tubes.

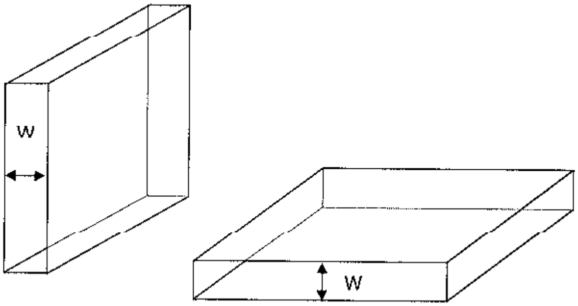

Figure 3. Illustration to show the definition of tube width (w) for vertical and horizontal tube orientations.

Fishes were induced to pass through vertical and horizontal rectangular tubes 0 (one fish length), 5, 10, and 20 cm long, of various widths. Widths were presented to the fish at random. A fish was herded toward the entrance of a tube by means of a small net (Figure 2). A fish escaped by passing through the tube. If a fish had not exited a tube after a period of 5 minutes, the tube was considered too small to negotiate. Tube width is defined as the smaller tube cross-section dimension irrespective of orientation (Figure 3). Minimum widths of tubes traversed were expressed as relative width, dividing actual width by total length of the fish (Webb et al. 1996).

Fish passage through tubes was recorded on videotape. The swimming behavior of each fish was recorded as it passed through the tube. The tape was analyzed field by field (field rate = 60 Hz) to determine the transit time, t, defined as the time of entry of the nose into the tube to the time of exit of the posterior tip of the caudal fin. This definition of t also defines the effective tube length as the physical tube length (TL) plus the fish length (FL). To further take into account possible effects of size, we define the non-dimensional relative tube length (RL) as:

$$RL = (FL + TL)\,FL^{-1}.$$

Mean transit speeds, u (FL per second), were also calculated.

Relative minimum widths traversed by each fish for both vertical and horizontal tubes were compared using a two-way ANOVA with one observation per cell. The two factors for this ANOVA were the mean relative minimum vertical or horizontal tube width, and tube length. A Tukey's multiple comparison test was used to identify pairwise differences among species (Neter et al. 1996). The same procedures were used to compare the ratio of vertical to horizontal minimum widths among species. Simple linear regression equations were used to relate log transit speed and log tube length. Slopes were compared using analysis of covariance. The assumptions of normality and homogeneity for all models were evaluated by graphical and analytical methods including the Lilliefors test, Bartlett's test, and examination of skewness and kurtosis values (Neter et al. 1996). No significant deviations were found. Significant differences are declared for $\alpha \leq 0.05$.

Table 1. Body dimensions of the three species of fish (n = 8) averaged from weekly measurements. Values are means ± 2 SE.

	units	Goldfish	Silver dollar	Angelfish
Mass	g	4.27 ± 1.69	6.8 ± 0.26	5.53 ± 1.54
Total length	cm	7.3 ± 1.0	6.6 ± 0.1	6.1 ± 0.7
Maximum body width	cm	1.08 ± 0.21	1.04 ± 0.02	0.92 ± 0.11

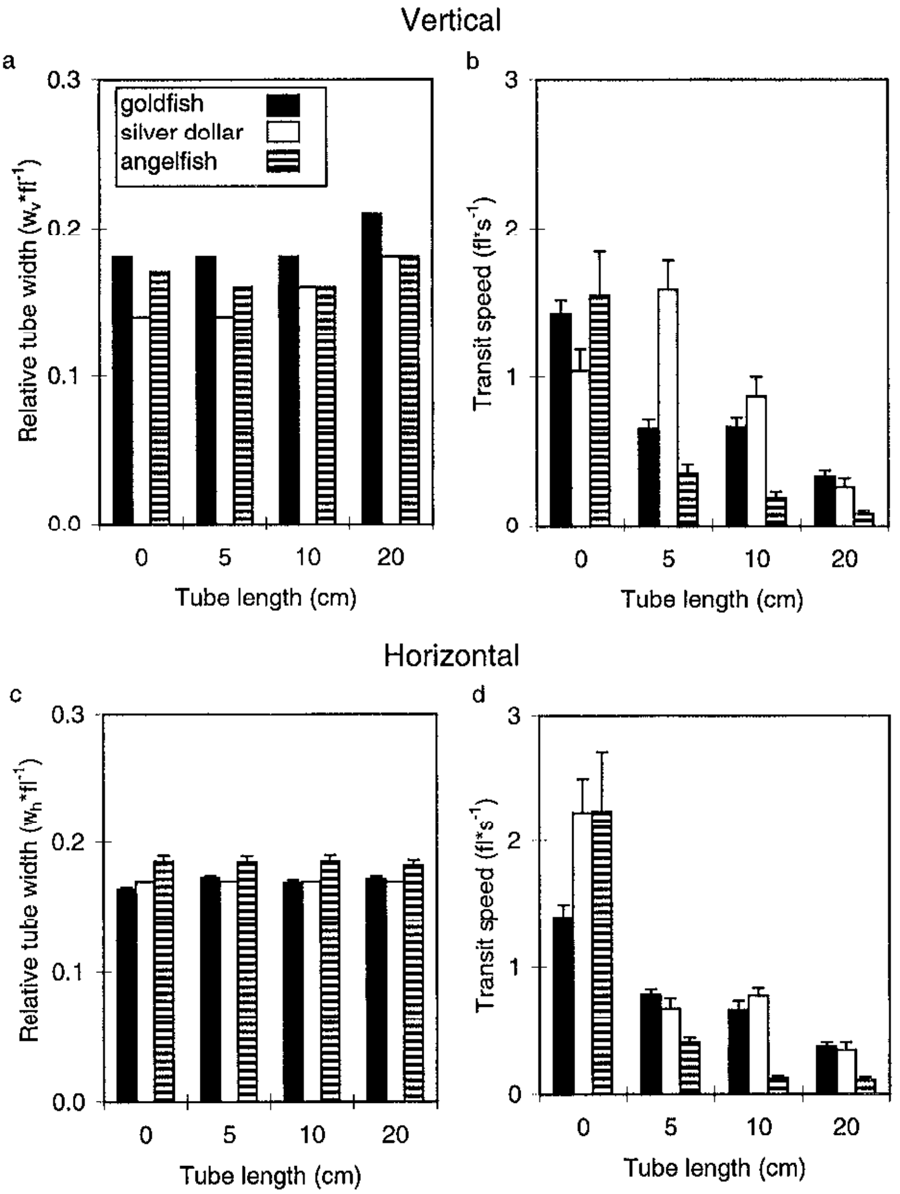

Figure 4. Relative vertical and horizontal tube widths (vertical or horizontal width * total fish $length^{-1}$) and transit speeds (fish lengths per second). Error bars are 2 standard errors. No error bars signify negligible variance.

Results

Swimming behavior

Swimming behavior differed among species during routine swimming and in transiting the tubes. During routine activity, goldfish usually swam using undulations of the body and caudal fin supplemented by the median and paired fins working singly or in any combination. Silver dollar swam using median and paired fins when hovering and with body and caudal fin movements for quick darts. Silver dollar tended to remain stationary until stimulated to move by the net. Angelfish typically hovered and swam slowly using small movements of the median and paired fins, including the caudal fin web, but rarely body and caudal fin undulation.

While traversing tubes, goldfish used behaviors

Table 2. Overall mean relative minimum tube widths for tubes of various lengths negotiated by three species of fish. 95% confidence intervals are ≤ 0.01 for these data.

	Goldfish	Silver dollar	Angelfish
Minimum vertical width	0.19	0.15	0.17
Minimum horizontal width	0.17	0.17	0.18
Minimum vertical width * minimum horizontal width^{-1}	1.10	0.91	0.91

similar to those seen in routine swimming, continuing to use body and caudal fin undulations. However these movements were at reduced amplitude because of the confinement of the tube walls. Silver dollar and angelfish attempted to coast through tubes with the body stretched straight and no fin movements, but this was not sufficient to transit longer tubes. Therefore these fish decelerated, and in the longer tubes fishes often came to a halt. When a fish halted, it attempted to restart and exit by swimming with those propulsors used in routine swimming. Silver dollar used small amplitude beats of the caudal fin followed by coasting, repeating this burst-and-coast behavior as necessary to exit the tube. Angelfish attempted to use the pectoral fins, but these were ineffective in the confined space. Sometimes these fish would spin in the lateral body plane or move back towards the tube entrance. Pectoral fin use was eventually succeeded by short periods of undulation of the median and paired fin webs followed by coasting. This low-speed burst-and-coast behavior sometimes took the fish to the exit, but on other occasions moved the fish towards the entrance. If the fish did not exit the tube using these median and paired fin motions, it began using body and caudal fin undulation which appeared to be the result of startle behavior in a restricted space. This eventually propelled the fish from the tube. When angelfish were re-tested in narrow tubes, the same behavioral patterns were repeated, and fish did not improve in their ability to pass through tubes with successive trials.

Minimum slit width

Relative minimum tube widths tended to increase with length for vertical tubes (Figure 4A). For example, mean relative minimum tube width was 0.18 for goldfish traversing tubes from 0 to 10 cm in length but 0.21 for 20 cm tubes. A more consistent increase in minimum width from 0.14 for a 0 cm tube to 0.18 for 20 cm tubes was found for silver dollar. Results were more variable for angelfish in that relative minimum widths decreased from 0.17 to 0.16 for tubes from 0 to 10 cm but increased to 0.18 for 20 cm tubes. The overall average minimum relative widths for vertical tubes decreased from 0.19 to 0.15 in the order goldfish > angelfish > silver dollar. Differences were significant only for the minimum relative tube width of 0.15 for silver dollar compared with that of 0.19 for goldfish ($p < 0.0008$).

Minimum relative tube width was independent of tube length for horizontal tubes (2-way ANOVA) (Figure 4C). Further analysis using a Tukey's t-test showed that the overall mean minimum relative horizontal tube width of 0.18 for angelfish was significantly greater than 0.17 for goldfish and silver dollar ($p < 0.0004$).

The ratio between relative vertical to relative horizontal minimum tube width (w_v/w_h) was significantly greater at 1.10 for goldfish compared with silver dollar and angelfish at 0.91 ($p < 0.05$) (Table 2).

Table 3. Regression equations relating log transit speed, u (fish lengths per second) to log relative tube length, RL. Means (± 2 SE) are given for regression coefficients.

Tubes	Goldfish	Silver dollar	Angelfish
Horizontal	$u = 0.16(\pm 0.16) - 0.41(\pm 0.17)TL$	$u = 0.33(\pm 0.26) - 0.62(\pm 0.28)TL$	$u = 0.28(\pm 0.33) \quad 1.16(\pm 0.35)TL$
Vertical	$u = 0.17(\pm 0.19) - 0.46(\pm 0.21)TL$	$u = 0.15(\pm 0.71) - 0.42(\pm 0.77)TL$	$u = 0.14(\pm 0.27) - 1.07(\pm 0.29)TL$

Transit speed

Mean relative transit speed generally decreased with increasing tube length (Figures 4B, D), although speeds were more variable for silver dollar traversing vertical tubes than for the other species. The relationships between speed and length were best described by power functions (Table 3). For horizontal tubes, slopes relating log speed to log tube length increased from − 0.41 to − 1.16 in the order goldfish < silver dollar < angelfish. Differences between goldfish and angelfish, and silver dollar and angelfish were significant ($p < 0.05$). For vertical tubes, slopes increased from − 0.42 to − 1.07 in the order silver dollar < goldfish < angelfish. Differences between goldfish and angelfish were significant ($p < 0.05$). Therefore, angelfish transit speed was affected most by tube length. In contrast, goldfish were slowest in traversing short tubes, but were the fastest through longer tubes (Figures 4B, D).

Discussion

Maneuverability of fishes is receiving increasing attention (Bandyopadhyay et al. 1997, Fish 1998, Webb 1998a, b), however, highly maneuverable vehicles tend to be unstable and vice versa. Therefore, maneuverability and stability should be considered together, especially stabilizing swimming trajectories during maneuvers. In previous experiments (Webb et al. 1996) fishes were induced to orient and negotiate vertical and horizontal slits, or tubes of one fish length. Passage through the horizontal slits required fishes to execute a rolling maneuver, but it was not necessary to stabilize posture for any substantial period of time. The present experiments induced fishes to pass through vertical and horizontal tubes, and hence stabilize posture during an extended maneuver required to pass through an enclosed space. For horizontal tubes, fishes controlled posture while swimming on their sides having executed an initial rolling maneuver. Fishes with better abilities to control the swimming trajectory would be expected to negotiate narrow tubes and to do so at higher speeds.

We are unable to show with these three species that one body and fin form is associated with superior trajectory stabilization. For example, goldfish required the largest relative minimum tube widths for vertical tubes, but among the smallest horizontal relative tube widths. Thus, the w_v/w_h ratio was greater than 1, which suggests that goldfish were best able to stabilize swimming after performing the rolling maneuver. Additionally, goldfish traversed the tubes at highest speeds. In contrast, angelfish required intermediate relative minimum vertical tube widths, the largest relative minimum horizontal tube widths, and had among the smallest ratios of w_v/w_h. However, angelfish were also the slowest in traversing longer tubes. Similarly there was no consistent pattern in the ability of silver dollar to traverse tubes. Overall, however, goldfish had the smallest relative tube widths and highest speeds for the most challenging tasks of negotiating longer tubes and horizontal tubes. Thus goldfish were somewhat better able to stabilize swimming in a long narrow space, especially after performing a rolling maneuver, than the other two species tested.

A similar lack of definitive differences in maneuvering through slits was found for the same three species. Nevertheless, goldfish were again somewhat better at completing maneuvers through slits while angelfish were least effective (Webb et al. 1996). As such, no inverse relationship between maneuverability and stability is apparent for fishes, supporting the belief that fishes can be both maneuverable and stable during swimming. Furthermore, the large differences in body and fin pattern of these three species are not associated with either large differences in maneuverability or trajectory stabilization, at least for rolling maneuvers.

Fishes use multipurpose flexible propulsors to both induce maneuvers and stabilize swimming trajectories. This multiple use of a common system (Webb et al. 1996) is probably effective for powered propulsion because both maneuvers and stability involve changes in state. Thus, both necessitate creation of forces to overcome an inertial resistance, either to initiate a maneuver or to correct a disturbance.

The most important factor affecting success in stabilizing the body during rectilinear swimming in a confined space was found to be locomotor behavior during routine activity. These same behaviors were used during maneuvers and in stabilizing posture. Thus goldfish normally swam using the body and caudal fin. This behavior proved to be required to negotiate physically restricted space by all species. Angelfish routinely swam using the median and paired fins. The walls of the tubes clearly prevented use of the paired fins. However these fish could have continued to use the median fins in the confined space, rather than axial undulations. As such, angelfish should have been able to traverse narrower spaces than when using axial undulations. Instead, angelfish shifted to body and caudal fin swimming. In these respects, swimming with the body and caudal fin apparently was superior for moving in physically confined space.

Studies of fish locomotion are typically made in open water, lacking structures. In practice, there is a continuum in the density of habitat structure from pelagic waters to dense stands of macrophytes and rocks and crevices in the substratum. As structure density increases, swimming behavior is modified, as shown here, and is eventually succeeded by burrowing (Moyle & Cech 1996). By making the physical spaces very small, we suggest our experiments require behavior more akin to the burrowing end of the fish response to habitat structure continuum. Throughout the animal kingdom, axial propulsion is used for burrowing (Wainwright 1988). Indeed, burrowing animals typically have lost or reduced appendages. Thus in preferring axial body and caudal fin propulsion, goldfish were most effective overall in moving through very confining spaces.

Acknowledgements

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