EFFECTS OF FIN SIZE ON SWIMMING PERFORMANCE, SWIMMING BEHAVIOUR AND ROUTINE ACTIVITY OF ZEBRAFISH DANIO RERIO

ITAI PLAUT*

Department of Biology, University of Haifa at Oranim, Tivon 36006, Israel

*e-mail: plaut@research.haifa.ac.il

Accepted 29 November 1999; published on WWW 26 January 2000

Summary

The zebrafish Danio rerio exhibits substantial morphological variability in the sizes and shapes of the body and the caudal fin. The present study describes swimming performance, swimming behaviour and routine locomotor activity patterns in three of the major morphotypes: wild-type, long-finned and no-tail. Wild-type and long-finned differ in total length (TL), fork length (FL), caudal fin length (CFL) and caudal fin height (CFH). No-tail has no caudal fin and is significantly smaller in standard length (SL) than the other types. Critical swimming speeds (Ucrit) were measured at 28 °C in a modified Brett-type water tunnel. Ucrit of wild-type fish was 56.0±4.8 cm s⁻¹ or 15.5 SL s⁻¹ (mean ± s.d., N=21), significantly faster than the Ucrit of long-finned fish (43.7±6.8 cm s⁻¹ or 12.5 SL s⁻¹, N=17); both were significantly faster than the Ucrit of no-tail fish (19.8±4.7 cm s⁻¹ or 6.9 SL s⁻¹, N=15). When forced to swim in the water tunnel, zebrafish tended to turn and swim downstream for short periods at slow water velocities. Turning frequencies (turns per minute, fT) at the slowest velocity (4 cm s⁻¹) were 10.1±6.5 min⁻¹ (N=63) and 8.6±4.7 min⁻¹ (N=51) for wild-type and long-finned, respectively, significantly different from that of the no-tail fish, 4.7±2.8 min⁻¹ (N=45). These frequencies decreased below 1 min⁻¹ at 56 %, 64 % and 61 % of Ucrit in wild-type, long-finned and no-tail fish, respectively.

Activity levels of wild-type fish were generally significantly higher than those of long-finned fish, and the levels of both were significantly higher than those of no-tail fish. The pattern of differences in relative activity levels between types was similar to that for Ucrit. The results show that the wild-type fish, on a size-scaled basis, is one of the fastest-swimming fishes ever measured, reaching the maximum predicted theoretical sustained swimming speed. Ucrit of long-finned fish was 22 % lower than that of wild-type fish, and Ucrit of no-tail fish was 65 % lower. Similar differences were found in turning frequencies and routine activity level.

Key words: fish, zebrafish, Danio rerio, swimming performance, activity, swimming behaviour, critical swimming speed.

Introduction

Many species of fish are characterized by fins of different shapes and sizes. Such variability is usually interpreted as reflecting evolutionary adaptations for either social purposes (Bischoff et al., 1985; Partridge and Endler, 1987; Price et al., 1987) or swimming capabilities (Beamish, 1978; Yates, 1983; Videler, 1993). The social significance of fin shapes and sizes has been studied mainly in the context of sexual selection, especially in guppies (Endler, 1980, 1983; Kodric-Brown, 1985; Nicoletto, 1991). However, the effects of different fin sizes and/or shapes on swimming capabilities within species are poorly understood (Webb, 1973; Nicoletto, 1991).

Fin sizes and shapes are expected substantially to affect swimming performance because the fins transfer to the water a large proportion of the propulsive power created by the muscles (Yates, 1983; Weihs, 1989; Videler, 1993). Larger fins may accelerate larger amounts of water in each stride, but larger fins may be less stiff, and the forces transmitted by the fins are negatively correlated to fin stiffness (Simons, 1970; Long, 1992; McHenry et al., 1995). Fin shape is also expected to affect swimming performance. For example, high aspect ratios (defined as the square of fin span/fin area) characterize fast-swimming fishes, while low aspect ratios characterize fishes with low swimming performance but better manoeuvring abilities (Weihs, 1989; Videler, 1993).

Social adaptations by fin enlargement may constrain swimming performance in fishes (Partridge and Endler, 1987; Price et al., 1987). There is a trade-off between evolution towards social success and towards better performance. This trade-off should be evaluated intraspecifically, but low intraspecific variation prevents such a comparison in most species.

Some studies have sought to evaluate the effects of fin size and area on swimming performance. Nicoletto (1991) measured critical swimming speeds of guppy Poecilia reticulata males that differed in their caudal fin shape, but not caudal fin area, and found no effects on critical swimming speed (Ucrit). Webb (1973) amputated the caudal fins of sockeye salmon Oncorhynchus nerka and found no significant
effects on swimming kinematics and on standard and active metabolic rate.

In zebrafish, *Danio rerio* (Barman, 1991), three morphotypes with different fin sizes occur (Fig. 1). One is the wild-type, 'short-finned' zebrafish, with standard body and fin shape. The second is a long-finned variant that has developed in Czechoslovakia. Tan and Phang (1994) found that the genetic segregation of long and short fins matches the classic monohybrid Mendelian pattern of inheritance, suggesting that these fish differ from wild-type fish only in their fin sizes. The third type has no tail. It is a well-known mutant that occurs spontaneously (Halpern et al., 1993; Schulte-Merker et al., 1994).

The present study describes experiments conducted to test the effects of fin shape and size on swimming performance, swimming behaviour and routine locomotor activity patterns in these three major morphotypes.

### Materials and methods

#### Fish and their maintenance

Wild-type and long-finned zebrafish *Danio rerio* (Barman, 1991) were obtained from commercial dealers. During breeding in the laboratory, the no-tail mutant occurred. Fish of the three types were reared in the laboratory (Westerfield, 1995) in 20 l aquaria equipped with biological filtration and temperature control (28±1 °C) at a photoperiod of 14 h:10 h L:D. Fish were fed twice a day with Tetramin tropical fish food. One-third of the water in each aquarium was replaced weekly with dechlorinated tap water. In the experiments, only healthy adult fish (aged 6–10 months) bred in the laboratory and with no body deformations or behavioural abnormalities were used.

#### Fish measurement

After each swimming experiment, a fish was anaesthetized in 0.25 ml l\(^{-1}\) 2-phenoxyethanol for 5–10 min (Summerfelt and Smith, 1990), and the following body measurements were made: total length (*TL*); standard length (*SL*); head length (from the snout to the median edge of the gill operculum, *HL*); caudal fin length (*CFL*); fork length (*FL*); maximum body height (*BH*); caudal peduncle height (*PH*); and maximum body width (*BW*). Measurements were taken using a mechanical caliper of 0.1 mm accuracy. Fish body mass (*BM*) was determined to an accuracy of 0.01 g. Caudal fin height (*CFH*) and caudal fin area were measured from video recordings (25 frames s\(^{-1}\)) of a single swimming fish (\(N=21\) for wild-type fish and \(N=17\) for long-tailed fish, speed 12 cm s\(^{-1}\)) taken against a scaled background and measured by hand. The square of caudal fin span divided by caudal fin area yielded the aspect ratio.

#### Swimming performance

Critical swimming speed (*U*\(_{\text{crit}}\)), defined as the maximum velocity a fish can sustain for a set period (Brett, 1964), was measured using a water tunnel (Fig. 2). Water was pumped from a reservoir (Tsurami submersible pump, model LB2-750, 750 W) through 40 mm diameter tubing to a junction. One exit from the junction led through a valve and a flow meter to the enclosed swimming chamber, the other led back to the reservoir through another valve. The working section was 6 cm × 7 cm × 70 cm (width × height × length) with a cross-sectional area of 42 cm\(^2\). Flow through the working section was made uniformly microturbulent by placing upstream a batch of 14 cm long straws. The accuracy of the flowmeter measurement of water flow velocity in the working section was confirmed by injection of dye into the water of the working section and analysis of the flow velocity using video recordings. A mesh screen located at the downstream end prevented the fish from leaving the working section.
corrections for blocking effects were made because the maximum cross-sectional areas of the fish were always less than 5% of the working section’s cross-sectional area (Bell and Terhune, 1970).

Fish were not fed for 24 h prior to measurements. One fish was then randomly selected by net from the holding aquarium, placed in the swimming chamber and allowed to recover for 2 h at a water velocity of 4 cm s\(^{-1}\). Previous studies have shown that \(U_{\text{crit}}\) is not affected by relatively short recovery periods (Kolok, 1991; Peake et al., 1997). During the last 5 min of the recovery period, the number of fish turns per minute (\(f_T\), see below) was measured. Water velocity was then increased in steps of 4 cm s\(^{-1}\) (approximately 1.5 \(SL \cdot s^{-1}\)) at intervals of 5 min until the fish were fatigued, could not hold position in the tunnel and attached to the downstream screen. The water temperature during experiments was 28±0.5 °C.

Critical swimming speeds were calculated using the equation (Brett, 1964):

\[
U_{\text{crit}} = U_i + \left[ U_i(T_f/T_i) \right],
\]

where \(U_i\) is the highest velocity maintained for the whole 5 min (cm s\(^{-1}\)), \(U_r\) is the velocity increment (4 cm s\(^{-1}\)), \(T_f\) is the time elapsed at fatigue velocity and \(T_i\) is the time between velocity changes (5 min).

**Behavioural analysis of fish swimming at different speeds**

Typically, most fish species swim steadily into the current in the water tunnel. Zebrafish, at low velocities, tend to turn and swim downstream for short periods and then return upstream. To evaluate the effects of varying water velocities on this behaviour, frequencies of turns were counted by direct observation during the second, third and fourth minute of each speed interval. The values obtained (\(f_T\), min\(^{-1}\)) were examined in relation to swimming speed and fish type.

**Routine activity measurement**

Routine activity levels of the fish were measured in three isolated identical aquaria, 28 cm × 14 cm × 18 cm (length × width × height), containing dechlorinated tap water at 28±1 °C with a photoperiod of 14 h:10 h L:D. Three infrared beam projectors and recording photocells were placed along the length of the aquarium opposite a reflector. A counter connected to a recorder attached to a computer recorded every time a fish crossed a beam. The computer recorded the accumulated beam-crossing events for every 15 min. Six fish of the same fin type were placed in an aquarium for 72 h prior to measurements. Measurements began 12 h after the experimenter left the room and continued for 72 h. Fish were not fed during the experiment. Three sets of measurements were taken. In each set, one group of each type of fish was placed randomly in one of the three measurement aquaria. Data for each type of fish were assembled for each hour of the day (24 h) for analysis.

**Data analyses**

Analysis of variance (ANOVA) and Tukey tests were used to compare \(U_{\text{crit}}\) for the three fish types. Similar analyses were used to compare routine activity levels between fish types at any hour of the day. Data from three successive days were treated as repeated measurements. Turning frequency (\(f_T\)) was regressed against log10(swimming speed) (\(U\)), and the regression equations were tested for homogeneity of slopes and analysis of covariance (ANCOVA). Significant differences were accepted at \(P<0.05\). Unless stated otherwise, results are presented as means ± s.d.

**Results**

**Body measurements**

Wild-type and long-finned zebrafish differed significantly only in their TL, CFL, CFH and FL (\(P<0.001\)) (Table 1). No-tail fish were significantly smaller than the other two types in TL, SL, FL and BM. Since they had no tails, tail measurements were not possible.

**Swimming performance**

Mean \(U_{\text{crit}}\) of wild-type zebrafish was significantly greater (56.0±4.8 cm s\(^{-1}\), \(N=21\)) than that of long-finned zebrafish (43.7±6.8 cm s\(^{-1}\), \(N=17\)); both were significantly greater than that of no-tail zebrafish (19.8±4.7 cm s\(^{-1}\), \(N=15\)) (Fig. 3). For

<table>
<thead>
<tr>
<th></th>
<th>Standard length (mm)</th>
<th>Total length (mm)</th>
<th>Fork length (mm)</th>
<th>Head length (mm)</th>
<th>Caudal fin length (mm)</th>
<th>Caudal fin height (mm)</th>
<th>Aspect ratio</th>
<th>Maximum body height (mm)</th>
<th>Caudal peduncle height (mm)</th>
<th>Maximum body width (mm)</th>
<th>Body mass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wild-type</td>
<td>36.0±2.3(^a)</td>
<td>44.3±2.5(^a)</td>
<td>41.5±2.4(^a)</td>
<td>8.8±0.5</td>
<td>8.3±0.7(^a)</td>
<td>8.3±1.9(^a)</td>
<td>2.0±0.5(^a)</td>
<td>9.3±1.2</td>
<td>3.8±0.5</td>
<td>5.2±1.0</td>
<td>0.90±0.25(^a)</td>
</tr>
<tr>
<td>((N=21))</td>
<td>(31.8–39.7)</td>
<td>(39.8–48.4)</td>
<td>(37.6–45.9)</td>
<td>(8.1–9.7)</td>
<td>(7.1–9.6)</td>
<td>(5.3–11.7)</td>
<td>(1.19–3.21)</td>
<td>(7.4–12.0)</td>
<td>(2.9–4.5)</td>
<td>(3.8–7.7)</td>
<td>(0.54–1.41)</td>
</tr>
<tr>
<td>Long-finned</td>
<td>35.1±2.0(^a)</td>
<td>52.4±3.8(^b)</td>
<td>44.2±2.8(^a)</td>
<td>8.5±0.5</td>
<td>17.5±3.9(^b)</td>
<td>12.9±3.5(^b)</td>
<td>1.5±0.5(^b)</td>
<td>8.8±1.2</td>
<td>3.8±0.3</td>
<td>5.3±0.8</td>
<td>0.86±0.20(^a)</td>
</tr>
<tr>
<td>((N=17))</td>
<td>(31.4–38.0)</td>
<td>(47.8–61.5)</td>
<td>(40.6–50.9)</td>
<td>(7.4–9.3)</td>
<td>(11.4–24.8)</td>
<td>(8.5–21.6)</td>
<td>(0.90–3.00)</td>
<td>(7.1–11.2)</td>
<td>(3.3–4.3)</td>
<td>(4.2–6.5)</td>
<td>(0.55–1.18)</td>
</tr>
<tr>
<td>No-tail</td>
<td>28.7±2.6(^b)</td>
<td>28.7±2.6(^b)</td>
<td>28.7±2.6(^c)</td>
<td>7.6±0.4</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>8.6±0.9</td>
<td>3.8±0.4</td>
<td>4.7±0.7</td>
<td>0.60±0.16(^b)</td>
</tr>
<tr>
<td>((N=15))</td>
<td>(25.0–33.3)</td>
<td>(25.0–33.3)</td>
<td>(25.0–33.3)</td>
<td>(7.1–8.4)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>(7.4–10.2)</td>
<td>(2.9–4.6)</td>
<td>(3.8–5.9)</td>
<td>(0.41–0.89)</td>
</tr>
</tbody>
</table>

Values are as means ± s.d., ranges are given in parentheses.

Values with different superscript letters are significantly different among fish type (\(P<0.05\)).
the range of sizes tested within a fish type, \( U_{\text{crit}} \) was not affected by body length: slopes of regression lines relating \( U_{\text{crit}} \) to \( SL \) were not significantly different from zero (for wild-type fish, \( r^2 = 0.030, P = 0.51 \); for long-finned fish, \( r^2 = 0.037, P = 0.40 \); for no-tail fish, \( r^2 = 0.020, P = 0.61 \)).

Swimming behaviour

In all types of fish, \( f_T \) was highest at the slowest speeds and decreased to zero by \( U_{\text{crit}} \) (Fig. 4). The relationship between \( f_T \) and swimming speed is best described linearly as a function of log 10 \( U \) (Table 2). The slopes for wild-type and long-finned were not significantly different (\( F_{1,923} = 3.48, P = 0.062 \)), but ANCOVA revealed a significant difference between the intercepts (\( F_{1,924} = 815.01, P < 0.001 \)). The slopes were significantly different between wild-type and no-tail fish and between long-finned and no-tail fish (\( F_{1,752} = 12.90, P < 0.001 \) and \( F_{1,401} = 12.58, P < 0.001 \), respectively). At 4 cm s\(^{-1} \), the turning frequency of wild-type fish was 10.1±6.5 min\(^{-1} \) (\( N = 63 \)), that of long-finned fish was 8.6±4.7 min\(^{-1} \) (\( N = 51 \)) and that of no-tail fish was 4.7±2.8 min\(^{-1} \) (\( N = 45 \)). \( f_T \) decreased below 1 min\(^{-1} \) at a water velocity of 32 cm s\(^{-1} \) (56 % of mean \( U_{\text{crit}} \)) in wild-type fish; in long-finned fish this decrease occurred at a water velocity of 28 cm s\(^{-1} \) (64 % of \( U_{\text{crit}} \)), and in no-tail fish at water velocity of 12 cm s\(^{-1} \) (61 % of \( U_{\text{crit}} \)). At any given swimming velocity, \( f_T \) of wild-type fish was higher than that of long-finned fish, and both were higher than that of no-tail fish. At \( U_{\text{crit}} \), no fish turned at all. These differences were not always significant, probably because of the high variability of this measurement and the relatively small sample sizes.

Circadian activity rates

The three zebrafish types showed distinct diurnal activity patterns with two activity peaks during the light period, at 09:00 h and at 15:00 h, and reduced activity at 12:00 h (Fig. 5). However, wild-type fish were more active than long-finned fish (significantly so at 12:00–14:00 h and 17:00–19:00 h) except at 08:00 h, but no significant differences were found at other times of day. During the night, wild-type and long-finned fish were similarly active, except at 02:00–03:00 h, when the wild-type were significantly more active, and at 05:00–06:00 h when long-finned fish were significantly more active. No-tail fish were always significantly less active than the other two types. Overall, for the 24 h period, the activity of long-finned fish was 88 % of that of the wild-type fish and the activity of no-tail fish was 46 % of that of wild-type fish.

Discussion

Fish comparability

Zebrafish are well adapted for high swimming performance. The larger fins of the long-tailed fish apparently reduced their \( U_{\text{crit}} \) by approximately 22 % relative to those of the wild-type, and caudal fin loss of the no-tail fish apparently reduced their

<table>
<thead>
<tr>
<th>Fish type</th>
<th>( N )</th>
<th>Regression equation</th>
<th>( r^2 )</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wild-type</td>
<td>819</td>
<td>( f_T = 17.69(\pm 0.65) - 10.48(\pm 0.45) \log_{10} U )</td>
<td>0.451</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Long-finned</td>
<td>631</td>
<td>( f_T = 14.32(\pm 0.64) - 9.04(\pm 0.48) \log_{10} U )</td>
<td>0.550</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>No-tail</td>
<td>419</td>
<td>( f_T = 7.63(\pm 0.55) - 5.81(\pm 0.50) \log_{10} U )</td>
<td>0.539</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

\( \pm \) S.D. is given in parentheses for the regression variables.

\( f_T \), turns per minute; \( U \), swimming speed.
Swimming and activity in zebrafish

Uₐₑᵣ by approximately 65%. Differences in turning behaviour and routine activity rates followed a similar pattern.

Wild-type and long-finned zebrafish have the same body sizes (excluding fins) and differ only in their fin measurements, so the differences between them are probably primarily due to different fin size. No-tail zebrafish were significantly smaller than the others in their body length and mass, but the differences were small and theoretically, because of their smaller body size, they might be expected to swim relatively faster (Goolish, 1991). Thus, the differences between no-tail fish and the other types are probably due to the absence of the caudal fin. It is also possible that the genetic differences that produce these different strains may have multiple pleiotropic effects on other aspects of the fish such as those measured here. However, since the fish appear to show similar behaviour, life span, reproductive success, etc., it is unlikely that this could explain the present results.

Fish performance

Although comparative data are few, the Uₐₑᵣ of wild-type zebrafish, expressed as body-length-specific relative swimming speed (15.5 SL s⁻¹), is the fastest reported to data for any small fish. Only four published studies report Uₐₑᵣ for fish with a small (less than 6 cm SL) adult body length (Table 3). Uₐₑᵣ of zebrafish is within the range of maximum steady swimming speeds of juveniles of some larger fishes (Videler and Wardle, 1991). It is also within the range of the theoretical predictions made for fish of similar body size (Wardle, 1975, 1977; Weihs, 1989; Goolish, 1991).

Zebrafish are indeed well adapted for fast, sustained swimming. Fuiman and Webb (1988) showed that mean and maximum routine swimming speeds of adult wild-type zebrafish measured in aquaria were 4.2 SL s⁻¹ and 6.5 SL s⁻¹, respectively. Plaut and Gordon (1994) showed that wild-type zebrafish can swim for more than 2 h at velocities of 40 cm s⁻¹ (approximately 13 SL s⁻¹) without fatigue and with no significant elevation in body lactate concentration.

The outstanding swimming capability of zebrafish is probably an adaptation for living in living in rapid streams in southeast Asia (Laale, 1977), where they have to resist the current to avoid being swept away from their habitat. In such habitats, the need for high swimming capacity is a substantial evolutionary force, especially for small fishes. To resist a given current speed, a small fish must swim relatively (measured as SLs⁻¹) much faster than a larger fish. Moreover, assuming that predatory fish are significantly larger than their prey, to avoid predation, the prey must swim or manoeuvre much faster and better than the predator. To determine whether this swimming capability characterizes only zebrafish or is a general trait of species with small body size as adults, studies should be conducted on additional similar species.

Uₐₑᵣ of long-finned zebrafish was 22% lower than that of wild-type zebrafish. One of several possible reasons for this difference may be the significantly lower aspect ratio of the caudal fin (Table 1), which would reduce the lift coefficient and, hence, any contribution of lift to thrust (Weihs, 1989; Videler, 1993). Second, observations during the swimming experiments showed that the caudal fins of long-finned zebrafish often had more than one wavelength of bending, compared with less than half a wavelength in wild-type zebrafish. This observation suggests that long caudal fins are more flexible than the shorter wild-type caudal fins. The magnitude of the forces transmitted by the fins depends on their relative stiffness (Simons, 1970). Fauci (1996) stated that the higher the stiffness constant, the less impact the drag forces have. Thus, long-finned zebrafish are likely to be more affected by drag forces and therefore to be less efficient swimmers. Third, long fins have larger wetted surface areas. This may also increase the effects of drag forces acting on the fish and, thus, decrease its swimming capability, assuming that, as a result of a lack of stiffness in the fin, the added area does not contribute significantly to thrust production. A similar effect was found in fishes tagged with anchor tags (Clancy, 1963; McCleave and...
The $U_{\text{crit}}$ of no-tail zebrafish was approximately 35% of that of the wild-type. As discussed above, the fins are the main transmitters of momentum from the muscles to the water. Without caudal fins, the active area that pushes the water is substantially reduced, and the obvious result is a reduction in swimming capability. From the present data, approximately 65% of the power transmitted to the water in wild-type zebrafish is derived from the tail, although we cannot rule out a role of possible pleiotropic effects of genetic variation.

Swimming behaviour

At low water velocities, zebrafish tended to swim both upstream and downstream in the swimming chamber. At higher speeds, they stopped turning downstream and swam continuously upstream (Fig. 4). This pattern of behaviour is similar to patterns observed previously (Plaut and Gordon, 1994). The ecological relevance of $U_{\text{crit}}$ measurements can be questioned because the procedure is far from representing the natural conditions a fish may encounter. However, as noted by Plaut and Gordon (1994), turning frequencies are of ecological relevance. Zebrafish tend to swim continuously in open water (Fuiman and Webb, 1988), and this is also the case in the water tunnel. However, they can swim and turn against the water current only until the current speed equals their natural routine maximum swimming speed. Fuiman and Webb (1988) measured this as 6.5 $\text{SL s}^{-1}$, similar to the current velocity at which the wild-type fish turned less than 1 min$^{-1}$ (7.2 $\text{SL s}^{-1}$). At this speed, exceeding their maximum routine swimming speed, the fish do not allow themselves to drift downstream and therefore do not turn. Therefore, this speed can be used as an estimate of the maximum routine swimming speed.

$U_{\text{crit}}$, control swimming speed; $\text{SL}$, standard length; $\text{BL}$, body length.

<table>
<thead>
<tr>
<th>Species</th>
<th>Size (SL unless marked differently)</th>
<th>$U_{\text{crit}}$ (cm$^{-1}$)</th>
<th>$U_{\text{crit}}$ (BL s$^{-1}$)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zebrafish (wild-type) <em>Danio rerio</em></td>
<td>28</td>
<td>36±2</td>
<td>56.0±4.8</td>
<td>15.5</td>
</tr>
<tr>
<td>Zebrafish (long-finned) <em>Danio rerio</em></td>
<td>28</td>
<td>35±2</td>
<td>43.7±6.8</td>
<td>12.5</td>
</tr>
<tr>
<td>Zebrafish (no-tail) <em>Danio rerio</em></td>
<td>28</td>
<td>29±3</td>
<td>19.8±4.7</td>
<td>6.9</td>
</tr>
<tr>
<td>Guppy <em>Poecilia reticulata</em></td>
<td>27–29</td>
<td>17.5±0.5</td>
<td>23.7±1.0</td>
<td>13.7</td>
</tr>
<tr>
<td>Delta smelt <em>Hypomesus transpacificus</em></td>
<td>21</td>
<td>35–53</td>
<td>28±5</td>
<td>6.6±1.6</td>
</tr>
</tbody>
</table>

*Table 3. Comparison of the critical swimming speeds of small fishes*

Stred, 1975; Lewis and Muntz, 1984; Mellas and Hynes, 1985; Serafy et al., 1995.

The $U_{\text{crit}}$ of no-tail zebrafish was approximately 35% of that of the wild-type. As discussed above, the fins are the main transmitters of momentum from the muscles to the water. Without caudal fins, the active area that pushes the water is substantially reduced, and the obvious result is a reduction in swimming capability. From the present data, approximately 65% of the power transmitted to the water in wild-type zebrafish is derived from the tail, although we cannot rule out a role of possible pleiotropic effects of genetic variation.
represent 64% of $U_{\text{crit}}$ for long-finned and 61% for no-tail zebrafish, similar to the value of 56% for wild-type zebrafish. These relationships may also indicate the effects of fin size on the maximum routine swimming speeds of the different types of zebrafish.

**Spontaneous activity**

Wild-type zebrafish showed a distinct diurnal activity pattern apparently with two peaks, similar to the results reported for zebrafish by Baganz et al. (1998). Long-finned zebrafish were usually less active (89% of wild-type) and no-tail zebrafish were significantly less active than the two other types (46% of wild-type). These results again demonstrate the behavioural effects of the different fin sizes and shapes. The trends are similar to those found for $U_{\text{crit}}$ and $f_{\text{r}}$ discussed above, and also likely to be of ecological relevance.

**General remarks**

Wild-type zebrafish are well adapted for fast sustained swimming. Longer fins reduce swimming capabilities, and the total absence of the caudal fin reduces them further. Similar effects, at similar levels, were shown on swimming behaviour and on routine activity levels. The levels at which longer fins affect the variables measured in this study also permit an estimation of some ecological and behavioural costs for fish with large fins. Many fishes that swim in the subcarangiform mode possess enlarged caudal fins (e.g. male guppies *Poecilia reticulata*, male Siamese fighting fish *Betta* spp., several killifish *Aphyosemion* spp., pearl fish *Cynolebias* spp., etc.), which serve mainly for mate attraction (Nicoletto, 1991). From the results presented here, one may estimate the cost of this fin ornamentation. A reduction of swimming capabilities, resulting in a reduction in activity rates, may decrease the ability to gather food and make the fish more vulnerable to predation. Such costs corresponding with increased chances of sexual selection may exemplify the handicap principle (Zahavi, 1975, 1977; Maynard Smith, 1985).

The author would like to thank Ms M. Shacham and Ms P. Shalev for technical assistance and Professor M. S. Gordon, Professor D. Weih, Dr A. S. Kolok and anonymous referees for their comments on the manuscript. This study was supported by the Israeli Ministry of Science, Program for New Immigrant Scientists.

**References**


