Intra-school positional preference and reduced tail beat frequency in trailing positions in schooling roach under experimental conditions

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Using three different swimming velocities and a school size of eight roach *Rutilus rutilus*, individual intra-school position and tail beat frequency were examined in a flume tank. Tail beat frequency was determined in defined leading and trailing positions. Individual roach showed consistent intra-school positional preferences which implied a sustained positional pattern where certain individuals took up front positions whereas other individuals swam in the rear part of the school. The positional preferences could not be attributed to inter-individual differences of the eight roach in terms of total length, mass or condition factor. At the tested swimming velocities of 2, 3 and $4 L_T s^{-1}$, roach in trailing positions swam with tail beat frequencies reduced by 7·3, 11·9 and 11·6%, respectively, compared to roach in leading positions. These results suggested that roach situated in trailing positions experienced energetic savings due to hydrodynamic interactions at a wide range of swimming velocities. This may be important during migrations or when a school of roach is holding its position against the current in a lotic habitat. The observed sustained positional pattern combined with a hydrodynamic advantage in trailing positions would indicate that these energetic savings might not be evenly shared among schoolmates of roach. A positive correlation between swimming velocity and stride length was found. The present study, however, does not support any conclusions concerning these findings.

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Key words: energy saving; hydrodynamics; intra-school positioning; *Rutilus rutilus*; stride length; vortex street.

INTRODUCTION

The costs and benefits of group living are not necessarily shared equally between all members of a group, where each member is selected to maximize its own fitness (Krebs & Davies, 1993). Theoretical work indicates that the position of an individual relative to that of others may have an important influence on fitness (Hamilton, 1971). In support of this, mortality risk and foraging efficiency have been demonstrated to vary on different spatial positions

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in fish schools (Krause, 1994). More recent investigations have emphasized the role of the spatial distribution of the individuals within schools in terms of foraging efficiency (DeBlois & Rose, 1996; Krause *et al*., 1998*a*) and mortality risk (Bumann *et al*., 1997; Krause *et al*., 1998*b*). Sustained intra-school positional preferences have been observed in a number of species (Pitcher *et al*., 1982, 1985; Krause, 1993*a*) including roach *Rutilus rutilus* (L.) (Krause *et al*., 1992, 1998*a*; Krause, 1993*b*). The potential for an unequal distribution of costs and benefits introduces an element of conflict, where individuals on one hand benefit from each other's presence in the group but on the other compete for obtaining the largest share of the benefits (Krause, 1994).

Activity costs often form a significant component of fish bioenergetics budgets (Koch & Wieser, 1983; Boisclair & Leggett, 1989; Boisclair & Sirois, 1993). Reduction in cost of swimming resulting from hydrodynamic interactions has been suggested several times as a possible advantage to schooling (Breder, 1965; Belyayev & Zuyev, 1969; Zuyev & Belyayev, 1970; Weihs, 1973, 1975; Partridge *et al*., 1983; Weihs & Webb, 1983; Abrahams & Colgan, 1985, 1987; Pitcher *et al*., 1985; Ross *et al*., 1992), but the issue remains debatable (Pitcher & Parrish, 1993). A more recent study has indicated a hydrodynamic advantage (van der Lingen, 1995) and Herskin & Steffensen (1998) provided evidence that hydrodynamic interactions may comprise an important energy-saving mechanism for fishes cruising in schools.

Cruising undulatory swimmers shed two vortices per completed tail beat forming a reverse Kármán vortex street where two consecutive vortices in the direction of motion are separated by half a stride length (*i.e.* the distance covered per tail beat) (Müller *et al*., 1997). Weihs (1973, 1975) predicted that schooling fishes should swim in a specific pattern of a rhombus with optimum bearings and distances between individuals to benefit from hydrodynamic interactions. Using digital particle image velocimetry, Wolfgang *et al*. (1999) measured the velocity field around and in the wake of a swimming giant danio *Danio malabaricus* (Jerdon). Within a laser-illuminated plane extending roughly one fish length downstream, they found average wake velocities in the swimming direction up to 15% of the fish swimming velocity. In a laboratory study on schooling horse mackerel *Trachurus mediterraneus* (Steindachner), Zuyev & Belyayev (1970) showed reduced tail beat frequencies for fish in trailing positions compared to fish in leading positions. Similarly, investigations by Fields (1990) revealed reduced tail beat frequencies of schooling Pacific mackerel *Scomber japonicus* Houttuyn compared to solitarily swimming individuals. Numerous studies have shown a positive correlation between swimming velocity and oxygen consumption (Brett, 1964, 1965; Smit, 1965) and between swimming velocity and tail beat frequency (Bainbridge, 1958; Hunter & Zweifel, 1971). Using schooling individuals of sea bass *Dicentrarchus labrax* (L.), Herskin & Steffensen (1998) determined that trailing individuals swam with reduced tail beat frequencies compared to leading individuals. By employing a correlation between tail beat frequency and oxygen consumption obtained from solitary individuals, they demonstrated that the reduced tail beat frequencies in the trailing positions were equivalent to a 9–23% reduction in oxygen consumption compared to leading individuals.

The observed sustained intra-school positional preferences combined with a reduced tail beat frequency in trailing positions suggest that swimming costs

may not be evenly shared among schoolmates. The aims of the present experiment were firstly to examine if individual school members of roach exhibit consistent intra-school positional preferences, and secondly to determine tail beat frequencies in leading and trailing positions. Individual intra-school position and tail beat frequency were measured in a flume tank using three different swimming velocities and a school size of eight roach. The positioning behaviour of schooling individuals was examined in relation to length, mass and condition factor (Tytler, 1969).

MATERIALS AND METHODS

EXPERIMENTAL ANIMALS

In total 200 schooling (Pitcher & Parrish, 1993) roach were captured with an umbrella net (a 1×1 m net stretched apart by two flexible metal rods) in April 2000 from Mølleåen ($55°48'$ N; $12°22'$ E), a slow flowing stream in northern Zealand, Denmark. Roach is a facultative schooling species (Haberlehner, 1988) that uses the subcarangiform swimming mode. In the laboratory the roach were kept in oxygen-saturated tap water in a circular 200 l holding tank. A circular current ranging from 0 to 13 cm s^{-1} was established by directing water from two mechanical filters along the wall of the holding tank. The holding tank was cleaned and water was replaced every second day. The roach were fed on frozen chironomid larvae to satiation in the afternoon on weekdays. The light regime was 12L : 12D and the water temperature was $15°$ C, range $\pm 1°$ C. From the 200 captured roach, 80 [mean $\pm$ S.D. total length (L_T) $= 7 \cdot 4 \pm 1 \cdot 8$ cm, mass (M) $= 3 \cdot 0 \pm 1 \cdot 1$ g and condition factor (K, derived from $K = 100 M L_T^{-3}$) $= 0 \cdot 73 \pm 0 \cdot 09$] were sampled and used in the experiment.

FLUME TANK AND CAMERA SET UP

Roach were tested in a recirculating flume tank containing a working section 47 cm long, 15 cm wide and 14·5 cm deep. The floor was covered with reflective material (3M, Scotchlite[TM] 6060) to enhance the image contrast. Additionally, the floor was marked with a grid of 5 cm squares to be used as reference points. An impeller, situated downstream of the working section, was driven by an external electric motor and generated the recirculating flow. Baffles, flow-straighteners and deflectors in the recirculation loop prevented large scale eddies. A honeycomb (7·5 cm long, 7 mm cell diameter) upstream of the working section promoted a rectilinear flow and a uniform velocity profile. In the downstream direction a plastic grid bounded the working section (Fig. 1). A mechanical flow meter (Höntzsch digital pocket format anemometer fitted with a W30 probe) was used to calibrate water velocity to voltage output from the external motor controller. Since floor and walls affect current velocity and therefore steady swimming kinematics and efficiency (Webb, 1993), a cone (20 mm diameter) was inserted upstream of the honeycomb. This rendered a 5% reduction of the water velocity in the centre of the working section. This reduction allowed a more homogenous distribution of water velocities across the working section and therefore minimized bias on roach positioning related to choice of current velocity. Continuous aeration of water from the flume tank was conducted in a separate tank. A thermostat kept water temperature at $15°$ C range $\pm 1°$ C. The roach in the working section were recorded dorso-ventrally with a SONY CCD video camera. A frame counter and time code were overlaid on the videotape by a HORITA time code generator. Time resolution was 0·02 s.

EXPERIMENTAL PROCEDURE

Eight size-matched roach were sampled from the holding tank. Each roach was tagged by gluing (3M, Vetbond[TM] Tissue Adhesive) a 5 mm diameter piece of reflective material (3M, Scotchlite[TM] reflective sheeting) onto the dorsal side of the head, and L_T was
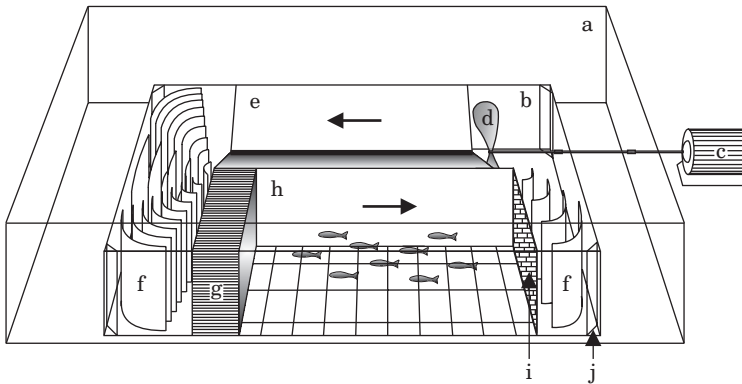
FIG. 1. The flume tank. a, ambient tank; b, flume tank; c, electric motor; d, impeller; e, baffles; f, deflectors; g, flow straightener (honeycomb); h, working section; i, bounding grid; j, fairing bars. Immediately upstream from the flow straightener (g) a cone (20 mm diameter), not visible in the figure, was placed centrally providing a more homogenous distribution of water velocities across the working section. ⟶, direction of the recirculating water flow downstream of the impeller and in the working section.

measured to the nearest mm. The tags had different colours and patterns and made each roach individually recognizable. Tagging lasted 20–30 s per individual. The eight roach were then introduced simultaneously to the working section to avoid the confounding influence of introduction order (Krause *et al.*, 1998*a*). Mean body length, L_{TM}, of the eight roach in the school was calculated and used as unit for setting of swimming velocity in the working section. Following a 2 h acclimation period (Herskin & Steffensen, 1998) with swimming velocity set to $1 L_{TM} s^{-1}$, the swimming velocity was increased incrementally to 2, 3 and $4 L_{TM} s^{-1}$. These swimming velocities were chosen because free ranging roach in lotic habitats have been observed to swim at similar velocities for extended time periods (Krause, 1993*b*), and because the relative influence of pectoral fins and a potential modulation of tail amplitude are minimized at these swimming velocities (Videler, 1993). The school was 'swum' for 40 min at each of the three different swimming velocities. Video recording was made continuously. The first 10 min at each swimming velocity was considered as an acclimation period (Herskin & Steffensen, 1998) and was not used in the post experimental analysis. When swimming velocity was increased it was done gradually during 30–60 s.

Following the experiment the eight roach were weighed (to 0·01 g). Corrections for solid blocking effects were not necessary since the eight roach in the working section had cross sectional areas that were <10% of the cross sectional area of the working section (Brett, 1964). This procedure was applied to 10 schools of eight roach using different roach in each school.

TRACKING AND RANKING

To obtain a two-dimensional horizontal set of co-ordinates of individual school members, stills were made from the video recordings. One still was made every third minute giving 10 stills per swimming velocity for each school. Each still was 202 pixels wide and 680 pixels long and covered the working section. The co-ordinate of the snout (Koltes, 1984) of each roach was recorded manually from every still. '*x*'-values defined the position in the flow direction while '*y*'-values defined the position perpendicular to the flow direction. From these co-ordinates, the mean longitudinal rank in line (ranked *x*-value) of each roach in each school and at each swimming velocity was calculated. All co-ordinates were subsequently transformed into units of cm. Roach in physical contact with the bounding grid were not included in the recordings.

TAIL BEAT FREQUENCY

One tail beat was defined as a complete oscillation of the tail (Hunter & Zweifel, 1971). The tail beat frequency was determined by analysing video recordings frame by frame (25 frames s^{-1}) for individuals in leading and trailing positions (Fig. 2). The present study defined a trailing roach as an individual swimming $0.5–2 L_{TM}$ downstream of the tail of an upstream individual (Herskin & Steffensen, 1998) within a horizontal bearing of 30°, which is in agreement with previously observed inter-individual distances (van Olst & Hunter, 1970).

Only steadily swimming roach, moving $<0.1 L_{TM}$ in the upstream or downstream direction (Herskin & Steffensen, 1998) and performing a minimum of five consecutive tail beats were used for determination of tail beat frequency. To minimize bias caused by wall effects, only roach swimming at least 2 cm from the walls (Fish *et al.*, 1991) were used for determination of tail beat frequency. Floor and ceiling effects were assumed to be equally shared among schooling individuals because the schools were observed to be predominantly two-dimensional with school members swimming in a single horizontal layer. Similar observations have been reported previously (Krause *et al.*, 1992; Bumann *et al.*, 1997; Herskin & Steffensen, 1998). Tail beat frequency was determined at 10 occasions for roach in a leading position and at 10 occasions for roach in a trailing position. This was accomplished for each school at each swimming velocity. The mean tail beat frequency in each position (trailing and leading) at each swimming velocity in each school was subsequently used as an endpoint value. The roach shifted spatial position in the flume continuously, which made it impossible to determine the tail beat frequency of every individual. The same individual was not included in the determination of mean tail beat frequency more than five times at each swimming velocity and no more than four times at either leading or trailing positions. This procedure secured that each endpoint value included measures taken from at least three different roach. In order to avoid pseudo-replication, the following measures as endpoints were used in the analyses. The mean tail beat frequency of each roach observed in each school and at each velocity was calculated first. This secured that individual roach entered the final analyses with only one value. These individual means were subsequently used for calculating the endpoint values, which were the overall mean tail beat frequencies for leading and trailing positions at each swimming velocity in each school. Calculation of a mean
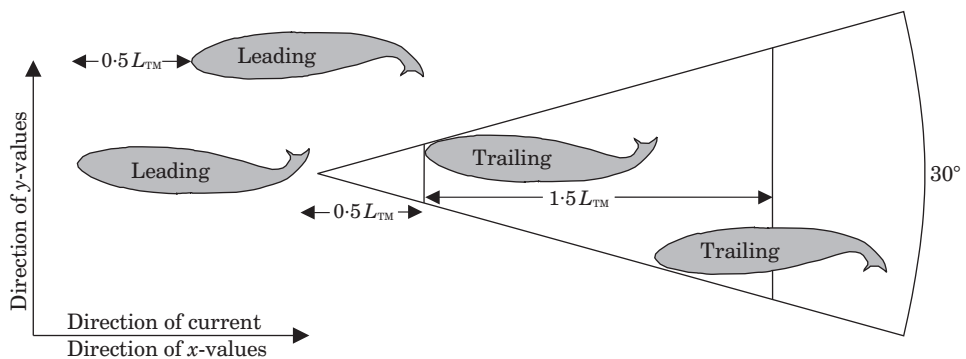

FIG. 2. Dorso-ventral view of individuals in the defined leading and trailing positions used in the present study. The trailing position was defined as the position within $0.5–2 L_{TM}$ from the tail of an upstream individual within a horizontal bearing of 30°. The head and at least 50% of the body of the trailing individual were situated within the bearing during tail beat determination. Roach in the leading position were defined as the foremost individual or an individual situated no more than $0.5 L_{TM}$, measured from snout to snout, downstream the foremost individual without being in physical contact with the defined bearing of any other individual.

stride length end point value (*i.e.* L_{TM} tail beat^{-1}) was done in the same way as the calculation of the mean tail beat frequency endpoint value.

RESULTS

Differences in individual L_T, M and K of the eight school members within each of the 10 schools varied between 7 and 14%, between 17 and 41% and between 12 and 38%, respectively. The roach did not perform burst and coast swimming (Videler, 1993), but performed steady swimming with continuous tail beats at the three investigated swimming velocities. In all trials it was evident that the roach were distributed throughout the length of the working section without preference for near-wall areas.

RANK

Spearman rank correlation showed a highly significant correlation between the individual mean rank number taken by a roach at $2 L_{TM} s^{-1}$ with that at 3 and $4 L_{TM} s^{-1}$ ($2 L_{TM} s^{-1}$ *v.* $3 L_{TM} s^{-1}$: $n = 76$, $r = 0.51$, $P < 0.001$; $2 L_{TM} s^{-1}$ *v.* $4 L_{TM} s^{-1}$: $n = 74$, $r = 0.39$, $P < 0.001$) (Fig. 3). The number of individual mean ranks at each comparison amounted to only 76 and 74 and not 80 (10 schools of 8 roach amount to 80 individual mean ranks per swimming velocity). This discrepancy is caused by the fact that at 3 and $4 L_{TM} s^{-1}$, four and six single individuals were not ranked due to permanent physical contact with the bounding grid.

Juvenile roach may locate particular areas with reduced flow in a laboratory flume (Garner, 1999). In order to test if the observed correlations between individual mean ranks at the different swimming velocities were not a by-product of preference for particular places in the working section, the standard deviation
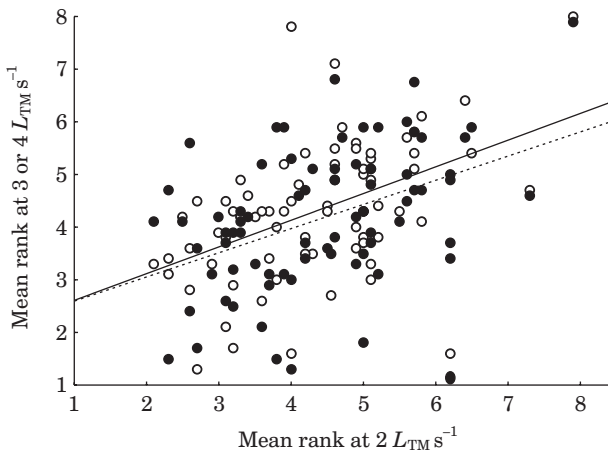

FIG. 3. Relationship between individual mean rank at 2 and $3 L_{TM} s^{-1}$ (○) and between 2 and $4 L_{TM} s^{-1}$ (●). The lines were fitted by: $3 L_{TM} s^{-1} = 2.10 + 0.51(2 L_{TM} s^{-1})$ (—); $4 L_{TM} s^{-1} = 2.17 + 0.45(2 L_{TM} s^{-1})$ (- - -).

s.d. of individual *x*-positions at each swimming velocity was analysed. Thus, a small s.d. of an individual's *x*-positions would reflect that a roach tended to stay at the same *x*-position, whereas a large s.d. would indicate the opposite. At each swimming velocity, the mean and s.d. of the 10 *x*-positions were calculated for each roach. Using only valid observations, this gave 74 individual s.d. at each swimming velocity ranging between s.d. $= 6.4$–13.2 cm. To test for effects of swimming velocity, individual s.d. were subjected to a repeated measure ANOVA using swimming velocity as repeated measure and school as a main factor.

The results revealed a significant effect of school ($F_{9,64} = 2.2$, $P = 0.032$) and swimming velocity ($F_{2,128} = 4.07$, $P < 0.019$) whereas the interaction between school and swimming velocity was not significant ($P = 0.106$). Additionally, to test if s.d. were similar throughout the tank and not depending on proximity to the honeycomb, an ANCOVA was conducted using individual s.d. as the dependent variable, school as a main factor and individual mean *x*-positions as the covariate. This analysis was carried out separately for each swimming velocity. The effect of the covariate was insignificant in all the tests ($P > 0.05$, all swimming velocities). Least square mean (mean of school means) s.d. of individual *x*-positions are pictured in relation to swimming velocity in Fig. 4. Compared to the size of the working section, individual s.d. of 8–10 cm during 30 min indicate that the roach did not stay in particular places within the working section but moved back and forth actively. The vast majority of this activity was characterized by roach moving upstream and downstream while swimming against the current, although roach turned around and swam downstream occasionally.

Steady swimming performance is positively correlated with body length (Beamish, 1978), which could result in size assortment within schools. In the present study, however, no significant correlation was found between individual mean rank number and L_T, M or K ($P \gg 0.05$ at all swimming velocities).
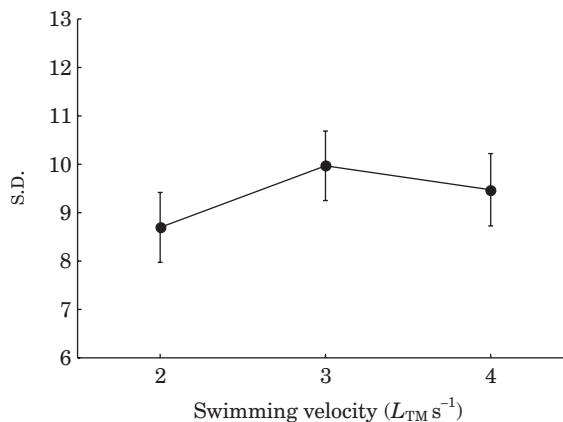

FIG. 4. Least square mean (mean of school means) $\pm 95\%$ CL s.d. of individual *x*-positions in relation to swimming velocity.

TAIL BEAT FREQUENCY

Mean tail beat frequency (leading and trailing position) of the 10 schools at each swimming velocity is shown in Fig. 5. Using swimming velocity as repeated measures and mean tail beat frequency at each position as repeated measures within swimming velocity, ANOVA showed a significant two-way interaction ($F_{2,18} = 4.9$, $P = 0.02$) implying that tail beat frequency in relation to position was not equally affected at each swimming velocity. Fig. 5 shows that this result is caused by a larger difference between mean tail beat frequencies in leading and trailing positions at 3 and $4 L_{TM} s^{-1}$ than at $2 L_{TM} s^{-1}$. *Post-hoc* tests demonstrated significant reductions in mean tail beat frequencies in trailing positions compared to leading positions at each of the velocities investigated. The mean reduction of tail beat frequency in trailing positions was [mean ± S.E. (Bonferroni test)] 0.28 ± 0.08 Hz at $2 L_{TM} s^{-1}$ ($P = 0.028$), 0.56 ± 0.08 Hz at $3 L_{TM} s^{-1}$ ($P < 0.001$), and 0.58 ± 0.08 Hz at $4 L_{TM} s^{-1}$ ($P < 0.001$). Expressed in percentages, these findings are equivalent to reductions of 7·3, 11·9 and 11·6%, respectively. Since tail beat frequency is affected by body length (Bainbridge, 1958; Hunter & Zweifel, 1971; Webb, 1977), it was also tested if the observed reduction in mean tail beat frequency could be attributed to differences between leading and trailing roach in terms of individual L_T, M or K. Using the ANOVA design explained above, however, no significant differences were found (L_T, $P = 0.829$; M, $P = 0.921$; K, $P = 0.957$). These findings infer that roach in the defined trailing position were able to keep the same swimming velocity with a reduced tail beat frequency as roach in the defined leading position.

STRIDE LENGTH

Analysis of mean stride length was done by ANOVA. The design considered swimming velocities as repeated measures and mean stride length in leading and trailing positions as repeated measures within swimming velocity. The mean stride length increased with increasing swimming velocity (ANOVA, $F_{2,18} = 99.63$,
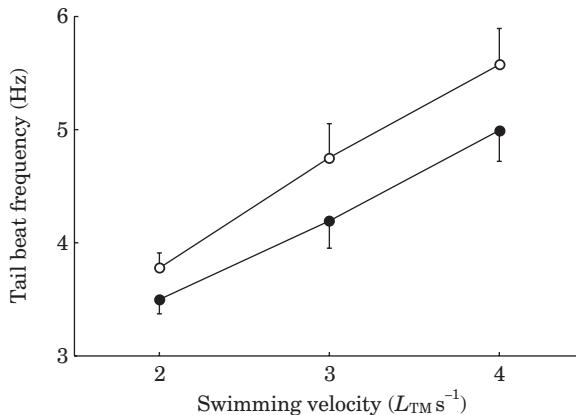

FIG. 5. Least square mean ± 95% CL tail beat frequency (mean of school means) in relation to swimming velocity in leading and trailing positions. ○, leading position; ●, trailing position.

$P < 0.001$) and stride length in trailing positions was significantly longer than in leading positions (ANOVA, $F_{1,9} = 82.57$, $P < 0.001$). The difference in stride length between roach in leading and trailing positions interacted significantly with swimming velocity (ANOVA, $F_{2,18} = 5.03$, $P = 0.018$) (Fig. 6).

DISCUSSION

The present study found highly significant correlations between the mean rank of each roach at $2\,L_{TM}\,s^{-1}$ with that of 3 and $4\,L_{TM}\,s^{-1}$ revealing strong positional preferences. This result suggest that roach exhibit sustained intra-school positional preferences as also demonstrated by Krause *et al.* (1992, 1998*a*) and Krause (1993*b*). These findings infer a sustained positional pattern where certain individuals take up front positions whereas other individuals swim in the rear part of the school.

Fish schools are often size assorted both within and between schools (Krause *et al.*, 2000*a*). The observed variation of individual L_T within each school in the present study (7–14%) is within the length variation in naturally appearing schools (Breder, 1976; Pitcher & Parrish, 1993; Krause & Godin, 1996), which indicates that the composition of the schools used in this experiment did not deviate from schools in the field. Assortment by size within schools may be associated with individual swimming performance and thereby body length (Krause *et al.*, 1998*a*; Ward *et al.*, 2002). Due to the lacking correlation between individual mean rank number and individual body length, the present study suggests that assortment by body length within schools is overridden by other assorting effects in the absence of large body length variation. Positional preferences in roach are strongly influenced by the nutritional states of the individuals (Krause *et al.*, 1992, 2000*b*; Krause, 1993*b*). Krause *et al.* (1998*a*) demonstrated that food-deprived individuals take up leading positions once the school is on the move. In the present study all roach were fed at least once before the swimming trials but different levels of hunger cannot be excluded as a partly explanation to the observed positional preferences because
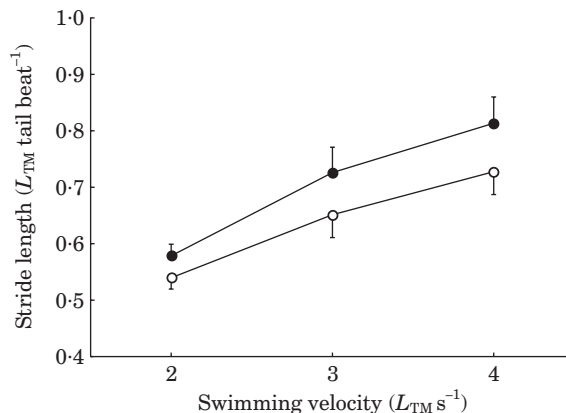

FIG. 6. Least square mean ± 95% CL stride length (mean of school means) in relation to swimming velocity in leading and trailing positions. ○, leading position; ●, trailing position.

of possible interactions between dominant individuals and subordinates (Ruzzante, 1994) in the holding tank. The condition factor was included as an attempt to reveal if any of the experimental roach had been deprived of food prior to capture. In sticklebacks *Gasterosteus aculeatus* L., a few days of food deprivation causes substantial mass losses (Krause *et al.*, 1998*c*) and *K* was therefore likely to be correlated with the hunger level of each roach. During starvation, however, the water content of fish may increase (Elliott, 1994) and this may explain the absence of a relationship between *K* and the observed positional preferences. Additional possible mechanisms behind positional preferences are given by Barber & Huntingford (1996); Krause *et al.* (2000*b*) and Ward *et al.* (2002).

The reduction of tail beat frequency for schooling roach in trailing positions was on average 7·3, 11·9, and 11·6% at the tested swimming velocities (2, 3 and $4 L_{TM} s^{-1}$, respectively). In support of the study by Herskin & Steffensen (1998) on sea bass, these findings strongly suggest that trailing roach may benefit energetically from hydrodynamic interactions at a wide range of swimming velocities. The alternative hypothesis that trailing roach do not benefit energetically from hydrodynamic interactions might be supported by the positive correlation between swimming velocity and stride length (Fig. 6) because it may indicate that the roach were modulating body kinematics other than tail beat frequency when swimming steadily at the different swimming velocities. If that is the case, it may also be the situation at the different spatial school positions. Fishes can sense near-wall hydrodynamic variables and quickly adjust muscular control of swimming motions to optimize efficiency (Anderson *et al.*, 2001) and may modulate kinematics during steady swimming (Videler, 1993). If such a modulation is somehow advantageous in trailing positions compared to leading positions, it could potentially counteract the saved energy indicated by the reduced tail beat frequency. This hypothesis clearly needs to be tested before any firm conclusions can be drawn.

Weihs (1973, 1975) considered three different hydrodynamic interactions, which may result in energy savings to schooling fishes. It is most likely that the reduced tail beat frequency of trailing roach in this study is due to the vortex street shed by one or more upstream individuals. Channelling effect due to the proximity of lateral neighbours cannot be excluded but this effect probably also affected the leading roach. Channelling effect could be investigated by comparing tail beat frequency of a leading fish in a school with that of a solitarily swimming fish.

Based on the findings of a sustained positional pattern and the reduced tail beat frequency for individuals in trailing positions, it is proposed that the swimming costs are not necessarily equally shared among schoolmates of roach. This may be enhanced by the opportunity of trailing individuals to take shortcuts (Bumann & Krause, 1993).

During fish migrations, efficient use of available energy is of great importance (Weihs, 1987). Correspondingly, it has been suggested that American eel *Anguilla rostrata* (LeSueur) use the boundary layer close to the bottom substratum to minimize energy expenditure when performing upstream migration (Barbin & Krueger, 1994). Similarly, Hinch & Rand (2000) speculated that sockeye salmon *Oncorhynchus nerka* (Walbaum) locate and exploit very small reverse-flow vortices created by rough substances or banks during upstream migration.

Roach are capable of exhibiting repeated reproductive homing between lacustrine and fluvial habitats with high precision (L'Abée-Lund & Vøllestad, 1985), and may undertake upstream migrations of several kilometres (Baade & Fredrich, 1998). The current study suggests that trailing individuals may enjoy energetic savings due to hydrodynamic interactions during such migrations, or in situations where a school of roach is holding its position against the current in a lotic habitat as observed by Krause (1993*b*). The observed positional pattern suggest that these energetic savings may not be equally shared among individuals in a school over time.

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