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Published in:
Fish and Fisheries

DOI:
[10.1111/faf.12072](https://doi.org/10.1111/faf.12072)

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Document Version
Publisher's PDF, also known as Version of record

Publication date:
2015

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Hemelrijk, C. K., Reid, D. A. P., Hildenbrandt, H., & Padding, J. T. (2015). The increased efficiency of fish swimming in a school. *Fish and Fisheries*, 16(3), 511-521. <https://doi.org/10.1111/faf.12072>

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The increased efficiency of fish swimming in a school

CK Hemelrijk¹, DAP Reid¹, H Hildenbrandt¹ & JT Padding²

¹Behavioural Ecology and Self-organization, Rijksuniversiteit Groningen, Nijenborgh 7, Groningen 9747 AG, the Netherlands; ²Multiscale Modeling of Multiphase Flows, Eindhoven University of Technology, 5600 MB Eindhoven, the Netherlands

Abstract

There is increasing evidence that fish gain energetic benefits from the hydrodynamic interactions when they swim in a school. The most recent indications of such benefits are a lower tail (or fin) beat at the back of a school and reduced oxygen consumption in schooling fish versus solitary ones. How such advantages may arise is poorly understood. Current hydrodynamic theories concern either fish swimming side by side or in a diamond configuration and they largely ignore effects of viscosity and interactions among wakes and individuals. In reality, however, hydrodynamic effects are complex and fish swim in many configurations. Since these hydrodynamic effects are difficult to study empirically, we investigate them in a computer model by incorporating viscosity and interactions among wakes and with individuals. We compare swimming efficiency of model fish (based on shapes of mullets of 126 mm) travelling solitarily and in schools at several interindividual distances in four different configurations (diamond, rectangular, phalanx and line). We show that these fish always swim more efficiently in a school than alone (except in a dense phalanx). We indicate how this efficiency may emerge from several kinds of interactions between wakes and individuals. As individuals in our simulations are not even intending to exploit the wake, gains in efficiency are obtained more easily than previously thought.

Correspondence:

Charlotte K Hemelrijk
Behavioural Ecology
and Self-organization,
Rijksuniversiteit
Groningen, Nijen-
borgh 7, Groningen
9747 AG, the
Netherlands
Tel.: +31 50
3638084
Fax: +31503633400
E-mail: c.k.hemelrijk@
rug.nl

Received 19 Sep
2013
Accepted 13 Dec
2013

Keywords Collective, computational model, energetic benefit, hydrodynamics, school of fish, wake

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Introduction

There is an increasing number of studies that show energetic benefits for fish swimming in a school versus solitarily (Belyayev and Zuyev 1969; Zuyev and Belyayev 1970; Herskin and Steffensen 1998; Svendsen *et al.* 2003; Johansen *et al.* 2010; Killen *et al.* 2012). Although such benefits may be arising through social causes via a reduction of stress, we here focus merely on benefits from hydrodynamic interactions. A theory is needed that indicates whether hydrodynamic benefits are specific to certain configurations and which ones, or whether energetic benefits are a general outcome of proximity between the fish. Such a theory is important not only scientifically, but also technologically because it may have implications for the optimization of coordinated swarms of robots that are used for surveillance of the environment underwater (Pimenta *et al.* 2008).

Empirical studies show that travelling in a school benefits individuals energetically, as demonstrated by a reduction of oxygen consumption in the school (Herskin and Steffensen 1998; Johansen *et al.* 2010; Killen *et al.* 2012) and of the frequency of beating a tail and fins by individuals at the back of the school (Zuyev and Belyayev 1970; Herskin and Steffensen 1998; Svendsen *et al.* 2003; Johansen *et al.* 2010; Killen *et al.* 2012). The mechanics underlying energetic benefits in a school may be related to the observation of reduced muscle activity when fish are slaloming between the vortices in the von Kàrmàn street or drag wake behind a pillar (Liao *et al.* 2003a,b; Liao 2007). Energetic advantages have been worked out by Weihs in an abstract, mathematical model of a two-dimensional school that is constrained to a single plane with fish that are beating their tail synchronously. He argues that it is beneficial for a third fish to swim midway between two preceding fish that swim next to each other, because at this midway location the two side-by-side thrust wakes of the preceding fish generate a von Kàrmàn vortex street midway between and behind them (Weihs 1973). In an infinite school, therefore, a diamond-like configuration of the positions of individuals is predicted to be energetically optimal. In this configuration, individuals are also expected to profit from their lateral neighbours through a channelling effect or wall effect (Weihs 1973; Webb 1993; Fish 1999; Liao 2007). Conversely, a disadvantageous position for swimming

is supposed to be straight behind another individual, because here the follower finds itself swimming in the reverse von Kàrmàn vortex street from its predecessor, receiving its backwards jet. Despite the elegance of this theory, there is little evidence that the predicted diamond-like configuration occurs in nature (Breder 1976; Partridge and Pitcher 1979) and it is known that the spatial configurations of individuals in schools are manifold and often irregular. Because in Weihs' theory, the fluid dynamics are strongly simplified, his theory may have been too abstract for its aim. Therefore, in the present paper, we pose the question whether including more of the complexity of hydrodynamic interactions in a model of a school may result in different predictions of the energetic advantages of travelling in a school versus solitarily. We perform a more detailed simulation that represents particulars of the fluid hydrodynamics, undulation and fish shape, and we compare the energetic efficiency of fish when swimming solitarily versus in schools of several spatial configurations, not only the diamond-shaped configuration.

To represent the fluid, we use a method that is new for fish schooling. It is a mesoscale particle-based simulation model, called Multi-Particle Collision Dynamics (MPCD). Our choice of method has several reasons. First, it realistically represents hydrodynamics and its particle-based grid-free nature makes it particularly suited to the simulation of multiple organisms that are moving and deforming (Malevanets and Kapral 1998, 1999; Kikuchi *et al.* 2003; Padding and Louis 2006). Second, in our earlier work on fish, we have shown that in case of several static shapes it accurately predicts the lift and drag forces (Reid *et al.* 2009) and in case of fish travelling solitarily, it reproduces quantitatively the reverse von Kàrmàn street behind a solitary, mullet-like fish in terms of the size and position of vortices, their circulation and their frequency of shedding (see Table IV in Reid *et al.* 2012; Müller *et al.* 1997). Third, it has proven to be useful in generating new explanations that can serve as hypotheses to guide empirical studies (Reid *et al.* 2012). We illustrate this with two examples. Firstly, it shows that slip ratio U/V increases with the tailbeat frequency (where U is the speed of the fish and V is the speed of its body wave). This we recently confirmed in a large-scale meta-analysis of empirical data (Reid *et al.* 2012; van Weerden *et al.* 2013). Our model explains the increase in slip ratio with

tail beat frequency as a consequence of the lower variation of instantaneous swimming speed, which may be due to the accompanying smaller deceleration during the reversal of the tail beat, which we attribute to the lower effect of viscosity at a higher Reynolds number (Reid *et al.* 2012; van Weerden *et al.* 2013). Secondly, our model has shown that the Strouhal number St decreases with tail beat frequency ($St = 2Af/U$ with A representing the tail beat amplitude and f the tail beat frequency). This we confirmed in our meta analysis and in results of others (Lauder and Tytell 2005; Borazjani and Sotiropoulos 2008; Rosenblum *et al.* 2011; Reid *et al.* 2012; van Weerden *et al.* 2013). We attribute this decrease to the stronger increase with tail beat frequency of the lateral power P_s than of forward thrust T . This increases the width of the wake more than the longitudinal distance between the vortices, meaning that vortices are closer together at higher tail beat frequency (Reid *et al.* 2012).

In this paper, we follow the theoretical work of Weihs. Therefore, we simulate infinite schools of fish confined to a single two-dimensional plane, with individuals swimming in phase (Weihs 1973). We compare the advantages of swimming solitarily versus in schools with individuals distributed in four configurations: swimming in a line behind each other, in a side-by-side phalanx, a rectangular configuration and a diamond-like configuration, and at several distances to each other. Based on the predictions by Weihs (Weihs 1973), we expect that hydrodynamic advantages are greatest in the diamond-shaped configuration. Advantages are also expected to exist in case of the phalanx and perhaps in case of the rectangular configuration, but not in case of the line.

Materials and methods

Species

We base our simulations on the shape and swimming characteristics of a mullet (*Chelon labrosus*) for several reasons. First, details of the wake of such a mullet (in this case a mullet of 12.6 cm) and the kinematics of its swimming have been reported (Müller *et al.* 1997) and have been shown to be similar to that in our model of a single mullet (Reid *et al.* 2012) regarding swimming speed and wake structure, namely the ring radius and angle of the vortices, their circulation, the

standard deviation of their positioning in the longitudinal and lateral direction and the Strouhal number (Reid *et al.* 2012). Second, when a mullet swims steadily at cruising speed, it relies on the undulation of its body without using its pectoral fins (Videler 1993). Third, a mullet is considered an obligate schooler.

The fluid model

Here, we describe the main aspects of our basic model of undulating fish moving in a fluid of which the hydrodynamics is represented by multi-particle collision dynamics (MPCD). More details are given in the supplementary material and in our earlier description (Reid *et al.* 2012). In MPCD, a fluid is represented by ideal point particles (for parameters see Table 1). After propagating the particles for a fixed time interval according to $\mathbf{x}_i(t + \Delta t) = \mathbf{x}_i(t) + \mathbf{v}_i(t)\Delta t$, the system is partitioned into cells, and in each cell, the velocities

Table 1 Parameters of the fluid and fish in the Multiz-Particle Collision Dynamics simulation. For units of length, mass and time we choose the collision cell size a_0 , particle mass m and collision time step Δt , respectively (second column). Real (SI) values (last column) are obtained by substituting $a_0 = 1.4 \times 10^{-4}$ m, $m = 1.83 \times 10^{-11}$ kg, and $\Delta t = 1.5 \times 10^{-4}$ s.

Property	Sim. value	Value
Particles per cell (avg.) γ	8	–
Rotation angle α	$\pi/2$	–
Dynamic viscosity of fluid μ	$1.15 m/(a_0\Delta t)$	10^{-3} kg m ⁻¹ s ⁻¹
Fish length L	$900 a_0$	0.126 m
Swimming speed, $U_{\text{single fish}}$	$0.188 a_0/\Delta t$	0.176 m s ⁻¹
Number of edges per fish N_E	1024	–
Simulation box length L_{area}^1	$2 L$	$2 L$
Wave number fish deformation k_L	$1.8 \pi/L$	$1.8 \pi L^{-1}$
Tailbeat frequency f	$5.7 \times 10^{-4}/\Delta t$	3.8 s ⁻¹
Tailbeat amplitude A	$90 a_0$	0.0126 m
Reynolds number	1180 in 2D	20.000 in 3D

¹Box length is always $2L$ except for the line formation, where boxes of several lengths depending on the distances between fish, range from 1.5 till 5.5 L .

are changed according to $\mathbf{v}_i = \bar{\mathbf{v}} + \mathbf{\Omega}(\mathbf{v}_i - \bar{\mathbf{v}})$. Here, $\bar{\mathbf{v}}$ is the mean velocity of the particles in the grid cell, and $\mathbf{\Omega}$ is a stochastic rotation matrix that rotates the velocities by either $+\alpha$ or $-\alpha$ (where α is a fixed system parameter), with equal probability. It is the same for all particles within a cell. The rotation procedure can thus be viewed as a coarse-graining of particle collisions over space and time. The procedure conserves mass, momentum, and energy, and quantitatively yields the correct hydrodynamic (Navier–Stokes) behaviour at least up till a Reynolds number of about 1500 (Malevanets and Kapral 1998, 1999; Kikuchi *et al.* 2003; Padding and Louis 2006).

An advantage of the MultiParticle Collision Dynamics method is that analytical expressions are available for several of its transport properties (Kikuchi *et al.* 2003, see supplementary material).

In our MPCD simulation, we have optimized the parameters for swimming at a medium Reynolds number (~ 1180) by making the viscosity as small as possible (Table 1). Note that the particle-based fluid is about 20 times less dense than a real liquid (for computational reasons) and thus more compressible. This leads to a lowered speed of sound (1.3 m s^{-1} for our parameter settings). This will have no consequences for the realism of our model because we made the maximum surface velocity of the fish (at the tip of the tail) less than 20% of the speed of sound in the fluid. Therefore, compressibility effects can be ignored (Lamura *et al.* 2001; Lamura and Gompper 2002; Padding and Louis 2006). We confirmed that all along the length of the fish, the thickness of the boundary layer is much larger than the scale of resolution (the size of the collision cell) of the model.

Note that the flow speed in the fluid of the model emerges entirely from the undulatory motion of the fish.

The fish model

We scale the fish in terms of fractions of its body length L , so that $x = 0$ at the front of the fish and $x = 1$ at its rear and the spine of the straight fish has a y -value of 0 (Fig. 1). Over time the lateral deviation from each point x on the spine of the fish from the central axis is given by

$$y(x, t) = \theta(x) \sin(k_L x - \omega t) \quad (1)$$

Here, $\theta(x)$ represents the amplitude envelope, which varies nonlinearly along the fish body, $k_L = \frac{2\pi}{\lambda}$ is the wave number, which indicates the number of complete sine waves on the body for a wavelength λ , and $\omega = 2\pi f$ is the angular frequency for the tailbeat frequency f . For undulating mullets, the amplitude of the wave is smallest behind the head and increases quadratically towards the tail:

$$\theta(x) = \theta_0 + \theta_1 + \theta_2 x^2 \quad (2)$$

where the coefficients are given by $\theta_0 = 0.02$, $\theta_1 = 0.08$ and $\theta_2 = 0.16$ after empirical data (Videler and Hess 1984).

The interactions between fluid and the undulating bodies are modelled through particle-wall collisions that lead to no-slip boundary conditions (Reid *et al.* 2012). As in our earlier model (Reid *et al.* 2012), we represent the fish as a deformable polygon consisting of line segments (Fig. 1) and parameterize the contours and (fixed) tail beat frequency after empirical data of (Müller *et al.* 1997).

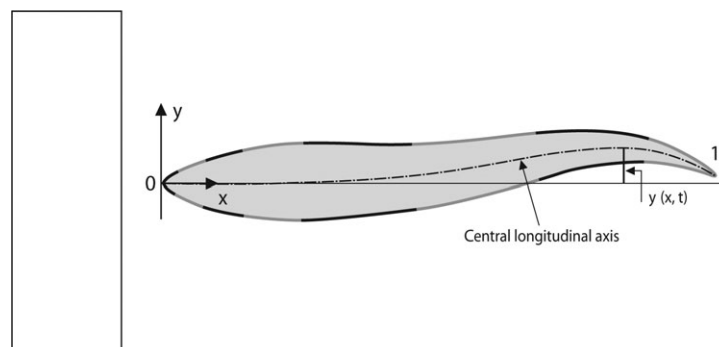


Figure 1 Schematic overview of the deviation from the central axis of the spine of an undulating mullet and of the representation of the mullet as a deformable polygon comprising line segments (indicated in grey and black). Note that line segments on the head are shorter than elsewhere on the body. The area ahead of the fish indicates the area of measuring free flow but is not drawn to scale.

It is important to note that the swimming speed of the fish (both forwards and sideways) emerges entirely from the reaction force of the fluid caused by the prescribed undulatory motion of the fish. It resembles the empirical speed U of a mullet as shown earlier (Reid *et al.* 2012).

Different school configurations and distances among individuals

To simulate an infinite school, we place one or two fish in a simulation area of width W and length L_{area} (Fig. 2a) and apply periodic boundary conditions. We organise the individuals in a diamond configuration, as studied by Weihs, by placing two individuals in diagonally opposite corners of the simulation area (Fig. 2a). In order to generate a rectangular configuration we place a single fish in the centre of the simulation area (Fig. 2b). To obtain schools that are infinite in only one direction, we apply periodic boundaries in one direction and scramble the fluid along the boundaries of the other direction.

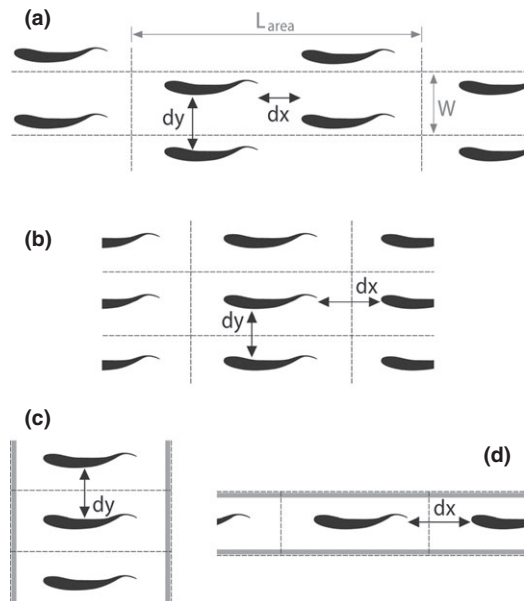


Figure 2 Periodic two-dimensional and one-dimensional arrangements of fish. (a) diamond, (b) rectangular, (c) phalanx and (d) line configuration. The discontinuous outline indicates the simulation area. Scrambled boundaries are marked by a wide band of light grey. L_{area} indicates the length of the simulation area, W indicates its width. Lateral distance between neighbours is given by dy and longitudinal distance by dx .

bling remove the structure and vorticity in the flow by resetting the positions and velocities of fluid particles to those of a homogeneous fluid. This is done by redistributing the current velocities of fluid particles randomly over new positions along the width of the wall. This procedure thus conserves the average velocity and maintains the average momentum flux across the boundary, as described earlier (Reid *et al.* 2012). Scrambling the boundaries ahead and behind a single fish (up to a distance of $150 a_0$ from the wall (Reid *et al.* 2012)) produces a phalanx, whereas scrambling the boundaries lateral of the individual leads to a line configuration (Fig. 2c, d). We study the hydrodynamic consequences of different inter-individual distances in all four configurations. For the line configuration, we study longitudinal distances ranging from 0.5 to 5 fish lengths L . For all other configurations, we keep the longitudinal distance fixed at the average distance for empirical data, namely one fish length L (Belyayev and Zuyev 1969; Zuyev and Belyayev 1970; Herskin and Steffensen 1998; Svendsen *et al.* 2003; Johansen *et al.* 2010; Killen *et al.* 2012) and we study lateral distances ranging from 0.4 fish lengths L (the distance considered optimal by Weihs) to $2L$ which is the maximum possible on our hardware.

Measurements

There is debate about how to measure swimming efficiency (Schultz and Webb 2002). One frequently used measure is the Froude efficiency, a dimensionless number, indicating the quotient of the useful power divided by the total power. If, however, useful power is based on the net thrust (thrust plus drag) during steady swimming, which is zero, then Froude efficiency is zero. Although thrust cannot be measured for steady swimming empirically, it can and has been measured in models, such as Elongated Body Theory and numerical models, like ours, see figure 14 of our earlier paper (Reid *et al.* 2012). The Froude efficiency separates for a steady swimming fish the useful force that the fish exerts forward (thrust) from the wasted power it exerts sideward (due to its sideways tail movement), thus calculating the fraction of the total power spent by the fish which is converted into forwards speed (Tytell and Lauder 2004; Borazjani and Sotiropoulos 2008). We use this modified version of the Froude efficiency η :

$$\eta = \frac{\bar{T}\bar{U}}{\bar{T}\bar{U} + \bar{P}_s} \quad (3)$$

with \bar{T} the average thrust force, \bar{U} the average forward speed (of the fish relative to the fluid) and \bar{P}_s the average lateral power per individual fish all taken over the beat cycle. Note that we need to take the average over the tail beat because even in steady state the forward velocity of the fish oscillates during each tail beat around its average \bar{U} .

We measure the thrust T , sideways power P_s , the forward speed of the fish U and Froude efficiency η after running the model until its steady state. We calculate average data over 20 tail beats.

The most relevant velocity for the estimation of the drag and efficiency is clearly the relative velocity between the fish and the water from the perspective of the fish. We name this speed U , with $U = U_{flow} - U_{fish}$. Here, U_{flow} and U_{fish} are both measured in the global frame, whereby U_{flow} is the speed of the oncoming flow ahead of it (averaged over an area in front of the fish that is sufficiently large for its estimation, as indicated in Fig. 1, and U_{fish} is the speed of the fish.

To measure thrust and sideways power, we decompose the forces on the skin of the fish. The total forward force F at any moment t is calculated by a summation over the line segments of the skin of the fish (Figs 1 and 3):

$$\mathbf{F}(t) = \sum_i \mathbf{F}_i \cdot \mathbf{e}_f = \sum_i (\mathbf{F}_n^i \cdot \mathbf{e}_f + \mathbf{F}_t^i \cdot \mathbf{e}_f) \quad (4)$$

where $\mathbf{F}_n^i = (\mathbf{F}_i \cdot \mathbf{n})\mathbf{n}$ is the force vector perpendicular to the skin at line segment i , $\mathbf{F}_t^i = \mathbf{F}_i - \mathbf{F}_n^i$ is

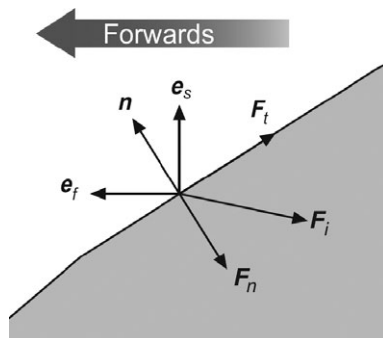


Figure 3 Decomposition of the force \mathbf{F}_i on line segment i of the skin of the fish into pressure (\mathbf{F}_n) and viscous (\mathbf{F}_t) components. The surface normal is indicated as \mathbf{n} and the unit vectors pointing forward and sideways are labelled \mathbf{e}_f and \mathbf{e}_s .

the force vector tangential to the skin and \mathbf{e}_f is a forwards-pointing unit vector. In the summation in Equation (4) the first element thus represents the contribution to the forward force of pressure and the second element that of the viscous force.

To separate the thrust and drag out of this total body force, we decompose it, depending on whether or not the forward force is positive (thrust) or negative (drag) (Borazjani and Sotiropoulos 2008):

$$\begin{aligned} T(t) &= \sum_i [F_n^i \cdot \mathbf{e}_f H(F_n^i \cdot \mathbf{e}_f) + F_t^i \cdot \mathbf{e}_f H(F_t^i \cdot \mathbf{e}_f)] \\ D(t) &= - \sum_i [F_n^i \cdot \mathbf{e}_f H(-F_n^i \cdot \mathbf{e}_f) + F_t^i \cdot \mathbf{e}_f H(-F_t^i \cdot \mathbf{e}_f)] \end{aligned} \quad (5)$$

where H is the Heaviside step function. For each edge, for both the perpendicular (pressure) and tangential (viscous) force on it, we add the forward component of the force to the thrust if it is positive, and to the drag if it is negative. The sum of thrust and drag is the total force $F(t)$ along the \mathbf{e}_f direction:

$$F(t) = T(t) - D(t) \quad (6)$$

That is, a positive $F(t)$ indicates net acceleration and a negative $F(t)$ a net deceleration in the \mathbf{e}_f direction. In steady state, the time average of $F(t)$ over a full swimming cycle is zero.

We calculate per time step Δt the sideways power P_s that the fish exerts:

$$P_s(t) = \sum_i \mathbf{F}_i \cdot \mathbf{e}_s V_{und}^i \quad (7)$$

where \mathbf{e}_s is a unit vector in the sideways direction, and V_{und}^i is the sideways velocity of edge i .

Results

Our model shows that for all configurations of schooling (apart from the phalanx) the Froude efficiency of individual fish (which is the percentage of total power converted in forward speed) is higher than for a solitary individual (Fig. 4a) and so is the speed (Fig. 4b), while thrust and sideways power are lower in all configurations in a group (apart from the phalanx) versus when swimming solitarily (Fig. 4c, d). We explain these findings by starting from the simplest configurations, the line and the phalanx.

The higher Froude efficiency η in the line-shaped school compared with a solitary fish is sur-

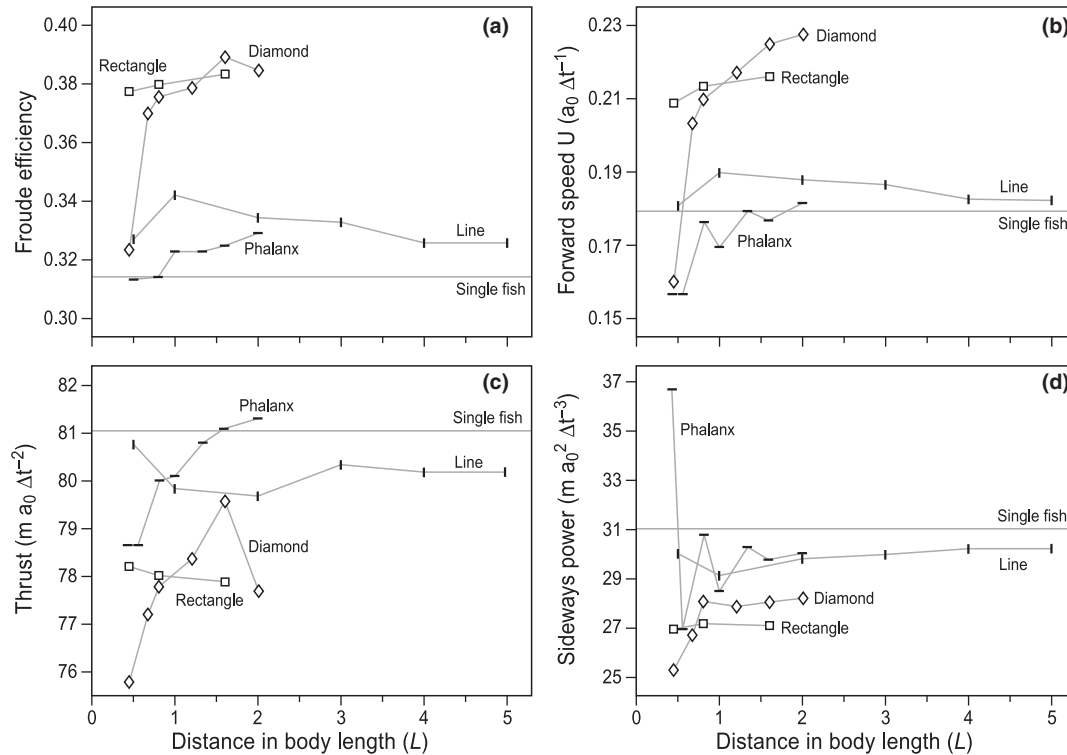


Figure 4 Average Froude efficiency η (a), average speed (b), average thrust (c) and average sideways power (d) of different configurations for different distances (in body length L) among individuals. The phalanx, rectangular and diamond configuration are studied at several lateral distances (dy) and the line formation at several longitudinal distances (dx). Note that the standard error of the mean, (being the standard deviation of the distribution of averages of each tail beat) is essentially zero due to the large sample size (20 tail beats of each 6.500 time steps).

prising, because when fish are swimming behind each other they are expected to slow down since they swim in the thrust wake of the predecessor and receive the jet of the predecessor on their nose. Our model shows that due to the undulation both the head of the follower and the jet of the predecessor move laterally back and forth. Here-with, the jet passes the body sometimes to the right, sometimes to the left. Sometimes the individual captures vortices in a beneficial way (Figs 5b, 6a, Movie S2). When the fluid passes the body at one side, it herewith causes a pressure difference, so that the individual experiences lift to the side where the fluid passes faster. Consequently, the individual will experience a lateral force, and indeed, there is an overall net drift laterally whereby the direction depends on the direction of the first beat (Figure S1).

The Froude efficiency of fish swimming in a (not too dense) phalanx is higher than when swimming alone which is in line with the channelling effect (Weihs 1973; Webb 1993; Fish 1999; Liao

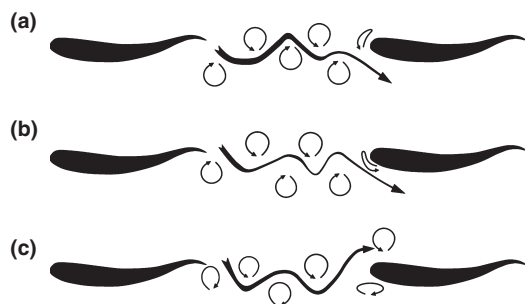


Figure 5 The structure of the wake in the rectangular and the line configuration over three independent tail beats. The follower fish (a) hits the vortex in its centre, (b) captures both vortices at one side advantageously, (c) swims in between both vortices. Arrows give the direction of local flow and their thickness indicates the speed of local flow. The fat, long arrow represents the jet. Information for the arrows was taken from snapshots of the flow field as in Movie S2.

2007) (Fig. 4a). Surprisingly, the Froude efficiency of the phalanx is lower than that of the line (Fig. 4a, Movie S3). This is probably due to an

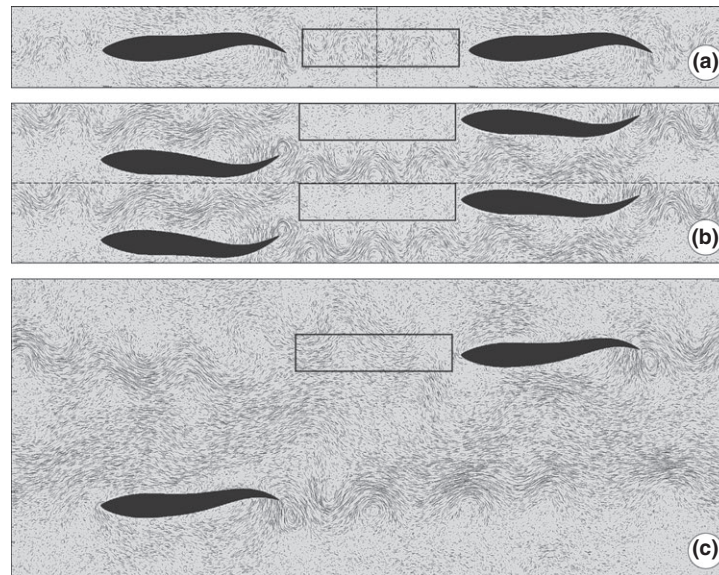


Figure 6 Flow in an infinite periodic school for several configurations. (a) rectangular configuration with small lateral distance ($0.4 L$), (b) diamond configuration with small lateral distance ($0.4 L$), and (c) diamond configuration with large lateral distance ($1.6 L$). For clarity the simulation area is shown twice in Fig. a and b, with horizontal duplication in (a) and vertical in (b) as indicated by the dotted line. Lines represent truncated streamlines, longer lines indicating faster speed. Areas ahead of each fish are marked by a black rectangle. For videos of moving fish, see the supplementary material.

increased resistance (on average per fish) of the phalanx to oncoming flow due to close proximity of lateral neighbours (for all lateral and longitudinal distances measured here). In agreement with this, the speed of the phalanx is usually lower than that of a solitary fish (Fig. 4b) and at larger lateral distances among individuals (where presumably resistance to oncoming flow is lower), both efficiency and speed increase not only in a phalanx, but also in a rectangular and diamond-shaped configuration (Fig. 4 a, b).

The rectangular configuration is more efficient than both the line and the phalanx. This may arise because in the rectangular configuration individuals benefit from neighbours in both directions, the longitudinal and the lateral one (Figs 4a, 5, Movie S4).

Remarkably, at short lateral distances (at $0.4 L$) in the diamond-shaped configuration fish are less efficient than in the rectangular configuration and they swim even slower than a solitary fish (Fig. 4a, b). This may arise because the fish receives an almost laminar structure in front of it (black rectangle Fig. 6b). This happens, because the undulating bodies of the neighbours one row (diagonally) ahead compress and disturb the wake of the predecessor straight ahead (two rows ahead,

Fig. 6b, Movie S5). Consequently, individuals benefit longitudinally less than in the rectangular configuration where they receive the wake of their predecessor on their laterally moving head. At larger lateral distances in the diamond configuration, however, the fish encounters a more intact wake structure generated by the predecessor straight ahead (Fig. 5c). Here, the “diamond effect” of swimming midway between others may work. This may explain why at large lateral distances, above $0.4 L$, the efficiency of a diamond-like configuration is similar to that of a rectangular configuration (Fig. 4a).

Discussion

Our model is the first model of an infinite school of fish that includes natural hydrodynamics. It confirms and rejects a number of theories of hydrodynamic benefits of schooling and generates new theories.

It confirms the higher efficiency of swimming in a diamond configuration and a phalanx (apart from the densest phalanx) compared with swimming alone (Weihs 1973).

Unexpectedly, in contrast with expectations based on the rotations of vortices in a thrust-like

vortex system (Weihs 1973), our model shows that it is efficient to swim directly behind another fish. This arises because following fish move their head sideward, and therefore, they do not exactly swim in a thrust wake in which they would experience only disadvantageous flow from the vortices. Instead they may sometimes, by bending their head sideward when a vortex arrives, capture the vortex such that they benefit from its flow (Fig. 5b). We may speculate that real fish may even exaggerate their lateral movements in a way synchronized to the shedding of vortices to capture their energy, thus performing a kind of 'reverse von Karman gait' (Liao *et al.* 2003b). Note that even at the largest distance studied here the beneficial effects do not yet decrease to the values of the single fish, due to the slow decay of hydrodynamic flow. Besides, in a dense diamond-like configuration close lateral proximity among neighbours ahead distorts the otherwise incoming vortex wake and ruins its beneficial effect by producing an almost laminar structure. Therefore, our model rejects that the optimal lateral distance of the diamond configuration should be $0.4 L$ as predicted by Weihs (1973). The difference between our results and Weihs' theory (Weihs 1973) is due to the different representation of hydrodynamics in both models; our present model takes into account viscosity, deformable body shape and interactions between wakes and individuals, none of which the theory of Weihs represents.

New is further that our model shows that swimming in a school is almost always more efficient than swimming solitarily, also when fish swim in a line and rectangular configuration, thus, irrespective of the precise spatial configuration of the school. Efficiency is almost independent of the lateral and longitudinal distance among individuals in our study, and apparently irrespective of the phase of the wake when it is received. Thus, in a school, the interaction between water and fish enhance forward movement in more ways than thought before, not only by exploiting a reverse von Karman street or drag wake and by the canalization effect, but also by exploiting a reverse von Karman street or thrust wake through the side-wards movement of the head.

Following the theory by Weihs, we chose to represent our model in two dimensions. As we showed in our former two-dimensional model, the wake behind a single fish resembles empirical values for a mullet of 126 mm as regards its ring

radius R , ring angle ϕ , circulation Γ , standard deviation of the vortex spacing dx and dy and Strouhal number (Reid *et al.* 2012). Results of two-dimensional models of this type of carangiform swimming fish, not only of ourselves related to mullet-like fish (Reid *et al.* 2009, 2012), but also of others, related to mackerel-like fish, saithe-like fish and fish-like foils, resemble those of real (three dimensional) fish remarkably well (Triantafyllou *et al.* 1993; Pedley and Hill 1999; Sui *et al.* 2007; Borazjani and Sotiropoulos 2008). The similarity of our results in two dimensions at a relatively low Reynolds number ($\sim 1.2 \times 10^3$) to experimental data of a mullet by Müller *et al.* (1997) at a much higher Reynolds number ($\sim 20 \times 10^3$) emerges from the reduction in dimension. This happens because there is one fewer degree of freedom for vortex dissipation. Consequently, all phenomena – such as recirculation, vortex shedding and turbulence – occur at lower Reynolds number compared with that in 3D (Reid *et al.* 2009; 2012).

Our results raise many further questions. How will the beneficial effect of schooling be influenced first, when, the size of the school is made finite, second, when individuals undulate asynchronously, third, when individuals actively exploit flow by adjusting their position and undulation, fourth, when the model were developed in three dimensions and fifth, when individuals actively coordinate with others? For active coordination, models of zone-based coordination among individuals (Parrish and Viscido 2005; Hemelrijk and Hildenbrandt 2012; Lopez *et al.* 2012) should be combined with an MPCD model like the one presented here. Such a combined model will also lead to a better explanation of details of the internal structure of the school than previous models of fish schools could do (Couzin and Krause 2003; Hemelrijk and Hildenbrandt 2012). New simulations are planned to study these questions.

In sum, incorporating in a computational model bodily movements, viscosity and interactions among wakes and individuals leads to novel findings regarding hydrodynamic advantages of schooling. Our model suggests that schooling is in general beneficial. Yet to know whether this holds in reality also, we still need to study the effects of the natural variation among individuals in their distances and angles to each other, their body sizes, their swimming phases and their tail (or fin) beat (Belyayev and Zuyev 1969; Zuyev and Bely-

ayev 1970; Herskin and Steffensen 1998; Svendsen *et al.* 2003; Johansen *et al.* 2010; Killen *et al.* 2012). As benefits in hydrodynamic efficiency in our simulations arise while individuals are not even intending to exploit the wake, hydrodynamic benefits are easier to obtain than previously thought and are therefore an important topic for further investigation.

Acknowledgements

We are grateful to the positive receipt of our work by Prof. Dr. D. Weihs. Our studies have been inspired by the enthusiasm about hydrodynamics of Prof. Dr. E. J. Stamhuis and Prof. Dr. J. J. Videler.

Financial support

We thank the Groningen University for an Ubbo Emmius grant to Daan Reid, and the Dutch Organization for Scientific Research (Nederlandse Organisatie Wetenschappelijk Onderzoek, NWO) NWO *Cognitie Pilot* project (051.07.006) for financial support to Hanno Hildenbrandt.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Lateral drift in fish length over time of the line formation. Two starting conditions with tail starting right and left. Small inset figures indicate where the wake passed by the fish at that point in time.

Movie S1. Solitary fish.

Movie S2. Infinite school of fish swimming behind each other in line configuration (forward distance 1L).

Movie S3. Infinite school of fish swimming side by side in a phalanx configuration (lateral distance 0.4L).

Movie S4. Infinite school in rectangular configuration (forward distance 1L, lateral distance 0.4L).

Movie S5. Infinite school in a diamond-like configuration (lateral distance 0.4L). See Fig. 4b.