

Analyzing fish movement as a persistent turning walker

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Abstract The trajectories of *Kuhlia mugil* fish swimming freely in a tank are analyzed in order to develop a model of spontaneous fish movement. The data show that *K. mugil* displacement is best described by turning speed and its auto-correlation. The continuous-time process governing this new kind of displacement is modelled by a stochastic differential equation of Ornstein–Uhlenbeck family: the persistent turning walker. The associated diffusive dynamics are compared to the standard persistent random walker model and we show that the resulting diffusion coefficient scales non-linearly with linear swimming speed. In order to illustrate how interactions with other fish or the environment can be added to this spontaneous movement model we quantify the effect of tank walls on the turning speed and adequately reproduce the characteristics of the observed fish trajectories.

Keywords Fish displacement model · Stochastic model · Nonlinear diffusion · Ornstein–Uhlenbeck process

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1 Introduction

The highly coordinated displacement of hundreds or thousands of fish in so-called fish schools has been the focus of many theoretical and some experimental studies. The spatial group cohesion, unless it is ensured by a confining environment, must be the result of interactions between the animals. As in any collective behaviour, these interactions should be considered as individual decision processes that synchronise the behavioural outputs [12].

Many authors have tried to understand these collective behaviours from a theoretical perspective. They propose biologically plausible (but nevertheless hypothetical) interactions that lead to a synchronization of the fish headings (moving directions), see [18, 61] and references therein. The interactions are implemented as a set of neighbour-dependent rules that modify a null-model of spontaneous and independent fish displacement. Such a null-model may gain particular importance in the case of fish groups with clearly identified leaders that swim rather independently ahead of the group, their null-model may therefore dominate the landscape of the collective patterns [18, 19, 24, 60].

In most of these studies this null-model is a random walk, that is the animal path is characterized by a series of straight moves separated by reorientation behaviour. In some cases, the new heading is simply uniformly distributed and the time series of headings obeys a Markov process of order 0 (pure random walk). More often, the new heading is a small deviation from the previous headings and the null-model corresponds to a correlated random walk or persistent random walker [34]. In this case, the time series of headings obeys a Markov process of order 1 (consecutive headings are auto-correlated), and the time series of the turning angles obeys a Markov process of order 0 (consecutive turning angles are independent).

However, most of these studies are only loosely linked to biological data. In order to move towards a biological validation some experimental studies have attacked the quantitative description of the collective swimming behaviour [3, 36, 49] and its comparison to model predictions. Only very few studies have directly addressed the experimental identification and quantification of the underlying interactions between individuals [26, 46], and they all used the pure random walk as the null-model.

It is important to note that the estimation of interaction parameters depends crucially on the choice of the null-model. The prerequisite for such an estimation is the existence of a validated null-model of spontaneous displacement since interactions are detected as the departures from such a null-model. We therefore advocate that a prior step to interaction analysis is to quantify this spontaneous behavior experimentally and to check whether the random walk model indeed holds for an isolated fish. Otherwise a better grounded spontaneous model must be developed. To be applicable, this model should work as much as possible at the same space and time scale as the suspected interactions.

To address this question, we quantify in the present paper the experimental trajectories of nine isolated fish that swim in a circular tank. The fish were Barred flagtail (*Kuhlia mugil*), a 20–25 cm pelagic fish that lives in schools along the coral reefs in La Réunion Island. In a data-driven approach we first develop a stochastic kinematic model of their swimming behavior in the form of stochastic differential equations

(sde): the persistent turning walker (PTW). This model is characterised by a constant swimming speed and an autocorrelation of the angular speed (turning angle per unit time) rather than autocorrelation of the heading as in the correlated random walk. The exploration of the model properties will help to identify the major differences to the random walk model, in particular the expected collective behaviour when many individuals move according to this null-model. In a second step we will also explore how to add interactions to this null-model by quantifying the interaction between the fish and the tank wall. This interaction takes the form of an additional term in the stochastic differential equation that bends the fish trajectory away from the wall. The extended model will be used to compare directly the net squared displacement between experimental and simulated trajectories.

2 Data collection

In the experiments described in [53], nine fish were filmed while swimming alone in a circular tank of radius $R = 2$ m, depth 1.2 m and filled with still clean sea water. The limited water depth ensured that the fish were swimming on a planar level, that is in two dimensions.

For each individual, two minutes were extracted from digital video recordings and the position of the individual's head was tracked every $1/12$ s (1,440 points per trajectory). Perspective errors were corrected, and oscillations of periods shorter or equal to $8/12$ s that are due to the beating mode of swimming were removed using wavelet filtering with Daubechies bank of length 10 (Wave++ package [22]). This filtering procedure yielded the trajectory of the fish body and was never farther than 2 cm from the tracked head (for a fish of length 20 cm). These trajectories appeared rather winding (spiral course) with no well-defined points of directional changes as would be expected in standard correlated random walks (Fig. 1). Some fish exhibited some kind of thigmotactic behaviour (wall following/attraction, see fishes 1, 4 and 5) whereas the others displayed simple wall avoidance type patterns.

Cartesian 2D coordinates are arbitrary with respect to the origin and orientation of the axis, they are therefore badly suited to analyze movement. To adopt the fish point of view they were converted into the intrinsic coordinates along the trajectories. Starting from the initial point $P(0)$ at $t = 0$, intrinsic coordinates $(S(t), \varphi(t))$ denote, respectively, the curvilinear abscissa and the heading at time t when the fish is at position $P(t)$. The curvilinear abscissa $S(t)$ is the length of the trajectory since $t = 0$ when $S(0) = 0$. Correspondingly, the heading $\varphi(t)$ is computed relative to the initial heading $\varphi(0)$ at $t = 0$ (see Fig. 2). The time derivatives of these intrinsic coordinates are, respectively, the swimming (tangent) speed $V(t)$ (m/s, which is the norm of the speed vector $\mathbf{V}(t)$) and the turning speed $W(t)$ (rad/s).

To minimize the error due to time discretization, we estimated the intrinsic coordinates at each point $P_i = P(i\Delta t)$, $i = 1, \dots, 1,338$, by fitting a circle to the three consecutive points P_{i-1} , P_i , P_{i+1} . We then recovered Δs_i and $\Delta\varphi_i$ (counter-clockwise coded as positive) for each middle point P_i as shown in Fig. 2. The instantaneous swimming speed V_i and turning speed W_i were then estimated by

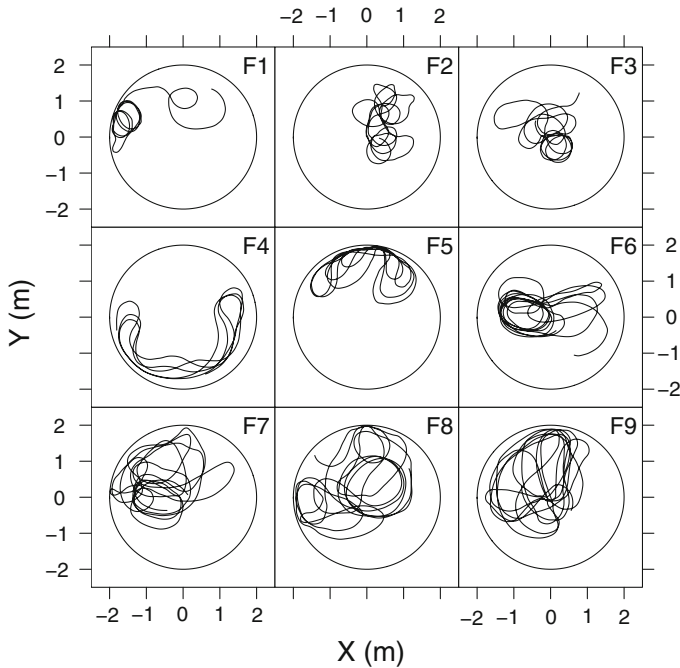


Fig. 1 Nine fish trajectories in the water tank. The trajectories are displayed ranked by the fish speed, from the slowest (fish 1, mean speed 0.16 m/s) to the fastest (fish 9, mean speed 0.56 m/s). The *outer circle* indicates the tank wall and axis units are in meters

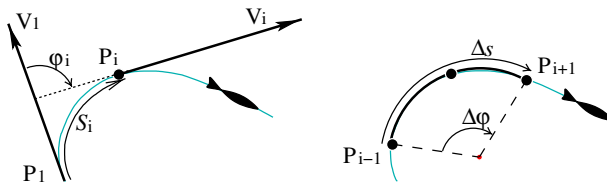


Fig. 2 Symbols used in the path analysis. $P(t)$ is the fish position at time t , $V(t)$ its speed vector and $S(t)$ the path length since the beginning of the path $P(0)$. On the *right side*, the fitted circle arc (*bold line*) used for quantifying the intrinsic coordinates was superimposed on the actual fish trajectory. P_i denotes $P(t_i)$, that is the position of the fish at time step i

$$\widehat{V}_i = \frac{\Delta s}{2\Delta t} \quad (1)$$

$$\widehat{W}_i = \frac{\Delta \varphi}{2\Delta t} \quad (2)$$

The curvilinear abscissa S_i and heading φ_i at point P_i were recovered by integrating the corresponding speeds over time, starting from the second point of the series

($P_1 = P(\Delta t)$), according to the equations

$$\widehat{S}_i = \int_{\Delta t < t < i \Delta t} dS(t) \simeq \sum_{j=1}^{i-1} \widehat{V}_j \Delta t \quad (3)$$

$$\widehat{\varphi}_i = \int_{\Delta t < t < i \Delta t} d\varphi(t) \simeq \sum_{j=1}^{i-1} \widehat{W}_j \Delta t \quad (4)$$

Note that this procedure yields a heading value φ_i which is relative to the heading at the starting point P_1 and can fluctuate away from the standard trigonometric limits $[-\pi, \dots, +\pi]$ because φ_i is not taken modulo 2π (e.g. three complete counter-clockwise revolutions would yield a φ -shift of $3 \times 2\pi$). Such a definition of heading is the most relevant one when dealing with rotational diffusion [9, 11, 47] because it is consistent with the continuous evolution of the heading (no artificial jumps at the transitions between $-\pi$ and π).

3 Kinematic model

3.1 Rationale for the model

The time evolution of $S(t)$ indicated that the swimming speeds could be considered as constant for each fish (Fig. 3a: constant slopes with some residual tracking noise) but different across fishes. As for the time evolution of the heading, we found that the autocorrelation of the turning speed $\langle W_i, W_{i+h} \rangle$ was significant over several seconds (Fig. 3b). Contrastingly, an essential property of random walks is that consecutive changes of heading are independent. Therefore, the autocorrelation of the turning speeds, defined as

$$\langle (\varphi_i - \varphi_{i-1})/\Delta t, (\varphi_{i+1} - \varphi_i)/\Delta t \rangle = \langle W_i, W_{i+1} \rangle, \quad (5)$$

would be negligible. This is obviously not the case in our data. Hence, the random walk model, whether correlated or not, could not account for the persistence of the turning speed in our fish and would be inadequate. Data rather suggest a process based on a correlated turning speed [1, 2] with constant swimming speed. Following the terminology of the persistent random walker (PRW) which denotes the random walk with an autocorrelation of the heading, we shall hereafter call the PTW this new kind of random walk with an autocorrelation of the turning speed. In its simplest form, this model states:

$$V_i = V \quad (\text{constant swimming speed}) \quad (6)$$

$$W_i = a W_{i-1} + b_i \quad (7)$$

where b_i is a random gaussian variable of mean 0 and variance s^2 , and a the one-step correlation coefficient of W_i .

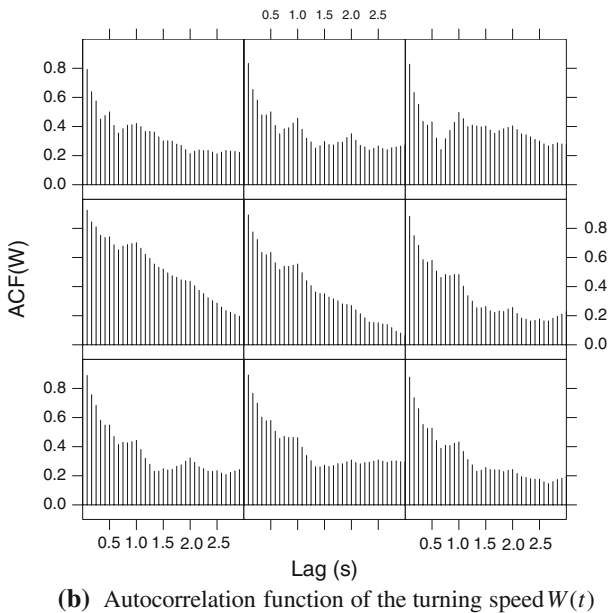
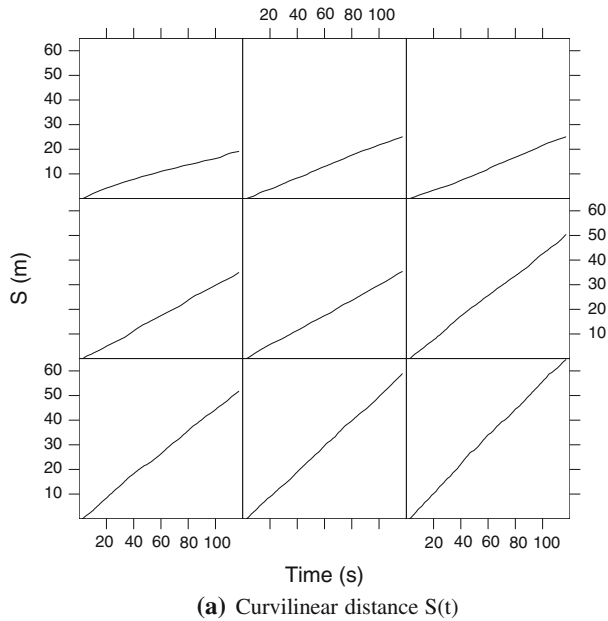


Fig. 3 Evolution of the intrinsic coordinates $S(t)$ (top) and the autocorrelation function of the turning speeds W_i (bottom, both graphs in the same order as Fig. 1). The linear slopes of $S(t)$ indicate a constant swimming speed and the autocorrelation of the turning speed is significant over several seconds

Equation 7 is an auto-regressive process of order 1 (AR(1) in the statistics literature). Its parameters a and s can be estimated from a time series (N points sampled

every Δt) by the standard equations

$$\hat{a} = \frac{\sum_i^{N-1} W_i W_{i+1}}{\sum_i^{N-1} W_i} \quad (8)$$

$$\hat{s}^2 = \frac{1}{N} \sum_i^{N-1} (W_{i+1} - \hat{a} W_i)^2. \quad (9)$$

For a continuous signal such as a moving fish, a and s depend on the discretization time step Δt , but this dependency can be resolved by computing their continuous-time equivalents α and σ :

$$\alpha = -\frac{\log(a)}{\Delta t} \quad (10)$$

$$\sigma^2 = s^2 \frac{2\alpha}{1 - e^{-2\alpha\Delta t}}. \quad (11)$$

α expresses the inverse of the autocorrelation time τ (that is $\tau = 1/\alpha$) and $a = e^{-\Delta t/\tau}$. Since $W(t)$ is a continuous-time process, (7) ought to be understood as the discretized solution over $[(i-1)\Delta t, \dots, i\Delta t]$ of the stochastic differential equation (sde):

$$dW(t) = -\frac{1}{\tau} W(t)dt + \sigma dB(t) \quad (12)$$

with $B(t)$ representing a Brownian process (white noise). This is known in statistical physics as the Ornstein–Uhlenbeck (OU) process [59] and as the Vasicek model in the financial economics literature [7]. In the stationary regime, this equation leads to a Gaussian random process of the turning speed with zero mean, variance $\tau\sigma^2/2$ and an exponentially decaying autocorrelation function with decay rate α .

3.2 Parameter estimation

In order to estimate the parameter values of this spontaneous moving behavior from the fish trajectories in Fig. 1 we had to take the confining effect of the wall into account. Taken a constant swimming speed for granted, this effect can only operate on the turning speed, acting as an external field which skews the turning speeds towards repulsive moves (for further details see next section). This might have biased the estimates of the autocorrelation time lag. Hence, we restricted this estimation by using only positions farther than 1 m from the wall (Fig. 4) and censored, i.e. treated as unknown values, the trajectories when the fish was outside the innermost 1 m wide disk. Those estimates are reported for each fish on Fig. 5 (bullets, ●). They were rather homogeneous across the fish, except for the individuals 1 and 4 that were identified above as exhibiting a strong attraction towards the wall with a rhythmic pattern to and from the wall (Fig. 1). To estimate the confidence interval of the parameters, we produced

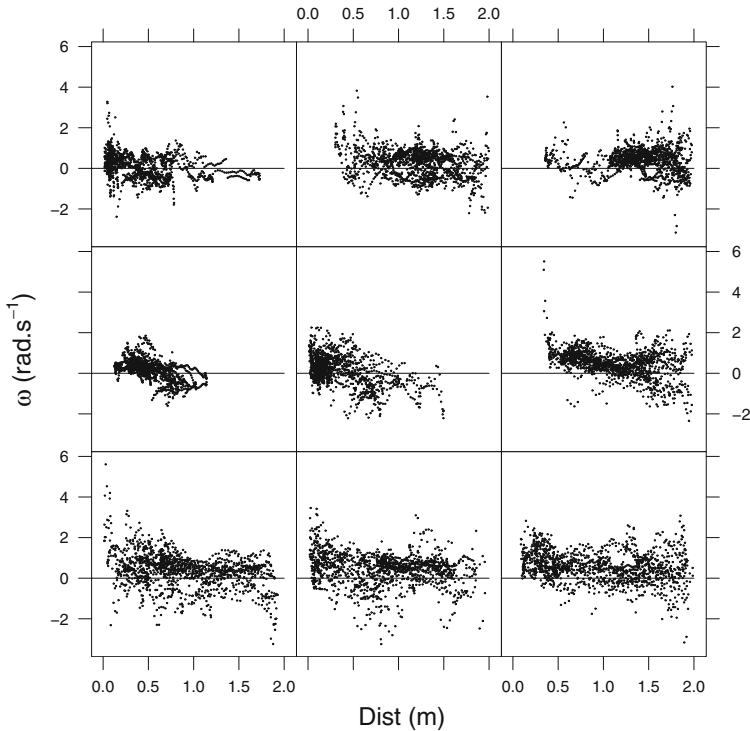


Fig. 4 Effect of the wall on the turning speed $W(t)$ (same order as Fig. 1). The sign of \widehat{W}_i was corrected so that positive values correspond to a fish steering away from the wall. The sign-corrected values $\widehat{\omega}_i$ are reported as a function of the shortest distance Dist from the fish to the wall. Near the wall (Dist < 1 m), $\widehat{\omega}_i$ is skewed towards positive values, indicating an effect of the wall up to 1 m away from it

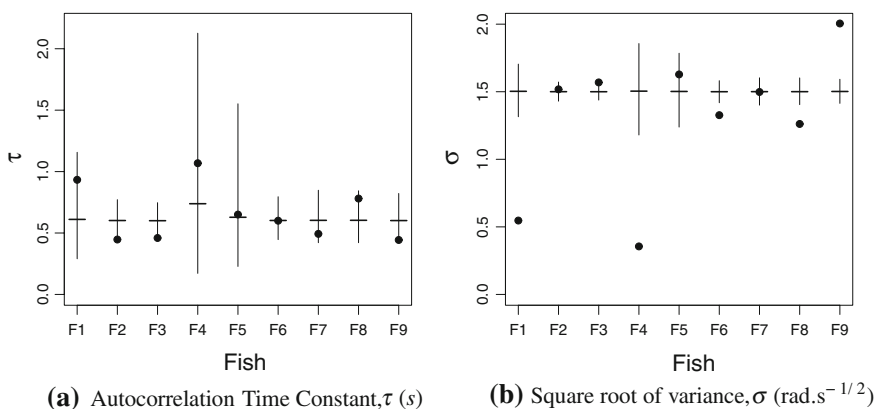


Fig. 5 Parameter estimates for each fish of the AR process representing the angular speed W , mean time lag τ **(a)** and turning speed standard deviation σ **(b)**. *Bullet* parameter estimate from the original data. *Lines* numerical predictions of the means and 0.95 confidence intervals for the common set (see text for further details)

repeated simulated series of W using (7) with a common set of parameters ($\tau^* = 0.6$ s and $\sigma^* = 1.5$ rad/s^{0.5}, same time step Δt), and applied to each fish the same censoring filter as to the original data. We then computed the corresponding mean and confidence interval at the 95% level (percentile method, estimated from 100,000 simulations each). These confidence intervals show that all fish have a τ -value that is not significantly different from a common autocorrelation time around τ^* . As expected, the outlier fish 1 and 4 depart clearly from the others (and their confidence intervals are much larger because of a lack of data in the inner 1-m disk). The individual variances σ^2 seemed more contrasted and were significantly less homogeneous than the correlation times. However, it is unlikely that these slight deviations from σ^* would actually raise significant differences at the level of the trajectories.

4 Properties of the spontaneous model

4.1 Macroscopic prediction

Degond and Motsch [20] have analysed the large time scale behaviour of a similar model (with an autocorrelation of the curvature instead of the turning speed). They have shown by a space–time rescaling technique that their model leads to a diffusion process at the macroscopic scale. Since our fish swim at constant speed, an autocorrelation of the curvature is equivalent to an autocorrelation of the turning speed, so their conclusion holds also for the PTW model and the mean square displacement scales linearly with time at large scale:

$$\text{Var} \left[\overrightarrow{x(t)} \right] \xrightarrow{t \rightarrow +\infty} 2Dt \quad (13)$$

where $\overrightarrow{x(t)}$ denotes the vector from the starting point to the position at time t . The diffusion coefficient D indicates how fast the fish spreads out from its initial position across the 2D-space.

Figure 6 reports the dependence of the associated macroscopic diffusion coefficient D on the swimming speed V and the autocorrelation time of the turning speed τ . An analytical derivation of this dependance is under study. In contrast to the macroscopic version of the random walk, the diffusion coefficient in the PTW model is not proportional to the swimming speed, but rather increases non linearly as the swimming speed increases. For a given speed V , an increase of the autocorrelation time of the turning speed τ yields a lower diffusion coefficient. This happens because the fish is more often trapped in a high value of turning speed and for a longer time, so it turns around more locally.

5 Inclusion of wall avoidance

The kinematic model presented above only applies to fish behavior in unconstrained open water. As an example of how additional components can be integrated into this model and quantified from data we added the wall avoidance behavior. Focusing on

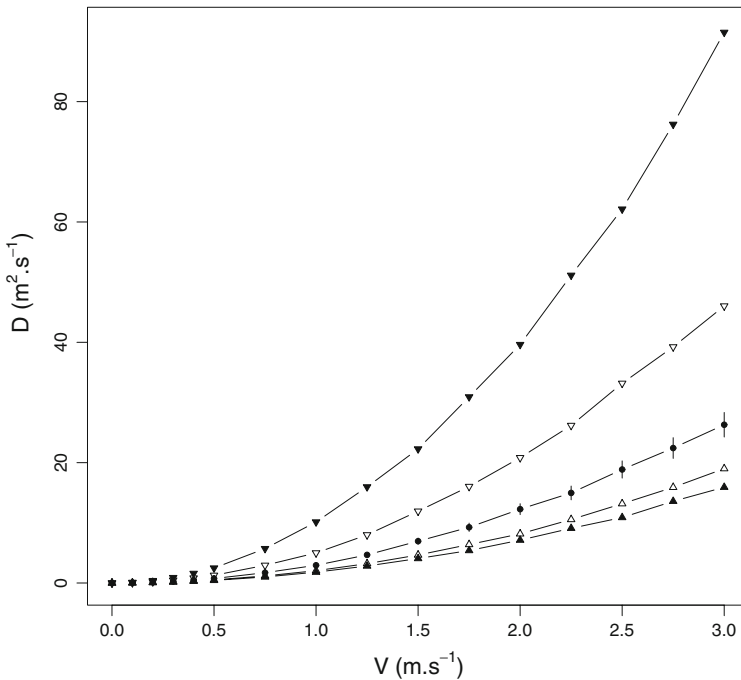


Fig. 6 Diffusion coefficient D for the PTW model as a function of the swimming speed V , and for different values of the autocorrelation time τ , but keeping the variance $\frac{\tau\sigma^2}{2}$ of W constant (filled downward triangle $\tau = \tau^*/4$; open downward triangle $\tau = \tau^*/2$; bullet $\tau = \tau^* = 0.6$ s; open upward triangle $\tau = 2\tau^*$; filled upward triangle $\tau = 4\tau^*$). Each value was estimated by the Monte-Carlo method, with 10,000 replicates of individual trajectories simulated with $\Delta t = 0.01$ s over 1,200 s and with random initial conditions (heading and turning speed). D was estimated by linear regression from the mean square displacement restricted to the time interval $[600, \dots, 1,200]$ s in order to avoid the ballistic part of the curve. Bars denote the 0.95 confidence interval for the case *bullet* $\tau = \tau^*$

the fastest fish (fish 9) we found that the wall had a salient effect only when the fish was close to and heading towards the wall. We consequently reconstructed the effect of wall repulsion as a function of the distance D_c before collision with the wall (if heading were not changed), i.e. the distance between the fish and the intersection of the heading line with the wall.

We assumed that the repulsive effect of the wall made the fish tend towards a turning speed $F(D_c)$ which bends its trajectory away from the wall. In order to keep the model independent of the time step, we adopted the sde formalism of Eq. (12) and introduced the new term $F(D_c(t))$ as

$$dW(t) = -\frac{1}{\tau} (W(t) - F(D_c(t))) dt + \sigma dB(t) \quad (14)$$

If the wall effect were constant over time (e.g. $F(D_c(t)) = F^*$) process (14) should be understood as a relaxation of $W(t)$ towards the equilibrium value F^* . Of course, since the fish position and its heading change over time, so does $F(D_c(t))$.

Over a small time step Δt , however, we can assume that $F(D_c(t)) \simeq F(D_i)$ (with $t = (i - 1)\Delta t$) is constant, and the discrete version of (14) is given in [7] by

$$W_{i+1} = a W_i + c F(D_i) + b_i \quad (15)$$

where $c = (1 - e^{-\Delta t/\tau})$, and a and b_i are defined as in (7). Given a from the spontaneous model we reconstructed $F(D_c)$ based on

$$\widehat{F(D_i)} = \frac{W_{i+1} - a W_i}{c} \quad (16)$$

plotted against D_i .

Finally, since the repulsive effect of the wall has to induce a change of the turning speed in the correct direction, we corrected the sign of $\widehat{F(D_i)}$ such that positive values

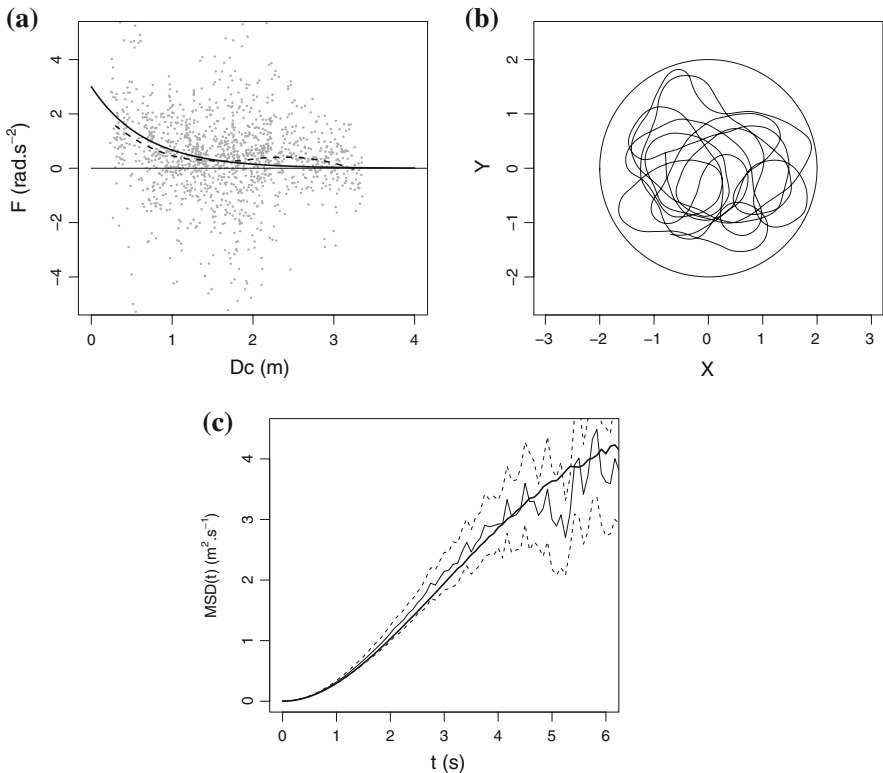


Fig. 7 Integration of the wall repulsive effect in the model for fish 9. **(a)** Wall effect on the angular speed. D_c : distance to collision. A positive F denotes repulsion. *Dotted line* loess estimate of $F(D_c)$. *Thick line* parametric approximation $3 \exp^{-1.5D_c}$, **(b)** Example of a typical simulated trajectory in the tank (equation 15, with $\tau = 0.6$ s, $\sigma = 1.5$ rad.s^{-1/2}, $\Delta t = 0.01$ s), **(c)** Mean Squared Displacement of model and experimental data (fish 9). *Thin line* experimental mean; *dotted lines* experimental 95% confidence interval; *thick line* model prediction estimated by Monte Carlo simulations (parameters as in b).

corresponded to a fish steering away from the wall (Fig. 7a). Following [9], we used a nonparametric locally weighted regression procedure (loess, [17]) to estimate the decay of this wall effect as the distance to collision increases. This decay could be adequately modeled by the parametric function $F(Dc) \simeq 3e^{-1.5Dc}$ (Fig. 7a).

We finally simulated the complete model, using the discrete version (15), and checked the simulated trajectories against the experimental one. A typical example is shown in Fig. 7b. Note in particular that the wall avoidance results from the time integration of the wall effect quantified above, with no ad-hoc correction in case of collisions (which do not happen with sufficiently small Δt). As a final test of the relevance of this model, we compared the experimental and the expected mean squared displacement (MSD). Both agreed perfectly well up to 6 seconds (i.e. 3.6 m, which is of the same order of magnitude as the tank width of 4 m) despite the fact that the statistical quantifications of the model were done on the turning speed fluctuations (third derivative of the position) whereas this test is performed directly with the integrated time series of the fish positions.

6 Discussion

6.1 Why a new kind of random walk model is needed?

Random walks and the associated diffusion models were originally developed in biology to describe the movements of single cells [44,45]. Later they were adopted by ecologists to model the displacement of animals [35,56], and particular attention was paid to the underlying behavioral mechanisms and how they are modulated by environmental conditions. Inspired from the model of gas particles that travel straight ahead between collisions, random walk models break the path into a series of consecutive straight moves, separated by random reorientation behavior. The biological rules determine, for each move, a direction, a duration and a length that can depend on the preceding move (in the case of the correlated random walk) but also on the animal's state and goals and the environmental conditions (including the presence of conspecifics). Most often, these discrete random walk models have equivalent continuous time formulations, either at the population level (macro-scale diffusion models) or at the individual level (stochastic differential equations and Langevin theory of Brownian motion [16]). They are especially useful when the focus is put on the interplay between the behavior and the environment at large time and space scales (e.g. how ovipositing butterflies respond to changes in the dispersion of their food plants [34]). More generally, simple random walks have proved to be appropriate to quantify the movement of animals or cells which exhibit clear bouts of straight moves separated by reorientation behaviour (e.g. in ants [13,14], cockroaches [32] or *Escherichia coli* [2]).

Our fish in the tank did not exhibit such clear bouts of straight moves nor clear reorientation behaviour. They are rather characterized by smooth variations of their heading. Of course, it would still have been possible to approximate their trajectory as a series of straight segments at some fine scale. This would have required a subtle choice where to break up the path, with a trade-off between inappropriate lumping of small displacements and excessive splitting of long ones. Excessive splitting yields

series of headings that are still highly autocorrelated which complicates statistical factor analyses and the translation of individual movements into population dispersal models [34,57]. To avoid this, Tourtellot advocates for instance to sub-sample trajectories of cockroaches in order to enhance the discrimination between “gait noise” (lateral, side-to-side wobble) and course changes [55]. Accordingly, Turchin suggests to resample the path at a lower rate until the autocorrelation structure disappears [6,56,58]. Such a procedure applied to our fish has led to an overly rough approximation of the true path, impeding accurate predictions of the fish trajectory at the short time scale. At finer scales, not only was the heading highly autocorrelated from one segment to the next (one-step correlation as in the correlated random walk model), but the heading change itself was autocorrelated, because the circular-shaped trajectories imply sustained changes of the heading towards the same clock-wise sign. Modelling such a moving behaviour with straight moves separated by an *ad hoc* tortuous reorientation behaviour (e.g. a Markov process of higher order as in [27]) would have been unduly complicated.

We adopted a more parsimonious approach in which the random fluctuations act directly on the turning speed (the derivative of the heading) rather than on the heading itself. This led us to the PTW model. Using this model, there were still two alternatives to express the random process at the individual scale, either as a discrete process or as a continuous process. We followed the two approaches and quantified the associated model parameters from experimental data. In the discrete alternative, the trajectory is split into a series of circular segments of random length (constant turning speed over a random time length), separated by a renewal process of the turning speed drawn from a Gaussian distribution. The associated quantification procedure yielded convincing results, but it involved the prior validation of methodological prerequisites, in particular the detailed development of the proper algorithm of path segmentation. It will be the subject of a future report. In the continuous alternative that is reported in the present paper, the fish path is considered as a curvilinear track whose parameters are continuously updated by the animal. The renewal process of the turning speed leads to a description by stochastic differential equations [10,48] where the turning speed follows an OU process. We used the discrete-time sampling of the path to estimate its parameters. This formalism allows predictions at any time scale.

Beyond the formalism, the experimental data have clearly shown that the classical random walk models (adjustments of headings) are inappropriate for the spontaneous movement of the fish species under study in which the steering process is based on adjustments of the turning speed. Obviously, this result has to be confirmed for other fish species and arguably in other experimental set-ups (e.g. varying the tank diameter). It is, however, a highly plausible model for many fishes that travel at constant swimming speed [23,54]. The model used to quantify this behaviour may also be considered to analyze movements in other animals that exhibit some circularity in their displacement (e.g. the desert isopod searching for its burrow [28,29] or the carabid beetles [51]) and to derive their properties at the macroscopic scale. Schimansky-Geier et al. [37,52] showed for instance that the intensity of research associated with a noisy constant turning speed is higher than possible with a piecewise linear random walk.

6.2 Towards the quantification of fish interactions

The principal aim of this study was to establish a biologically grounded model of the spontaneous displacement of a fish against which the interactions with neighbors can be quantified. Since the null-model is directly based on the turning speed it is reasonable to address interactions also from this point of view. The presence of a neighbor would simply make a fish turn more or less quickly, either to avoid, to align with or to approach it. In this case the interactions should not be modeled as attraction or repulsion forces (in the Newtonian sense, which would affect the swimming and the turning speeds), but rather as attraction or repulsion torques (which would affect the turning speed only).

To illustrate this idea and as a first step towards an ad-hoc methodology to quantify fish interactions we addressed the interaction of isolated fish with the tank wall. This takes the form of an additional term in the stochastic differential equation governing the turning speed process ($W(t)$). The repulsive effect of the wall has been formally described as an OU process relaxing $W(t)$ towards $F(D_c(t))$ (which represents a mean turning speed away from the wall, $D_c(t)$ being the distance before wall collision if the heading were not changed) rather than towards 0 (which represents a mean turning speed that is independent of the wall as in the open space case). For an animal interacting with its environment, steering away might be the most natural mean to avoid obstacles since it can work without altering swimming speed (accelerate and decelerate might be more costly than just steering away). The estimated intensity of $F(D_c(t))$ displayed an exponential decay as the distance to collision with the wall increased. The simulations of the model showed that its integration over time is sufficient to avoid collisions in the normal regime. Some fish (1, 4, 5) failed to be correctly modeled within this simple framework since their trajectory clearly showed a tendency to be not just repulsed but also attracted by the wall (which is sometimes labeled thigmotaxis [32]). This attractive effect may be due to the stress induced by isolation or represent a natural behavior in the fishes' usual habitat in coral reefs. We did not further investigate this special case since we were not interested to model the effect of the wall per se, but simply used it to illustrate that interactions can actually be taken into account by a simple additional term in the $W(t)$ process.

The focus of the present paper on changing rates of rotation evokes the use of gyroscopic forces in control theory that were recently applied in the context of bio-inspired swarm robotics [4, 5, 25, 31, 33, 38, 40, 41, 50]. Especially the theoretical studies of systems with constrained speed capabilities (nonholonomic mobiles) [8, 21, 39, 42] or the studies that explore the minimal design that allow such coordination [15, 30, 43] may prove interesting for further insights into the modeling of fish interactions.

7 Conclusion

We showed that the fish *K. mugil* follows in the experimental tank a particular kind of random walk: the PTW. Even if this result has to be confirmed for other species and biological contexts, our results suggest that the standard null-models (random walks)

that are used in interaction studies and in models of collective fish movements might be less representative than suggested by their predominance in the literature.

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