




# Heterogeneous Group of Fish Response to *Escape Reaction*

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**Abstract.** The response of heterogeneous groups of fish including a few leaders, several followers, and a few fish initiating *escape reaction* is investigated. This alarm response is often observed in animal groups where exposure to strong stimuli such as a predator can force a few individuals to initiate sudden and abrupt turns to move to safer locations. In this work, a coupled stochastic process is leveraged to recreate this behavior and investigate their effects on the group collective dynamics. At the vicinity of a synchronized state, for small perturbations introduced by *startled* fish, a closed-form expression of the polarization order parameter is determined and shown effective in predicting group alignment. A numerical analysis suggests that a variation of the frequency and the amplitude of the jumps introduced by escaping fish can result in a transition to several states including an ordered state where individual align their heading direction, a disorganized state where they move in random direction, and two other states where the group split up resulting either into a change of leadership or individuals swimming away from the startled fish and therefore recovering their initial synchronized state. The findings from this work are in line with observations on fish groups exposed to a predator where initially a completely disordered state can be observed but groups tend to progressively recover a synchronized state.

**Keywords:** Bio-inspired systems · Collective dynamics · *Escape reaction* · Heterogeneous group

## 1 Introduction

Individual differences are often listed among important factors at the origin of collective behavior in biological groups. These differences can be characterized based on morphological or physiological traits, an individual position within the group, the knowledge of the environment, or individual social dominant statute [1–3]. The effects of individual traits on group response are either observed in nature through observations or tested in controlled laboratory environments [4, 5]. In recent years, to address ethical issues about the use of animals in laboratory studies, *in-silico* experiments [6] have become popular. These computational study allow to reduce significantly the number of subjects by pretesting hypothesis in order to better

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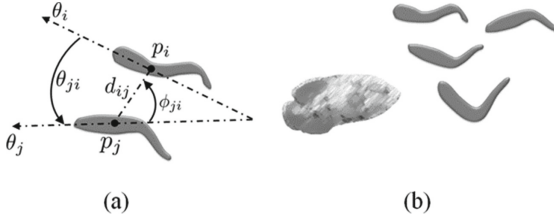
plan experimental studies with real life subjects. In addition, they have allowed to unravel some microscopic factors explaining the emergence of groups collective behavior [7–10] such as leaders-followers relationships and information flow within groups [11].

In biological groups, *escape reaction* [3], is classified among alarm responses originating from exposure to fear-inducing stimuli such as animal exposure to a predator [12]. This behavior has been observed in fish groups causing individuals to exhibit erratic or zig-zagging swimming [13] before maintaining a coordinated swimming behavior [14, 15]. In the literature, computational models have been utilized to dissect fish kinematics during *fast-start swimming* [3, 16–18] or to unravel group collective response during *escape reaction*. The authors in [19] working on group collective response have leveraged a mathematical model to observe a propagation wave following the initiation of *escape reaction*.

Different from most prior works [3, 16–18] dissecting fish kinematics or the response of homogeneous groups, this work investigates the collective response of a heterogeneous group of fish to the observable *escape reaction* [20] characterized by sudden and fast-turns away from a strong stimulus source [21]. The heterogeneous group of fish includes a few individuals denoted *leaders* having a dominant statute [3] or a good knowledge of their environment [4] to guide other team members denoted *followers* implementing local updating rules to maintain alignment with other fish in the group [22, 23]. In addition to *leaders* and *followers*, the group includes a few *startled* fish initiating sudden and fast-turning maneuvers after exposure to a strong stimulus. These bursts of activity are captured through a stochastic jump-diffusion process introduced in [24] and adapted here with a biased distribution to stir a *startled* toward a preferential heading direction.

Group response to small perturbations at the vicinity of a synchronized state is conducted allowing to establish a closed form expression for the polarization order parameter introduced in [25, 26] to measure group of fish tendency to swim in the same direction. The closed form expression is validated against numerical simulations which in addition revealed unexplored forms of state transitions in addition to the traditional transition from a state of complete order to a disorganized state [25, 26]. Further, as observed in the literature [3], the modeled *escape reaction* is shown capable to induce new form of leadership defined as the initiation of new directions of motion by a few individuals followed by other fish in the group [4].

Section 2 introduces the mathematical modeling framework recreating *escape reaction*. Section 3 analyzes group response to small perturbations introduced by *startled* fish leading to the derivation of a closed form expression for the polarization order parameter. Section 4 presents results from the numerical analysis and Sect. 5 discusses the main findings and concludes the work.



**Fig. 1.** Pair of fish  $i, j$  interaction (a) with positions  $p_i, p_j$ , heading angles  $\theta_i, \theta_j$  with respect to a fixed reference frame, their inter-distance  $d_{ij}$ , difference heading angle  $\theta_{ji} = \theta_j - \theta_i$ , and relative angular position of fish  $i$  with respect to fish  $j$  heading angle  $\phi_{ji}$ ; and initiation of *escape reaction* (b) by a group of fish exposed to a predator.

## 2 Fish Individual and Collective Behavior

### 2.1 Mathematical Modeling of the Heterogeneous Group

A group of  $N$  fish swimming in a 2D unbounded and non-periodic open water domain at a constant speed is considered. A fish  $i$  position is captured at any time instant  $\tau$  by the 2D vector  $p_i$  of the position and the scalar  $\theta_i$  representing the heading angle in a fixed frame as illustrated in Fig. 1(a). The group of fish includes a few *leaders* well aware of their environment [22] to move freely similar to dominant fish [3] and guide the rest of the group [9, 27] towards set location such as migration route or foraging source. These fish are not coupled to the rest of the group which can interact with them creating a sort of potential difference forcing individuals implementing a social interaction function with closer neighbors to follow them. Another subset of fish is denoted as *startled* fish initiating *escape reaction* (see Fig. 1(b)) characterized by sudden and fast turns with frequency  $\nu$  and intensity  $\delta$ . The remaining fish are denoted as *followers* which concomitantly to *startled* fish update their heading angle through the predefined social interaction function.

A stochastic jump-diffusion process introduced in [24] to capture the fast turn rate  $w(\tau)$  observed in the swimming locomotion of small fish species is adapted here to model fish exhibiting *escape reaction* in term of a dimensionless coupled system [28]:

$$dw_i(\tau) = -(w_i(\tau) - w_i^*(\tau)) d\tau + \varsigma dW_i(\tau) + dJ_i(\tau), \quad (1a)$$

$$w_i^*(\tau) = \sum_{j \in \mathcal{N}_i(\tau)} \frac{1}{|\mathcal{N}_i(\tau)|} [\kappa_v \sin(\theta_{ij}(\tau)) + \kappa_p \bar{d}_{ij}(\tau) \sin(\phi_{ij}(\tau))], \quad (1b)$$

where  $\varsigma$  is the noise intensity;  $w^*$  the interaction function with coupling gains  $\kappa_v$  and  $\kappa_p$ ;  $|\mathcal{N}_i(\tau)|$  the number of fish interacting with fish  $i$ ;  $\bar{d}_{ij}$  the inter-distance between pair of fish;  $W_i(\tau)$  is the Wiener process which is defined such that the increments  $dW_i(\tau)$  follow a normal distributed random variable with standard deviation  $\sqrt{d\tau}$ ; and  $J(\tau) = \sum_{j=1}^{\nu_i(\tau)} \delta_i Z_j$  is the jump diffusion process with  $\nu_i(\tau)$

defining a counting process with parameter  $\iota_i$  capturing the frequency of the fast turns while  $\delta_i$  is a scaling coefficient of the jumps.

In the model above, the heterogeneous fish behavior is captured by a single parameter  $\varsigma_i$  for the *informed fish*, three parameters  $\varsigma_i, \kappa_{vi}$ , and  $\kappa_{pi}$  for *followers*, and by five parameters  $\varsigma_i, \kappa_{vi}, \kappa_{pi}, \iota_i$  and  $\delta_i$  for the *startled fish*. The parameters of the jump-diffusion process in [24] have been calibrated on experimental trajectories of a small fish species to reproduce sudden and fast-turns [24]. However, the jump term in [24] randomly take either positive or negative values such that they do not favor a preferential heading direction as observed during *escape reaction*. This problem can be solved by selecting appropriate distribution to model the jumps.

## 2.2 Distribution of the Jumps to Recreate *escape Reaction*

Departing from the process model in (1), *escape reaction* is modeled by considering a biased distribution and notably the half-normal distribution defined as:

$$Z_j(t) = \begin{cases} z, & \text{if } Z = z \geq 0, \\ -z, & \text{if } Z = z < 0. \end{cases} \quad (2)$$

where  $Z$  is the standard normal distribution. The resulting skewed distribution induces turns in average in a preferential direction of motion as observed in the literature [13] after fish exposure to a strong stimulus such as a predator. Note that, other biased distributions including skewed distribution or symmetric distribution with non-zero mean can be considered.

Note that, fish initiating *escape reaction* and *follower* fish share identical interaction parameters such that, before the initiation of the *escape reaction*, *startled* fish are assimilated to *followers* as suggested in [3] where social subordinated fish are observed to be more favorable to exhibit such a behavior. In addition, the sign of the expected value of the distribution of the jump determines in which direction the *startled* fish will turn. In particular, using the distribution in (2), the expected mean of a fish  $i$  turn rate is evaluated as  $\mathbf{E}[w_i, \Delta\tau] = \iota\delta\Delta\tau\sqrt{\frac{2}{\pi}} > 0$  while for a *follower* not subject to any additional disturbances, one has  $\mathbf{E}[w_i, \Delta\tau] = 0$ . Thus, at steady state, one expects that the coupled system in (1) will move either in a direction determined by the long-term mean of the abrupt turns introduced by fish initiating *escape reaction*, in a direction prescribed by the *leaders*, or will simply split-up with followers following either group *leaders* or *startled* fish. These transitional states tend to characterize the various responses observed during *escape reaction* in nature where the fast and large turns initiated by a few fish can significantly affect the collective response of a group [3, 13, 14, 29].

### 2.3 Discrete Time Approximation

The stochastic system in (1) is solved using a discrete-time Euler-Maryuma approximation scheme [30]. In particular, assuming that  $\Delta\tau$  is small enough such that at most a single jump is observed in a time step, the discrete time approximation of the turn rate process in (1) allows to estimate a fish  $i$  position at any time step  $\tau_k, k \in \mathbb{N}$  by a forward Euler scheme [6, 9]:

$$\begin{aligned} x_i(k+1) &= x_i(k) + \Delta\tau \cos \theta_i(k) \\ y_i(k+1) &= y_i(k) + \Delta\tau \sin \theta_i(k) \\ \theta_i(k+1) &= \theta_i(k) + \Delta\tau w_i(k), \\ w_i(k+1) &= w_i(k)(1 - \Delta\tau) + w_i^*(k)\Delta\tau + \varsigma_i \sqrt{\Delta\tau} \varepsilon(k) + \delta_i \Delta\nu_i(k)\zeta(k), \end{aligned} \quad (3)$$

where  $\tau_{k+1} = \tau_k + k\Delta\tau$ ,  $w_i^*(k) = w_i^*(\tau_k)$  is the social interaction function,  $\varepsilon(k)$  and  $\zeta(k)$  are i.i.d. Gaussian random variables, and for simplicity  $\tau_k$  is replaced by  $k$ . The discrete time process  $w_i(k), k \in \mathbb{N}$  converges weakly to the continuous time process  $w_i(\tau)$  [24]. Note that, using the above discrete-time scheme, except for the *startled* fish, when  $\nu_i$  and  $\delta_i$  are null, the expectation and variance of a *follower* fish turn rate are  $\mu_i(w_i(k+1), \Delta\tau) = w_i(k)(1 - \Delta\tau) + w_i^*\Delta\tau$  and  $V_i(w_i(k+1), \Delta\tau) = \varsigma_i^2 \Delta\tau$ , respectively.

## 3 Analysis of Group Coordination

Group coordination is analyzed at the vicinity of a synchronized state when all fish tend to move in the same direction and shared a common heading angle denoted  $\theta_0$ . The stability of the group is evaluated by introducing to the system in equations (1) small perturbations. To simplify the analysis, a single *leader* and a single *startled* fish are considered. Note that for such a system to achieve group coordination, all *leaders* should move in the same direction. Similarly, a single strong stimulus is considered and all *startled* fish swim in the same direction to maintain a consistent escaping route. With the above considerations, given that  $\theta_0$  represents the *leader* heading direction, the stability study of the local disagreement  $\theta_i - \theta_0$  can be conducted for the rest of the  $N - 1$  fish.

### 3.1 Measure of Group Coordination

Group coordination is evaluated with a traditional order parameter introduced in [25, 26] to measure group alignment in self-propelled particles and denoted as the polarization with expression determined as:

$$\text{Pol} = \frac{1}{N} \left\| \sum_{i=1}^N \mathbf{v}_i \right\|, \quad (4)$$

where  $\|(\cdot)\|$  defines the norm of the unit velocity vector  $\mathbf{v}_i$ . The values of the polarization order parameter [25, 26]  $P(\tau)$  range from 0 to 1 with values closer to 1 indicating that all fish moving in the same heading direction and values closer to 0 when they move in completely different heading directions.

### 3.2 Group Response to Small Perturbations

Using the polarization order parameter  $\text{Pol}$ , group response to small perturbations denoted as the Pol-susceptibility is equivalent up to a constant factor to the fluctuation of the order parameter  $\text{Pol}$  [31], that is:

$$N [\langle P^2 \rangle - \langle P \rangle^2] = \frac{\partial P}{\partial x} \Big|_{x=0}, \quad (5)$$

where  $\langle \text{Pol} \rangle = \lim_{T \rightarrow \infty} 1/(T - T_r) \sum_{k=T_r}^T \text{Pol}(k)$ , and  $x$  is related to the perturbation field. For a fixed value of  $\varsigma$ , the perturbation field for the system in (1) is captured by the jumps parameters  $\iota$  and  $\delta$  as further elaborated below.

At closer proximity of the coordinated state, when all individuals share a similar heading direction, let say  $\theta_0$ ,  $\theta_{ij} = \theta_i - \theta_j \simeq 0$  for all  $i, j$ . Denoting  $\tilde{w}_i(k) = w_i(k) - w_i^*(k)$ , the discrete-time system in (3) reduced to:

$$\begin{aligned} \theta_i(k+1) &= \theta_i(k) + w_i^*(k)\Delta\tau + \tilde{w}_i(k)\Delta\tau \\ \tilde{w}_i(k+1) &= \tilde{w}_i(k)e^{-\Delta\tau} + \varsigma\sqrt{\frac{1}{2}(1 - e^{-2\Delta\tau})}\varepsilon_i(k) + \delta\Delta\nu_i(k\Delta\tau)\zeta_i(k), \end{aligned} \quad (6)$$

where for simplicity,  $w_i^*(k) = w_i^*(\tau_k)$ . For smaller values of  $\Delta\tau \ll 1$ , the system can be further reduced to:

$$\begin{aligned} \theta_i(k+1) &= \theta_i(k) + w_i^*(k)\Delta\tau + \tilde{w}_i(k+1)\Delta\tau \\ \tilde{w}_i(k+1) &= (1 - \Delta\tau)\tilde{w}_i(k) + \varsigma\sqrt{\Delta\tau}\varepsilon_i(k) + \delta\Delta\nu_i(k\Delta\tau)\zeta_i(k), \end{aligned} \quad (7)$$

In addition, for small misalignment between pair of fish  $i$  and  $j$ , one can approximate  $\sin(\theta_{ij}(k)) \simeq \theta_{ij}(k)$  and  $\phi_{ij}(k) \simeq \frac{\pi}{2}$ . These approximation allows in turn to get the following discrete-time double integrator system:

$$\begin{aligned} \theta_i(k+1) &= \theta_i(k) + \kappa_v\Delta\tau \sum_{j \in \mathcal{N}_i(k)} \theta_{ij}(k) + \tilde{w}_i(k)\Delta\tau \\ \tilde{w}_i(k+1) &= (1 - \Delta\tau)\tilde{w}_i(k) + \varsigma\sqrt{\Delta\tau}\varepsilon_i(k) + \delta\Delta\nu_i(k\Delta\tau)\zeta_i(k). \end{aligned} \quad (8)$$

The mean square stability analysis of a stochastic system similar to the one in (8) has been thoughtfully investigated in [32, 33] for the vectorial network model (VNM) [34] which is considered as a simplification of the celebrated Vicsek model at the limit of large speed. In the VNM model, particles are thought to move fast enough such that they can interact at any time instant with any other randomly selected particles in the group. Such a consideration holds in particular for small particle sizes. Using the expression of the polarization in (4), writing the velocity vector in polar coordinates assuming a unit constant speed of 1, a linear approximation of the polarization is given for the remaining  $N - 1$  particles excluding the leader as [32, 33]:

$$\text{Pol}(k) = \frac{1}{N-1} \sum_{i=1}^{N-1} \mathbf{v}_i = \frac{1}{N-1} \left| \sum_{i=1}^{N-1} e^{j\theta_i(k)} \right| \simeq 1 - \frac{1}{2(N-1)}\rho(k),$$

where  $\mathbf{v}_i$  is the unit velocity vector;  $j$  is the imaginary index; and  $\rho(k) = \mathbf{E} \left[ \sum_{i=1}^{N-1} (\theta_i(k) - \theta_0)^2 \right]$  defines the steady state deviation from the synchronized state  $\theta_0$ .

### 3.3 Closed Form Expression

The steady state deviation  $\rho$  has been shown in [32, 33] to converge towards a finite value at the vicinity of a synchronized state for  $0 < (1 - \Delta\tau)^2 < 1$ . For the dimensionless model considered here, such a condition holds for  $0 < \Delta\tau < 2$ . After identification from the expression obtained in [32], a closed form expression of the polarization order parameter can be obtained as:

$$\text{Pol} \simeq 1 - \frac{(\zeta^2 \Delta\tau + \lambda\gamma^2) N - 2}{2(N-1)}, \quad (9)$$

where the number of connected neighbors is set to  $|\mathcal{N}_i| = N - 1$  for small group sizes. For group size of  $N \gg 2$ , the expression in (9) can be reduced to

$$\text{Pol} \simeq 1 - \frac{(\zeta^2 \Delta\tau + \iota\delta^2)}{2}$$

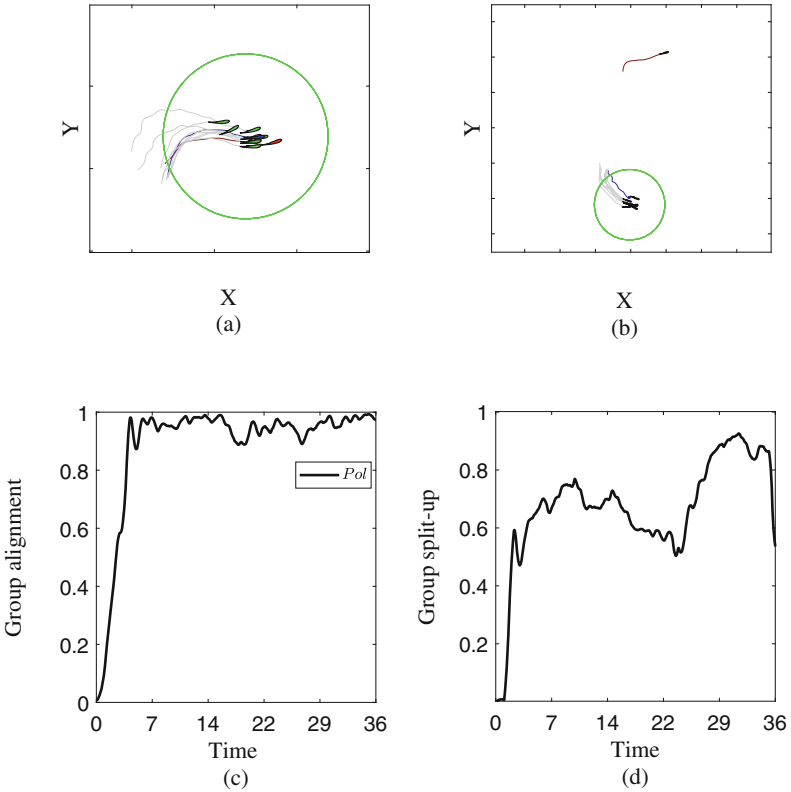
indicating that group response is mainly explained by the noise intensity  $\zeta$  and the jumps frequency  $\iota$  and intensity  $\delta$ . Doing a simple transformation to obtain  $\iota\delta^2 \simeq 2(1 - \text{Pol}) - \zeta^2 \Delta\tau$ , the closed-form expression above suggests that both  $\iota$  and  $\delta$  tend to be related by a negative power law. In addition, the closed form expression obtained above suggests that the expected variance of the jumps computed as  $\iota\delta^2$  can be leveraged to explain the transitions observed in the group in terms of a single parameter characterizing the level of noise in the system given a fixed value of the noise scaling coefficient  $\zeta$ .

**Table 1.** Model parameters retained in the simulations. The letter codes L, F, and S are used to indicate parameters required to model *leaders*, the *followers*, and *startled* fish behavior respectively.

| Model               | Behavior | Parameter  | Description          | Value    |
|---------------------|----------|------------|----------------------|----------|
| Individual dynamics | L-F-S    | $\zeta$    | Noise intensity      | 0.40     |
|                     | S        | $\iota$    | Jumps frequency      | [0 0.28] |
|                     | S        | $\delta$   | Jumps Intensity      | [0 4.18] |
|                     | L-F-S    | $v$        | Average speed        | 3.546    |
| Social behavior     | F-S      | $\kappa_p$ | Attraction gain      | 0.036    |
|                     | F-S      | $\kappa_v$ | Alignment gain       | 4.24     |
|                     | F-S      | $R$        | Interaction distance | 12.74    |

## 4 Numerical Analysis

Group coordination is analyzed for small group size of 10 fish which for simplicity included a single *leader* and a single *startled* fish initiating *escape reaction*. The reader is referred to [35] for results on larger group size. In all simulations, each fish type is set to share identical parameters as indicated in Table 1 with  $\varsigma_i = \varsigma$ ,  $\kappa_{vi} = \kappa_v$ ,  $\kappa_{pi} = \kappa_p$ ,  $\iota_i = \iota$ , and  $\delta_i = \delta$ . The polarization order parameter  $Pol$  is evaluated at steady state by computing the average values over 100 sample trajectories by varying values of  $\iota$  and  $\delta$  sampled in a discrete  $100 \times 100$  grid size. Only the last 180-time steps of the simulations were considered to allow the group to reach a steady state.



**Fig. 2.** Sample trajectories illustrating group response to (a) small jumps ( $\iota = 0.04$ ,  $\delta = 0.17$ ) and to (b) larger jumps ( $\iota = 0.12$ ,  $\delta = 0.50$ ) introduced by the *startled* fish and time trace of the corresponding group polarization  $Pol$  for small jumps (c) and for larger jumps (d). The circles in (a) and (b) indicates the interaction radius from the *followers* averaged position.

In the analysis, simulations are always started with individuals coordinating their motion before introducing the fish initiating *escape reaction* after a few time steps. In particular, departing from a random location within a circle of radius  $R$

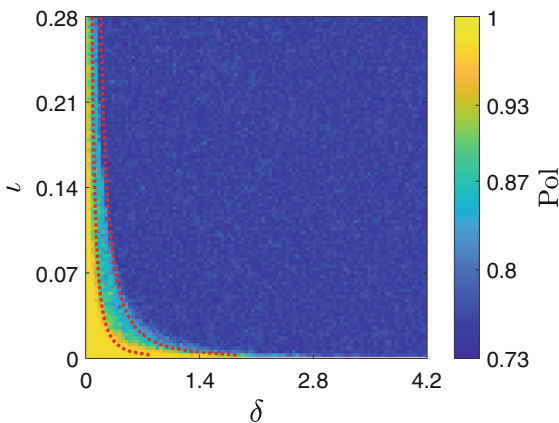
from the origin, fish initial positions are generated within the interaction radius of their neighbor. The *leader* position is set at a random location near the origin. The fish initiating *escape reaction* is introduced at a time step corresponding to 7.18 time units at a random position within a distance corresponding to half of the interaction radius of  $R$  from the group center. The initial heading direction of *followers* is randomly set between  $[-\pi, \pi]$  rad. Simulations are conducted in an unbounded and non-periodic domain with the interaction radius set to 12.74 length units. The latter value was selected to avoid group splitting in the absence of jumps. Note that, the choice of an interaction radius rather than a vision cone allows group response to be independent of the position of individual fish within the group. In addition, for larger group sizes, a topological approach for the interaction [36] can be considered by setting a fixed number  $K$  of connected neighbors within a fixed radius  $R$ .

#### 4.1 Time Trace of the Group Response to *escape Reaction*

Figure 2 presents two exemplary simulated trajectories and the corresponding time trace of the polarization order parameter (Pol). The plots indicates a high level of group alignment for small variations of the frequency  $\nu$  and intensity  $\delta$  of the jumps while for increased values of  $\nu$  and  $\delta$  the polarization order parameter tend to highly fluctuate. For the larger parameter values selected, one can observed a group split-up after a few time steps where *followers* and *startled* fish synchronize their motion in order to swim away from the initial group *leader*.

#### 4.2 Group Response to a Variation of the Jumps Parameters

Figure 3 illustrates group response measured by the polarization order parameter in (4) as the frequency  $\nu$  and intensity  $\delta$  of the jumps are increased. The

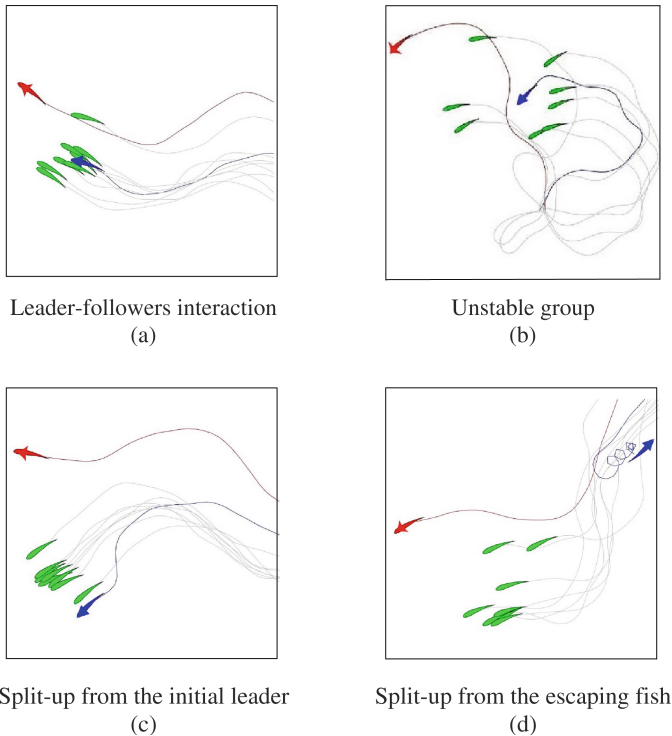


**Fig. 3.** Contour plot of group polarization (Pol) as the frequency  $\nu$  and intensity  $\delta$  of the jumps are varied. See Table 1 for model parameters.

contour plot of the polarization in Fig. 3 indicates a transition from a highly to a less coordinated state. As suggested by the closed form expression in (9), Fig. 3 indicates a negative power law relation between  $\iota$  and  $\delta$  for given values of the polarization order parameter Pol. In addition, the different coloration pattern in Fig. 3 tends to indicate that group coordination transitions through several states as  $\iota$  and  $\delta$  are increased from smaller to larger values. Two illustrative cases depicted by the red dashed lines are plotted in Fig. 3 to show how the closed form expression in (9) can be utilized to predict the level of order in the system as  $\iota$  and  $\delta$  varies. The first line corresponds to a value of Pol = 0.965 predicts the transition bound between the yellow area and the green area and the second line corresponding to a value of Pol = 0.805 predicts the transition bound between the green colored area and the blue colored area.

### 4.3 Transition States Observed as the Jumps Are Increased

Four distinct states illustrated in Fig. 4 are observed as the expected variance of the fast turns  $\iota\delta^2$  is increased and characterized by the following behaviors:



**Fig. 4.** Illustration of the transition states observed for selected value of the expected variance of the turn  $\iota\delta^2$  in various colored areas of Fig. 3 including yellow for (a), between yellow to green and green to blue for (b), green for (c), and blue for (d).

- **(a) leader-followers relationship** illustrated in Fig. 4(a) depicted by a strongly coordinated state where all group members including *leader*, *followers*, and *startled* fish align their heading to move all-together in the same direction;
- **(b) unstable state** illustrated in Fig. 4(b) where the group collective response is highly unstable and fish group likely to split-up apart and disperse;
- **(c) group split-up and switching leadership** illustrated in Fig. 4(c) where the group split-up with the modelled *leader* and the *followers* tend to coordinate their motion in a direction prescribed by the *startled* fish;
- **(d) group split-up from the *startled* fish** illustrated in Fig. 4(d) where the fish initiating *escape reaction* cannot coordinate their motion with *followers* which tend to align their heading direction with the modelled *leader*.

Note that the states observed above result from simulations always departing from an ordered state where  $\iota\delta^2 = 0$  prior to introducing *escape reaction* such that  $\iota\delta^2 > 0$  after a few time steps. The values of  $\iota\delta^2 > 0$  used in the illustrative cases in Fig. 4 are extracted from the colored area in the colormap in Fig. 3.

## 5 Discussions and Conclusions

*Escape reaction* investigated here is an alarm reaction behavior [13, 14, 29] characterized by fast turns and increased speed. This work shows that a stochastic process [9, 24] with biased jumps can be utilized to reproduce a similar behavior observed during *escape reaction* [16]. By introducing small perturbations to the group at the vicinity of a synchronized state where all individuals shared a common heading angle, a closed-form expression has been proposed depicting that, for fixed values of the noise intensity  $\varsigma$ , the expected variance of the jumps evaluated as  $\iota\delta^2$  can be used to predict the level of order in the system. The proposed closed-form expression has been validated against numerical simulation and shown effective to predict the transition between various states observed.

The numerical results from this work indicate that *escape reaction* can maintain a strong level of coordination for smaller values of  $\iota\delta^2$  where the group exhibits a synchronized leader-follower formation. *Escape reaction* can force the group to diverge from the *leader* heading direction and *followers* to align their heading with the *startled* fish. In this case, the sudden and fast turns initiated by the *startled* fish are observed to stir *followers* away from the *leader* prescribed heading direction. This results in leadership switching from the modeled *leader* to the *startled* fish and the new synchronized group moving in a toroidal circular formation pattern as described in the literature [37]. In this scenario, the leader becomes isolated and vulnerable to the predator [12]. *Escape reaction* can also cause a synchronized group to transition to a highly unstable state with a highly volatile polarization value and where individuals can split up and disperse. This situation can result in individuals being isolated and at risk in the presence of a predator. As the expected variance of the jumps become larger, *escape reaction* can force the *startled* fish to swim away from the group which then maintains

its initial *leader-followers* synchronized state away from the disturbances introduced by the *startled* fish. This tendency to swim away from the group might put the *startled* fish into a vulnerable position.

The work proposed in this manuscript contrasts with other attempts to model *escape reaction* such as the one in [19] where the behavior is initialized by setting the *startled* fish a velocity significantly larger in amplitude and opposite direction to the averaged group heading. Such a modeling approach results in a propagation wave typical to cascading behaviors observed in nature on large herds [38]. The stochastic model proposed here results instead in circular or toroidal motion patterns typically observed in fish groups [37] in the presence of a predator [12]. The results from this work are thus in line with many prior works where *escape reaction* can initially destabilize a group of fish but can also favor strong group coordination in the long run [13] allowing groups to stay resilient when facing a predator.

The method proposed in this work to recreate *escape reaction* can be utilized in other model of collective behavior to recreate antagonistic interactions or switching leadership [39]. These behaviors are relevant when a group of fish is exposed to a strong stimulus or when the group must negotiate a drastic change of heading direction. The findings from this work also suggest that the expected variance of the turn can be utilized as a single parameter to characterize the level of disturbances introduced by the *startled* fish. This single parameter can be utilized to design appropriate controllers in order to either improve or disrupt group coordination in several unmanned multi-vehicle systems. In future works, the framework considered here can be extended to study group responses to various sources of disturbances resulting into several fish exhibiting sudden and fast turns with different probability distributions.

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**Data statement.** All data used in this work are generated from the discrete time approximation (3) of the model in (1) using the parameters reported in Table 1.

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