

# Self-reorganization and Information Transfer in Massive Schools of Fish

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**This file contains all reviewer reports in order by version, followed by all author rebuttals in order by version.**

**Attachments originally included by the reviewers as part of their assessment can be found at the end of this file.**

Version 0:

Reviewer comments:

Reviewer #1

(Remarks to the Author)

Please see attached PDF ("review\_Hang.pdf")

(Remarks on code availability)

I do not see any code available in the ZIP file.

Reviewer #2

(Remarks to the Author)

This manuscript is a real puzzle: there are some interesting and nice results (especially one, see below), but unfortunately these are diluted within a mix of irrelevant, misleading and (in some cases) plain wrong claims.

This makes the final decision about the manuscript very hard. In principle, I am not totally opposed to publication in Nat. Comm. but:

- certainly not in the current form
- the Authors should convince me that the supposedly interesting results are compelling enough

Hence, as I said, I recognize that the manuscript contains interesting contributions. However, the presentation is terrible, making it exceedingly difficult to extract the key messages without a lot of effort. A heavy revision, focused on summarizing the content, highlighting the main insights and novelty, and streamlining the text, would significantly strengthen the manuscript and \*possibly\* make it ok for Nat Comm.

Let me start by listing here what are (in my opinion) the only three interesting results of the paper:

1. flow interaction destabilises polarization as  $N$  increases, leading to fragmentation; this is quite interesting.
2. a drop of the correlation length occurs \*prior\* to fragmentation; this is VERY interesting and it should be the punchline of the paper: the Authors have found a precursor of fragmentation, which seems great.
3. flow interaction increases information propagation speed, mildly interesting.

The Authors need to rewrite the manuscript using 1-2-3 above as a roadmap.

On the contrary, these are the problematic points of the manuscript:

A. The introduction must be rewritten putting the emphasis on 1-2-3 above, and cutting all the vague and pseudo-holistic parts, which do not add any significance.

B. It is unacceptable that NO details of the model are given in the main text. This is still a scientific paper, so the main

mathematical details MUST be given in the main text; because much of the rest of the material can be cut (see below) there will be ample space to do that. I cannot recommend publication if this is not done: this is an exclusively numerical paper, the model must be in the main. I am totally against equation-free science.

C. I completely fail to get the relevance of non-reciprocity here; I realise that nowadays non-reciprocity is a hot topics, but again - it is quite misleading in this context. Information propagates because of interaction, be it reciprocal or not (see below).

D. Using "More is different" as a title of a Section is not helpful at all, and quite rhetorical. The Authors should use titles summarizing the content of the section, not a famous paper by a Nobel prize.

E. I am completely baffled by the statement that the school swims faster than the individual. Even after reading [16], I find no sense in this statement. We have been taught at school the inequality:

$$|\sum_i v_i| \leq \sum_i |v_i|$$

because here  $|v_i| = U$  for each  $i$ , we get:

$$(1/N) |\sum_i v_i| \leq (1/N) \sum_i |v_i| = U$$

meaning that the mean speed of the group is smaller than the individual speed.

so, what is going on here?

this seems completely wrong, or - at best - very poorly explained. If this is due to the interaction with the flow, then there is something wrong in the way the mean velocity is defined. Anyway, the point is completely irrelevant for the rest of the paper, hence I would cut it entirely (but I am still curious about how the above high-school-level inequality is violated)

F. The 'more is different' section is too long; the Authors should keep only the material strictly needed to talk about the rest.

G. In this disgraced Section there is another very suspicious - in my opinion wrong - claim, namely that the density increases with size. According to the Supp Info no effort has been done here to cure and take care of the border bias. Therefore I am 90% sure that what the Authors found here is simply an effect of the border bias; this is a very old bias indeed, that was already recognised in the book Stoyan, D. & Stoyan, H. 1994. Fractals, Random Shapes and Point Fields. Chichester: J. Wiley. To see this bias at work in a spectacular way see Fig.6 of Animal Behavior 76 (1), 237-248 (2008) and relative discussion on how to eliminate the bias. Therefore, either the Authors cure the border bias, or they cut any statements about how density depends on size (which are irrelevant anyway).

H. That scale free correlations break down when there is fragmentation is \*completely\* trivial, hence putting the emphasis on this as the Authors do is very misleading. The Authors clearly know that scale free correlations of the orientations are due to Goldstone modes, because they write that; so, it is obvious that when there is fragmentation, one loses completely the spontaneous symmetry breaking of the Goldstone theorem, hence no Goldstone models, hence no scale free correlation. As I said, this is trivial. As I said above, what is FAR from trivial is that the correlation length decreases PRIOR to fragmentation. This is the only reason I am not recommending straight out rejection of the paper: if true, this result is really compelling. So, I strongly recommend to the Authors to concentrate the paper on this result, and on the handful of truly essential ancillary results. However, because this result is so important, I urge the Authors to make an effort to strengthen the result with more and better numerical evidence: Fig.4F is definitely not enough to convince me.

I. I think that the part (three sections) on information propagation is far far too long, and it should be cut entirely, or considerably trimmed, if the Authors insist on keeping it. Also it does not go together very coherently with the result on the precursor of fragmentation above. But, if the Authors decide to keep it and trim it, I recommend at least to cut - or make very very short - the section about the fact that fragmentation slows down propagation: this too is completely obvious.

J. The statement that inertia is not necessary to have linear propagation is wrong. Even though here there is no behavioural inertia, there is of course inertia nevertheless due to the interaction with the flow. Hence, this claim should be cut, or at least completely reworded, as in the current form it is not true.

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(Remarks on code availability)

Version 1:

Reviewer comments:

Reviewer #1

(Remarks to the Author)

Please see attached PDF for comments.

(Remarks on code availability)

I still could not find any code uploaded with the manuscript (despite "Supporting code available as supplementary materials with the paper."), so I am unable to review it.

## Reviewer #2

### (Remarks to the Author)

The Authors have made several steps forward, although more is needed for me to recommend publication in Nature Communication. More specifically:

\* I am still completely baffled by the statement that the school swims faster than the individuals, and I see from Ref.1 report that I am not alone. In what reference frame this statement applies?

Anyway, the current "clarification" in the amended version is not clear at all to me. I again suggest that this (old, by the way) result be removed from the paper.

\* The way the Authors take care of the boundary in the amended version of the manuscript is NOT the correct one: removing from the statistics points of the border is not the right way to go and not the one used in Animal Behavior 76 (1), 237-248 (2008), which clearly was not "carefully studied".

The correct way to cure the border bias is, for each point  $i$  to calculate its distance from the border, let call it  $R_i$ , and then - when counting all the pairs of points formed by  $i$  with its neighbours - to ignore all points beyond  $R_i$  from  $i$ .

Hence, either the Authors proceed with the correct procedure or - given the \*very\* weak decrease of NND with  $N$  and given the irrelevance of this result in the bigger picture of the paper - I suggest that this is removed.

\* I appreciate the additional data to support that  $\langle \xi \rangle$  decreases before the loss of cohesion. As I said, this is very interesting.

\* Regarding linear propagation, now that I see the equation in the main text, yes, I finally understand what is going on (see? equations helps after all!). Due to the anisotropy of perception, this is a \*first\* order equation in time and in space, hence, yes, there is a traveling solution. HOWEVER, this is not a wave equation at all and its unusual form means that propagation is exclusively in one direction, hence drastically anisotropic, and - most importantly - unlike anything recorded in real experiments, as disturbance waves are known to propagate in any direction. This must be explained more directly and explicitly than it is done at the moment.

\* Regarding splitting in two the manuscript, I am all in favour of that, but - once my remarks are addresses - I would recommend publication in Nat Comm only of the first part on scale-free correlations.

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A final remark regarding the reply to Ref.1 (if it can be forwarded to them).

The Authors write:

"By construction, we are building our correlation function based on fluctuation of individual velocity, and thus, the average or mean of velocity fluctuation is exactly zero. According to Goldstone modes, the correlation function should cross zero, and the integration of correlation function over space should be zero."

There are two very wrong statements in this paragraph, which is worrying, because it suggests that the Authors do not have the physics of correlation functions fully under control. Here they are:

1. Goldstone Theorem (GT) by itself has nothing to do with the fact that the correlation function must cross zero. GT only states that the correlation must be long range, i.e. power law. If the correlation were calculated with a bona fide statistical ensemble (i.e. Boltzmann), then that GT power law correlation function would NOT cross the zero, as well as an exponential correlation function.

The fact that the correlation function computed here - with this particular experimental definition which lacks an ensemble - must cross the zero at some point is true for any kind of shape, power law (as in the case of GT), or exponential. And the reason why this correlation must cross the zero brings us to the second wrong statement:

2. It is true that the mean of the velocity fluctuation is by definition zero, but the integral of the correlation function over  $r$  is NOT zero, just check the algebra. On the other hand, if we call NUM the numerator in the definition of the correlation function, then the integral of NUM over  $r$  IS zero, because one gets the square of the mean fluctuation. Because the integral of NUM is zero, this means that the function NUM must have a zero itself, so that the whole function  $C(r)$ , of which NUM is the numerator, must have a zero.

Whenever the ensemble correlation function is short-range (exponential), this zero is irrelevant and practically impossible to distinguish from the many zeros due to the noise/fluctuations of the correlation decayed to zero. On the other hand, when the ensemble correlation is scale-free (power law), then this zero becomes very evident, its position scales with  $L$ , which is the best indicator of scale free correlations.

(Remarks on code availability)

Version 2:

Reviewer comments:

Reviewer #1

(Remarks to the Author)

The authors have satisfactorily answered all of my questions. I have no further comments on the manuscript.

Siddhartha Verma.

(Remarks on code availability)

Reviewer #2

(Remarks to the Author)

All my points have been satisfactorily addressed, hence I now support publication in Nat Comm.

I also congratulate the Authors for their great patience and cold blood in dealing with me, but I think that the final manuscript is significantly better than the original version.

(Remarks on code availability)

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## SUMMARY of REVISIONS

We thank the referees for their careful consideration of our manuscript and helpful suggestions.

## RESPONSE TO REFEREES

Reviewer #1 (Remarks to the Author):

In this manuscript, the authors study the collective behaviour of a large number of point swimmers (on the order of  $\sim O(1k)$  to  $\sim O(10k)$  mostly) to better understand the behaviour of fish schools. The authors use a potential flow model combined with biased visual sensing and a set of empirical behavioural rules, to implement the motion of each individual point swimmer. The primary focus is to examine scale-free correlations of the motion, group cohesion, and information transfer among the swimmers.

Response: We thank the referee for their careful and constructive review of our work and for their support of this manuscript.

I have the following questions and comments for the authors:

1. For the readers' benefit, the authors should clarify in the main body of the text (not supplementary) that the "school of 50,000 fish" is actually a collection of massless point particles, and that the 'flow interactions' or 'hydrodynamic interactions' specific to this study are based on simplified two dimensional potential flow assumptions.

Response: We thank the referee for this suggestion. We revised the manuscript to include a "Mathematical Model" section that clearly spells out the details of the model.

2. The mention of potential flow also brings another question to mind: how are the flow interactions damped in the simulations? Usually the influence decays with distance, but viscous damping is not allowed in potential flow. This would allow the flow-mediated disturbances to accumulate indefinitely over time, leading to unrealistic behaviour.

Response: Thank you for bringing up this issue. In our model, flow interactions are instantaneous – each particles creates a dipolar field along its heading direction (as shown in Fig. 1A). There is no vorticity that is shed in the fluid medium that needs to be damped. The fluid has no inertia; there is no accumulation over time or fluid inertia. This is a purely kinematic model where the far-field signature of a swimmer is captured by a dipolar flow singularity. This is

a hallmark of the potential flow model that we use: fish are self-propelled flow “singularities” that are fundamental solutions to the Laplace equation. We clarify this in the revised manuscript.

3. The authors make an important point when they state “...in the context of our model...” at one point in their manuscript. This should be clarified very early on in the main body, and maybe even in the abstract, to ensure that readers fully appreciate that the conclusions being drawn are dependent on the model parameters.

Response: We thank the referee for this suggestion. We revised the manuscript to clarify in multiple locations that all conclusions are drawn from our model and are rooted in quantitative results, that are robustly produced by the model.

4. The primary model for point swimmer motion depends on the three free parameters “( $I_n$ ,  $I_a$ ,  $I_f$ )”. This brings about the question of having to manually tune these coefficients until the desired/expected behaviour is achieved. For example, Fig 3D shows that changing the value of  $I_f$  can change the behaviour substantially. So how is the generalizable ‘correct’ value of these parameters determined, besides tuning to desired behaviour? The authors mention using parameters that maintain polarity for small groups, but then why would the same parameters expected to be applicable in the 50k case, where the behaviour is very different?

Response: We thank the reviewer for bringing up point.

In our previous work (Audrey Filella, François Nadal, Clément Sire, Eva Kanso, & Christophe Eloy (2018) PRL), we conducted a parametric study over the parameter space of  $I_a$  and  $I_n$ , which we reproduce here for the referee’s convenience.

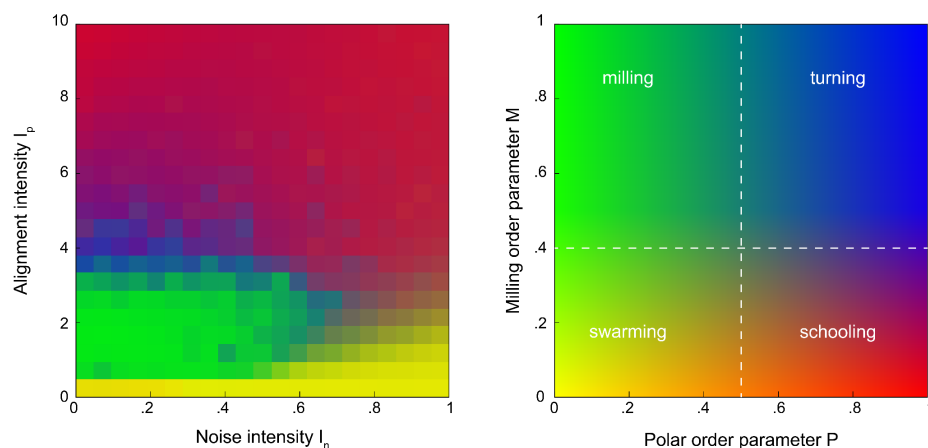


Figure 1 Reproduction of phase diagram for the collective behavior model with hydrodynamic interaction for 100 fish from Filella et al. PRL (2018). Depending on the alignment intensity  $I_a$  and noise intensity  $I_n$ , the school self-organizes into milling, schooling, turning and milling patterns. Parameter ranges are  $I_a \in [0,10]$  and  $I_n \in [0,1]$ ,  $I_f = 0.01$ , and  $N=100$ .

By changing ( $I_n$ ,  $I_a$ ), the fish school falls in disorganized swarming (low polar order parameter  $P$ , and low milling order parameter  $M$ ), polarized schooling (high polar order parameter  $P$ , and low milling order parameter  $M$ ), rotationally ordered milling (low polar order parameter  $P$ , and high milling order parameter  $M$ ), and polarized turning pattern (high polar order parameter  $P$ , and intermediate milling order parameter  $M$ ), with the last one only existing when hydrodynamic interaction is present.

In the current manuscript, we focus on the polarized schooling pattern and analyze how the group-level behavior changes with the increase in number of fish. We use parameter sets that generate polarized schooling pattern ( $I_a = 9$ ,  $I_n = 0.5$ ,  $I_f = 0.01$ ) for  $N=100$ . With increasing  $N$ , the emergent behavior of the fish school is different. The polarized school fragments and reorganizes themselves with the increase in number of swimmers. This behavior is robust as long as the parameters  $I_a$ ,  $I_n$ ,  $I_f$  produce polarized schooling in smaller fish groups.

In Fig.3, we performed parametric study of collective motion as a function of  $I_n$  and  $I_f$ . We found that with larger  $I_f$ , the school fragments at smaller number  $N$ , and changes in  $I_n$  does not significantly influence the collective behavior. In Fig. 4D, we showed that at several discrete parameter sets ( $I_a$  and  $I_n$ ) and same hydrodynamic intensity  $I_f$ , the polarized school have the same scale-free correlation. In Fig. 6, we showed that information transfer speed scales linearly with  $I_a / I_n$ .

As to why we don't expect these parameter values with increasing number of fish, this is because we are probing exactly the physics of what happens when the individuals are the same, but we increase their number.

Fixing the hydrodynamic intensity  $I_f = \pi (a/2)^2 U$ , where  $a$  is body length and  $U$  is swimming speed, means simply that we are fixing the size and speed of the swimmers.

Fixing the alignment intensity  $I_a$  means fixing the response of a swimmer to its immediate neighbors, which is limited by the individual's sensory and response abilities [1,2]. This interaction model should work equally well for 100 fish and for 50,000 fish as a prior, unless there exists some experimental finding that rejects this hypothesis (we are not aware of any). In fact, [3,4] show based on experimental evidence in fish schools and bird flocks that the coupling strength does not change over the number of individuals.

The noise intensity  $I_n$  may change over the number of fish, say due to crowding effects [5], but as we show in the manuscript, the change in noise intensity does not have significant effect in the results (Fig. 3C) – noise is not the mechanism that drives fragmentation and reorganization.

[1] Dickinson, Michael H., et al. "How animals move: an integrative view." science 288.5463 (2000): 100-106.

[2] Burden, Samuel A., et al. "Why animals can outrun robots." *Science Robotics* 9.89 (2024): eadi9754.

[3] Gautrais, Jacques, et al. "Deciphering interactions in moving animal groups." (2012): e1002678.

[4] Bialek, William, et al. "Statistical mechanics for natural flocks of birds." *Proceedings of the National Academy of Sciences* 109.13 (2012): 4786-4791.

[5] Sosna, Matthew MG, et al. "Individual and collective encoding of risk in animal groups." *Proceedings of the National Academy of Sciences* 116.41 (2019): 20556-20561.

5. Line 50: "In physical models of flow-coupled ..." – I am having some trouble understanding the meaning of 'physical models'. I assume the authors are referring to fish-shaped models used for laboratory experiments? Also, I am a bit unclear on '...perturbations get amplified as they propagate...' – perturbations die out due to viscous effects, then getting amplified would likely violate conservation of momentum.

Response: Yes, the referee is correct. By physical models, we mean fish-shaped models used for laboratory experiments, as well as fish-shaped mathematical models with flow interactions.

Several recent studies (including work from our group) [1,2,3] have recently shown that swimmers interacting with each other through the fluid as medium can self-organize and position themselves at regular spacing relative to each other. However, these equilibria are not stable. The fluctuations in the relative positions of these swimmers get amplified. This instability grows downstream with more swimmers, yet there is not violation of conservation of momentum. Conservation of momentum and balance laws do not prohibit growth of instabilities.

[1] Tsang, A. C. H., Shelley, M. J., & Kanso, E. (2018). Activity-induced instability of phonons in 1D microfluidic crystals. *Soft Matter*, 14(6), 945-950.

[2] Newbolt, J. W., Lewis, N., Bleu, M., Wu, J., Mavroyiakoumou, C., Ramanarivo, S., & Ristoph, L. (2024). Flow interactions lead to self-organized flight formations disrupted by self-amplifying waves. *Nature communications*, 15(1), 3462.

[3] Heydari, S., Hang, H., & Kanso, E. (2024). Mapping spatial patterns to energetic benefits in groups of flow-coupled swimmers. *Elife*, 13, RP96129.

6. Line 71: The authors liken message transmission to the game of telephone, and indicate that the message becomes distorted as it is passed among a large number of individuals. How does this happen in the authors' model? Is there a stochastic component involved that leads to message distortion? Does the cumulative 'noise' grow with number of times the message is propagated?

Response: We thank the reviewer for asking this question. The collective turning emerges from the local noise and local interaction. The "message" is the turn itself. The message does not get

distorted (see Fig.6 inset): the curved trajectories of all swimmers are similar despite the time delay in when a given swimmer in the group executes the turn.

To further convince the referee of this, we calculate here the correlation between curvatures as

$$Q_{ij} = \max_{\tau} \frac{\int_{t=t_1+\tau}^{t_2} k_i(t) k_j(t-\tau) dt}{\int_{t=t_1+\tau}^{t_2} k_i(t) dt \int_{t=\tau}^{\tau} k_j(t) dt}$$

If this value is close to 1, it means that the curvatures are perfectly matched.

In the figure below, we show  $Q$  for the group of 1000 fish turning. We calculate  $Q$  between the first ranked fish and all other fish as a function of their turning order  $o$ . There is very little distortion of the turning message ( $Q \approx 0.9$ ).

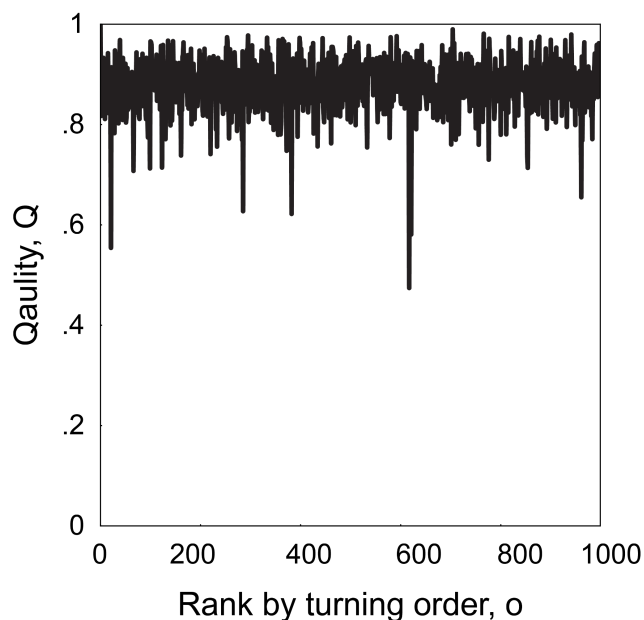


Figure 2 Correlation between the curvature of each fish relative to the first-ordered fish shows nearly no distortion in the message (the curvature of the turn itself).

7. Line 105: I am having some trouble understanding why the summation for  $P$  involves the complex exponential function (I assume 'i' represents  $\sqrt{-1}$ ). Why is the imaginary part useful? Also, " $\theta_j$  is the orientation of swimmer  $j$ " with respect to what precisely, i.e., the group axis, the lab frame, or something else?

Response: The polar order parameter  $P$  measures how strong the alignment of the school is. In vector form, it is

$$P = \left| \frac{1}{N} \sum_{j=1}^N (\cos \theta_j, \sin \theta_j) \right|$$

Alternatively, and for conciseness, we wrote it in complex form in the manuscript

$$P = \left| \frac{1}{N} \sum_{j=1}^N e^{i\theta_j} \right|$$

By definition,  $\theta_j$  is measured in the lab frame (line 84-85 in main text of revised manuscript and line 604 in original SI document). However, the choice of frame would not influence the value of polar order parameter  $P$  after taking the norm, namely,  $P = \left| \frac{1}{N} \sum_{j=1}^N e^{i(\theta_j + \Delta\theta)} \right| = \left| \frac{1}{N} \sum_{j=1}^N e^{i\theta_j} e^{i\Delta\theta} \right| = \left| \frac{1}{N} e^{i\Delta\theta} \sum_{j=1}^N e^{i\theta_j} \right| = \left| \frac{1}{N} \sum_{j=1}^N e^{i\theta_j} \right|$ , where  $\Delta\theta$  is an arbitrary angle. We modified the text using the vector notation and clarify the definition of orientation.

8. Lines 110 and 114: “we found that, on average, schools swam faster than the individual swimming speed  $U$ ” – this is a bit puzzling to me, how can the average speed be faster than that of the individuals? Being slower would be understandable since not all individual velocity vectors may be parallel to each other, but I don’t fully understand the school being faster.

Response: We thank the reviewers for pointing this out. We corrected this sentence by saying “we found that, on average, schools swam faster than the self-propelled speed  $U$ ”.

In our model, the self-propelled speed  $U$  is fixed for each swimmer. When hydrodynamic interaction is involved, each swimmer  $j$  is also advected by the flow field created by other swimmers with velocity  $U_j$ , thus, the speed of each swimmer is  $|U(\cos \theta_j, \sin \theta_j) + U_j|$ , which can be larger than  $U$ . For the same reason, the magnitude of group velocity can also be larger than 1. In both prior work and current work, we found that, in polarized groups, hydrodynamic interaction increases the group speed.

9. Line 138: “the school turned frequently” – what exactly induces a turning event in the authors’ model? Is this driven by an external catalyst, or is it based on an internal mechanism? Also, a brief description of why the lead swimmers turn instead of those in the middle of the group would be helpful – I assume it is due to the biased vision and the imposed rules to maintain alignment with neighbours?

Response: There is no external catalyst. All reported behaviors arise spontaneously in the model. Turning arises naturally due to individual level noise and flow interactions. When noise is not present (Fig. S3), collective turning, fragmentation and rejoining arise from hydrodynamic interactions, which are known to induce similar effects as noise (Filella *et al.* (2018) PRL).

In our model, and according to our analysis, the anisotropic information transfer in the longitudinal direction is always from the front of the group to the back. Thus, turning is always initiated at the front of the group because it is a vision-based effect. Perturbations initiated at the back of the school don’t propagate forward.

The fact that turning arises from the boundary of the school has been commonly observed in biological and physical systems [1,2].

[1] Cavagna, Andrea, Irene Giardina, and Francesco Ginelli. "Boundary information inflow enhances correlation in flocking." *Physical review letters* 110.16 (2013): 168107.

[2] Fahimipour, Ashkaan K., et al. "Wild animals suppress the spread of socially transmitted misinformation." *Proceedings of the National Academy of Sciences* 120.14 (2023): e2215428120.

10. Line 187: The calculation of  $C(r)$  is limited to group sizes of 1000 or smaller, and only to instantaneous snapshots of the data when the group is highly polarized. Doesn't limiting the analysis to  $P > 0.9$  introduce a bias? It would be helpful if the authors clarify the rationale for doing so. Also, I think small group sizes are considered since they remain coherent and polarized, but then again, what is the benefit of selecting these? Wouldn't it be more generalizable to consider 10k individuals, since the authors state that group behaviour changes minimally beyond this number?

Response: We thank the reviewer for asking this! This is a deep point. It is perhaps not very well appreciated outside the statistical physics community: scale-free correlations in velocity fluctuations are guaranteed in cohesive and highly polarized groups (for which  $P > 0.9$ ). Scale-free correlations in velocity fluctuations are related to Goldstone modes: it is imperative to start from a highly polarized state, for which there is a continuous symmetry breaking (rotational symmetry is broken), and thus slow spatially-varying rotations cost little energy and produce Goldstone modes. For more details, we refer the review to read the original research paper of Cavagna *et al*, PNAS (2010) and excellent review paper Cavagna *et al*. Physics Reports (2018) – full citation listed below.

With this as our starting point, we first verified that indeed scale-free correlations arise in our model in cohesive and highly polarized groups (whether they are of 1000 fish or 10000 fish – see figure below)

The important contribution of our work is that when fragmentation occurs, there is a decrease in scale-free correlation prior to the fragmentation event.

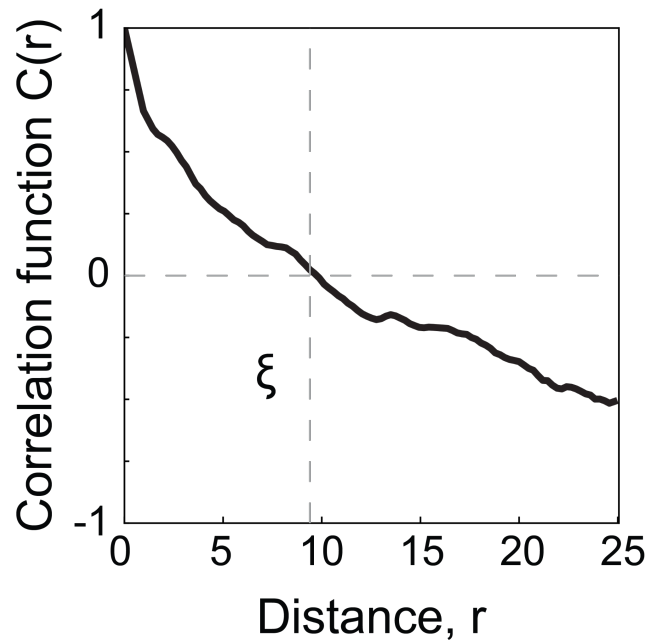


Figure 3 Correlation function over distance for a cohesive and highly polarized school of 10,000 fish without hydrodynamic interaction.

11. At short distances, the correlation coefficient being close to 1 makes perfect sense since the point swimmers are instructed to maintain alignment using the motion model. But a correlation coefficient of -1 at extremely large distances is very surprising. What is the cause of this?

Response: We thank the reviewer for asking this question! This is actually the key point of scale-free correlation.

By construction, we are building our correlation function based on fluctuation of individual velocity, and thus, the average or mean of velocity fluctuation is exactly zero. According to Goldstone modes, the correlation function should cross zero, and the integration of correlation function over space should be zero  $\int_0^L C(r) dr = 0$ .

The meaning of having an anti-correlation at large distance means that the velocity fluctuation at different ends of the school are anti-parallel, as illustrated in Fig.4B. This indicates that the school acts as an entity, where any perturbation can propagate through the school.

For more details, we refer the review to read the original research paper and excellent review paper:

1. Andrea Cavagna, Alessio Cimarelli, Irene Giardina, Giorgio Parisi, Raffaele Santagati, Fabio Stefanini, Massimiliano Viale "Scale-free correlations in starling flocks" PNAS (2010).
2. Andrea Cavagna, Irene Giardina, Tomas Grigera "The physics of flocking: Correlation as a compass from experiments to theory" Physics Reports (2018).

12. Line 211: "...the slope of the best fit of  $\xi$  vs L is nearly one-third, similar to the slope..." – What would happen if the authors consider the individual datasets shown in Fig 4D and get their corresponding slopes, i.e., separate slopes for dataset X, O, square, etc.? Do they show the same value of 1/3? Looking at the images, it seems to me the slopes would be very different, but a numerical value would be helpful to confirm. If they are not the same, then again the issue arises of what the 'correct' model parameter values are, since they can be selected arbitrarily.

Response: Yes, there is indeed difference in the fitting of different datasets:

For all the data, the slope is 0.365;

For  $I_a = 9$ ,  $I_n = 0.5$ , the slope is 0.336;

For  $I_a = 7$ ,  $I_n = 0.5$ , the slope is 0.406;

For  $I_a = 5$ ,  $I_n = 0.5$ , the slope is 0.284;

For  $I_a = 9$ ,  $I_n = 0.3$ , the slope is 0.346;

For  $I_a = 9$ ,  $I_n = 0.7$ , the slope is 0.345;

Clearly, the difference is not big. We included this data in SI Table. 2 in the revised manuscript.

13. Line 268: The analysis (this time for turning) is again limited to groups with a small number of individuals (<2000). As the authors state, the behaviour changes considerably for 10k swimmers, including fragmentation and merging. It is difficult for me to understand why the smaller groups were selected, especially since the conclusions are presented as if they should be generalizable to all schools.

Response: We first analyzed these turning maneuvers on smaller schools of less than 2,000 fish that stay cohesive during the turn for two reasons:

1. To establish a baseline from which to compare what happens when the school splits and merges.
2. Because in larger school, the clusters that form do undergo collective turns, sometimes without splitting and rejoining, hence the analysis of a cluster of fish that turns is also relevant in the context of the large schools that fragment, reorganize and reassemble.

The tools that we present for analyzing the turning only, splitting and turning, or merging and turning, are generally applicable to any group size.

14. Also, in that vein, the statement in Line 348 (and similar elsewhere) "...massive schools of fish, consisting of up to 50,000 individuals..." - while technically true due to the use of 'up to', could be tempered a bit, given that the majority of the analysis regarding correlation and information transfer is done using groups that are more than an order of magnitude smaller.

Response: Yes, the reviewer is correct about this: the simulation of 50,000 fish is very costly. The point of doing this simulation is to show our computational prowess but importantly to show that beyond a certain number of swimmers, the phenomena of fragmentation and reassembly are always similar. Therefore, the analysis tools and the results that we present are applicable to any school size. Indeed, the analysis tools we employ in the current manuscript do not depend explicitly on the total number of swimmers and are equally applicable to the observed phenomena, whether in a school of 10,000 or a school of 50,000.

15. Line 296: The authors claim that “our theory predicts an anisotropy in the information transfer” – in my opinion it is not a prediction of theory, but rather a result of the sensing model imposed on the swimmers using biased vision.

Response: We thank the reviewer for bringing this up. We moved the theoretical derivation of the continuum equation describing information propagation from the Supplemental to the Main manuscript. Starting from “the sensing model imposed on the swimmers using biased vision” and deriving a continuous model, the latter reveals an anisotropic transfer of information. We reworded the sentence to be more accurate.

16. Line 374: “Here, we went beyond reporting the fragmentation-rejoining process to proposing a flow-based mechanism that drives...” – Maybe the authors could provide some more discussion of the flow-based mechanism in the main text? I may have missed it, and I don’t remember the precise flow mechanism being discussed.

Response: We thank the reviewer for asking. In Fig.3, Fig.S2, Fig.S3, we showed that the flow interaction is crucial for the fragmentation and reorganization of the school. Without hydrodynamic interaction, the school will always swim cohesively together more swimmers.

In Fig.S2, we showed that a school composed of 10k swimmers remains cohesive without hydrodynamic interactions. In Fig.3, with hydrodynamic interactions, we showed that with larger hydrodynamic interactions, the school splits at smaller number of swimmers. In Fig.3 and Fig. S3, we showed that when hydrodynamic interaction is present and fixed in intensity, noise intensity does not have a large influence on collective behavior, and reorganization is present even if noise is completely removed.

All these results show that hydrodynamic interactions are the main mechanism responsible for fragmentation. We edited the manuscript to better explain this.

Reviewer #2 (Remarks to the Author):

This manuscript is a real puzzle: there are some interesting and nice results (especially one, see below), but unfortunately these are diluted within a mix of irrelevant, misleading and (in some cases) plain wrong claims.

This make the final decision about the manuscript very hard. In principle, I am not totally opposed to publication In Nat.Comm. but:

- certainly not in the current form
- the Authors should convince me that the supposedly interesting results are compelling enough

Hence, as I said, I recognize that the manuscript contains interesting contributions. However, the presentation is terrible, making it exceedingly difficult to extract the key messages without a lot of effort. A heavy revision, focused on summarizing the content, highlighting the main insights and novelty, and streamlining the text, would significantly strengthen the manuscript and \*possibly\* make it ok for Nat Comm.

Response: We thank the referee for their careful and constructive review of our work and for their support of this manuscript. We thoroughly revised the manuscript to address all the concerns raised by the referee. We hope that these revisions convince the referee that all the claims we make in the manuscript are rooted in strong mathematical and numerical arguments. We are thankful for the referee for pointing out that our presentation style might have given the impression that some of the statements we made sounded “plain wrong.” We revised the manuscript to clarify that all our statements and claims are rooted in statistical results or analytical derivations based on our self-propelled particle model.

Let me start by listing here what are (in my opinion) the only three interesting results of the paper:

1. flow interaction destabilises polarization as  $N$  increases, leading to fragmentation; this is quite interesting.

Thank you, we are also excited about this result. We revised the manuscript to clearly highlight this finding.

2. a drop of the correlation length occurs \*prior\* to fragmentation; this is VERY interesting and it should be the punchline of the paper: the Authors have found a precursor of fragmentation, which seems great.

Thank you for this positive and constructive feedback – we are thrilled that you find this very interesting (with a capital VERY). We revised the manuscript and added Figure 5 to clearly explain and support this finding.

3. flow interaction increases information propagation speed, mildly interesting.

Thank you! It is quite curious that flow interactions destabilize polarization, while at the same time increase information propagation.

The Authors need to rewrite the manuscript using 1-2-3 above as a roadmap.

Response: Thank you very much for this careful and constructive feedback on the manuscript. We are very grateful to the referee for their advice. We revised the manuscript accordingly and we think the revised version is much stronger thanks to the referee's comments.

On the contrary, these are the problematic points of the manuscript:

A. The introduction must be rewritten putting the emphasis on 1-2-3 above, and cutting all the vague and pseudo-holistic parts, which do not add any significance.

Response: We revised the introduction per the referee's suggestion.

B. It is unacceptable that NO details of the model are given in the main text. This is still a scientific paper, so the main mathematical details MUST be given in the main text; because much of the rest of the material can be cut (see below) there will be ample space to do that. I cannot recommend publication if this is not done: this is an exclusively numerical paper, the model must be in the main. I am totally against equation-free science.

Response: We included a mathematical description of the model in the main text.

C. I completely fail to get the relevance of non-reciprocity here; I realise that nowadays non-reciprocity is a hot topics, but again - it is quite misleading in this context. Information propagates because of interaction, be it reciprocal or not (see below).

Response: Ah! This is an interesting result. We feel terrible that we didn't explain it clearly enough in the first version of manuscript. This is not a pseudo-result. Non-reciprocity in the vision field is the mechanism that allows ballistic information transfer in the school, with

information propagating from the front to the back of the school. We revised the manuscript to explain how non-reciprocity affect information travel speed.

D. Using "More is different" as a title of a Section is not helpful at all, and quite rhetorical. The Authors should use titles summarizing the content of the section, not a famous paper by a Nobel prize.

Response: Indeed, we were playing on the title of the famous 1972 paper by physicist Philip W. Anderson. We are big fans of this paper – can you blame us? – and we thought that the concept presented in his paper captures the spirit of what happens in our schooling models as you increase the school size. If the referee is strongly opposed to this, no problem. We changed the title of the section.

E. I am completely baffled by the statement that the school swims faster than the individual. Even after reading [16], I find no sense in this statement. We have been taught at school the inequality:

$$|\sum_i v_i| \leq \sum_i |v_i|$$

because here  $|v_i| = U$  for each  $i$ , we get:

$$(1/N) |\sum_i v_i| \leq (1/N) \sum_i |v_i| = U$$

meaning that the mean speed of the group is smaller that the individual speed.

so, what is going on here?

this seems completely wrong, or - at best - very poorly explained. If this is due to the interaction with the flow, then there is something wrong in the way the mean velocity is defined. Anyway, the point is completely irrelevant for the rest of the paper, hence I would cut it entirely (but I am still curious about how the above high-school-level inequality is violated)

Response: Indeed, the school swims faster than the individual. The reason for that is that the individual's velocity is a combination of two effects: (1) its self-propelled velocity and (2) the advection velocity due to the flow field at its location. On average, these flow interactions enhance the speed at which individuals move when polarized, thus enhancing the speed of the entire school (up to 20% for our choice of  $I_f$ ). This flow-induced enhancement of overall speed is documented in Fillela et al PRL 2018 and mentioned in Huang et al PNAS 2024. We clarify this in the revised manuscript.

F. The 'more is different' section is too long; the Authors should keep only the material strictly needed to talk about the rest.

Response: Done!

G. In this disgraced Section there is another very suspicious - in my opinion wrong - claim, namely that the density increases with size. According to the Supp Info no effort has been done here to cure and take care of the border bias. Therefore I am 90% sure that what the Authors found here is simply an effect of the border bias; this is a very old bias indeed, that was already recognised in the book Stoyan, D. & Stoyan, H. 1994. *Fractals, Random Shapes and Point Fields*. Chichester: J. Wiley. To see this bias at work in a spectacular way see Fig.6 of *Animal Behavior* 76 (1), 237-248 (2008) and relative discussion on how to eliminate the bias. Therefore, either the Authors cure the border bias, or they cut any statements about how density depends on size (which are irrelevant anyway).

Response: We thank the reviewer for pointing out this effect of border bias -- we were ignorant of it. We carefully studied the paper suggested by the reviewer (Cavagna *et al.* (2008) *Animal Behavior*). To test whether this boundary bias plays a role in our results on the distance to nearest neighbor, we repeated our calculation, disregarding altogether the boundary fish in summing over the nearest neighbor distance. The figure attached shows that, excluding the boundary fish, results only in a slight decrease in nearest neighbor distance, but does not influence the overall trend that we report in the manuscript, namely, that the nearest neighbor distance is constant on average. We thus conclude that the effect mentioned by the referee is not dominant here.

As a side note, we agree with the reviewer that scaling of density and nearest neighbor distance with N is not a key point of our paper, but this data served as a basis for us to evaluate information transfer speed and connect to our analysis. We revised the manuscript to diminish the prominence of these results and put them as a supplementary figure.

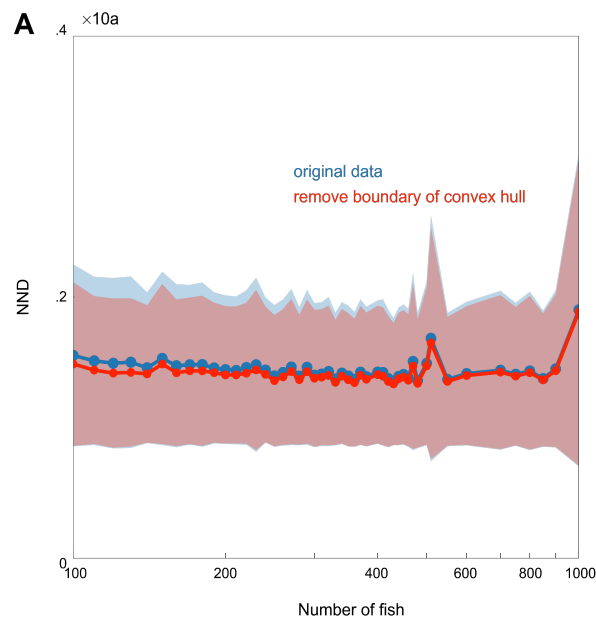


Figure 4 Comparison between nearest neighbor distance with and without removing the boundary points.

H. That scale free correlations break down when there is fragmentation is \*completely\* trivial, hence putting the emphasis on this as the Authors do is very misleading. The Authors clearly know that scale free correlations of the orientations are due to Goldstone modes, because they write that; so, it is obvious that when there is fragmentation, one loses completely the spontaneous symmetry breaking of the Goldstone theorem, hence no Goldstone models, hence no scale free correlation. As I said, this is trivial. As I said above, what is FAR from trivial is that the correlation length decreases PRIOR to fragmentation. This is the only reason I am not recommending straight out rejection of the paper: if true, this result is really compelling. So, I strongly recommend to the Authors to concentrate the paper on this result, and on the handful of truly essential ancillary results. However, because this result is so important, I urge the Authors to make an effort to strengthen the result with more and better numerical evidence: Fig.4F is definitely not enough to convince me.

Response: We thank the referee for their constructive feedback. Yes, it is not surprising that scale free correlations break down when fragmentation occurs, but it is very interesting that the correlation length decreases prior to fragmentation.

In the revised manuscript, we provide additional data in support of the decrease in correlation length prior to fragmentation. Specifically, we run additional Monte Carlo simulations with 1000 fish, where the school occasionally fragments and re-assembles, as shown in the figure below. We chose this school size because the fragmentation events are isolated as opposed to the school of 10,000 fish, where multiple fragmentation events could occur simultaneously.

In the figure below, we show the time evolution of polar order parameter, school size, correlation length and ratio of correlation length to school size after steady state was reached in a sample simulation of 1000 swimmer. Intervals where the school fragments and reassembles are highlighted in grey. During these intervals, the overall school size increases then decreases. Away from these events, the school undergoes cohesive polarized schooling and the school size is relatively stable.

To quantify the drop in correlation length prior to fragmentation, we took the time average of  $P$ ,  $L$ ,  $\xi$ , and  $\xi/L$  over a time interval that long preceded a fragmentation event (namely, we averaged these quantities over a time window ending 100 time units prior to a fragmentation occurred). Then, we repeated this calculation over a time window that ended at the onset of a fragmentation event. For the latter, we tested four different time windows consisting of the 10 time units prior to fragmentation, 30, 50 and 100. We found that the polar order parameter  $P$

and school size  $L$  were largely insensitive to the temporal placement of the averaging window, far or right before a fragmentation event. However, the correlation length  $\xi$  and ratio  $\xi/L$  decreased significantly right before a fragmentation event. These results reinforce our conclusion that the correlation length decreases prior to fragmentation.

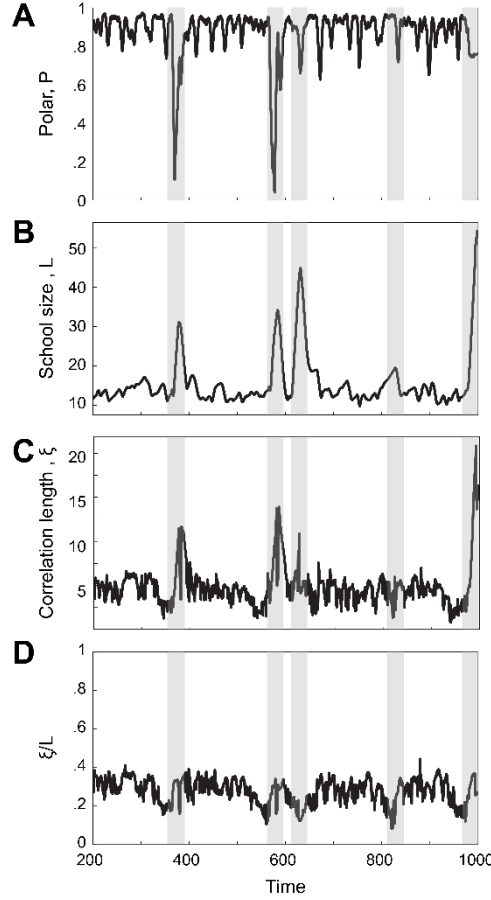


Figure 5 Time evolution of **A** polar order parameter  $P$ , **B** school size  $L$ , **C** correlation length, and **D** ratio of correlation length to school size for a school of 1000 fish.

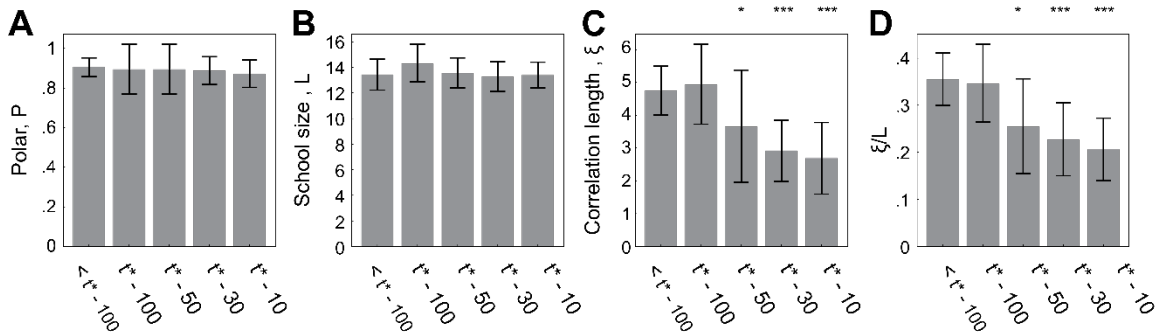


Figure 6 Statistics of **A** polar order parameter, **B** school size, **C** correlation length and **D** correlation length over school size for 10 MC simulations of school of 1000 fish. The first column hind shows the results in time snapshots at least 100 unit time from any splitting events; and the rest show the results within 100/50/30/10 time unit before a splitting event at time  $t^*$ . To evaluate the difference in statistical properties between close to splitting and far from splitting, a two-sample t-test is used [1,2]. The null hypothesis states that there is no significant difference in success rates. A smaller p-value indicates stronger evidence against the null hypothesis, suggesting a more significant difference in performance. \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

[1] Student. (1908). The probable error of a mean. *Biometrika*, 1-25.

[2] Fisher, R. A. (1922). On the interpretation of  $\chi^2$  from contingency tables, and the calculation of P. *Journal of the royal statistical society*, 85(1), 87-94.

I. I think that the part (three sections) on information propagation is far far too long, and it should be cut entirely, or considerably trimmed, if the Authors insist on keeping it. Also it does not go together very coherently with the result on the precursor of fragmentation above. But, if the Authors decide to keep it and trim it, I recommend at least to cut - or make very very short - the section about the fact that fragmentation slows down propagation: this too is completely obvious.

Response: Thank you for this feedback. The motivation behind these last three sections is to discuss the dynamics of information propagation, as opposed to the static spatial correlations.

The manuscript is organized in two parts: the first part discusses spatial correlations and the second part discusses the dynamics of information propagation in the school.

The sections on the dynamics of information propagation are important because they provide the following novel insights and contributions:

1. Information propagates linearly from the front to the back of the school. The underlying mechanism is non-reciprocal vision. This mechanism is different from behavioral inertia where information propagates in both directions (Attanasi et al 2014).
2. Information propagates faster when clusters merge together (not a priori obvious) and slower when a cluster fragments (predictable as noted by the referee).
3. Flow interactions enhance information travel speed (not a priori obvious).

We agree with the referee that the manuscript covers a lot of ground, but we think that these findings are important. Removing this discussion would take away fundamental understanding of the mechanisms driving information propagation in this schooling model.

We would not be opposed to splitting the manuscript into two papers:

- Self-reorganization in Massive Schools of Fish: I. Scale-free Correlations
- Self-reorganization in Massive Schools of Fish: II. Information Transfer

But we think that this should be an editorial decision. If the editor of Nature Communications is open to this idea, we would pursue it.

J. The statement that inertia is not necessary to have linear propagation is wrong. Even though here there is no behavioural inertia, there is of course inertia nevertheless due to the interaction with the flow. Hence, this claim should be cut, or at least completely reworded, as in the current form it is not true.

Response: We appreciate the referee's comments, but with all due respect, the referee is mistaken about this. Our statement that "inertia is not necessary to have linear propagation" is a mathematical statement. This statement is supported by:

- **Numerical simulations of our self-propelled particle model, where there is no inertia:** in our potential flow model, each swimmer generates an instantaneous potential dipole flow and is advected by the flow velocity field generated by all other swimmers at its location (Eq1, 2). There is no inertia in the fluid. Importantly, when in simulations, we set flow coupling to zero, we still obtain linear propagation of information.
- **Continuum equation based on our kinematic self-propelled particle model:** The analytical model we derived in Eq 4 is purely based on the alignment interactions with frontal bias, without hydrodynamics. Accounting for non-reciprocal vision introduces an advection term responsible for information propagation from the front to the back of the school.

Importantly, the behavioral inertia introduced in Attanasi *et al.* (2014) Nature Physics leads to information propagation that is different from that due to non-reciprocal vision that we uncover in this work: the propagation of information in Attanasi *et al.* (2014) is bi-directional and at a speed that scales with  $\sqrt{I_a}$  while in the vision-based mechanism we uncover, information propagates from front to back at a speed that scales with  $I_a$ .

## SUMMARY of REVISIONS

We thank the editor and referees for their effort in reviewing the manuscript. We further revised the manuscript as follows:

1. We clarify the reason for the enhancement in the average speed of polarized groups.
2. We clarify the differences between the linear information propagation in our non-reciprocal vision model (leading to a first-order transport equation) and the inertial model proposed in Attanasi et al. 2014 (leading to a second-order wave equation).
3. We provide references to empirical evidence that support the front-to-back propagation of information we observe in our model.
4. We made slight modifications to improve Figure 6 and its caption.
5. Haotian Hang and I went very carefully over the Goldstone theorem and made sure we all understood the comments raised by referee 2 – the erroneous statements were made in the previous response letter, and not reflected in the manuscript – I apologize for this oversight.

## RESPONSE TO REFEREES

Reviewer #1 (Remarks to the Author):

The inclusion of a well-written ‘Mathematical Model’ section in the main body is an excellent decision by the authors, and it clears up several of the questions that I had previously.

Response: We thank the referee for their positive comments.

Regarding perturbations/fluctuations, it is now clear to me that it is mentioned in the context of the stability of the group. The authors should clarify this very explicitly at least once in the manuscript. For instance, “...a perturbation, say, caused by an attacking predator...” leaves it open to interpretation whether the perturbations being mentioned are related to changes in velocity, pressure, vorticity (not applicable in this study), or some other quantity. Hence my original comment.

Response: We thank the referee for this comment. The perturbation can be related to any physical mechanism that causes a change/fluctuation in the individual heading direction. In the model, we account for the position and heading direction of each swimmer, with vision-based behavioral rules and minimal flow interactions. In reality, a perturbation can be caused by any of the mechanisms mentioned by the referee. The statement that the referee mentions “an animal group exhibits maximal responsiveness to a perturbation, say, caused by an attacking predator, when correlations are scale-free, that is, when the range of spatial correlations scales with the linear group size” is agnostic to the source of perturbation.

I also support the authors’ decision to remove references to the ‘telephone game’, it seemed a bit too informal to be included in a journal paper.

Response: We thank the referee for their support and reassurance.

Regarding school speed being larger than individual speed, I now understand that the individual speed does not account for the background speed that the individual might be getting advected with. I feel that this is still not clarified explicitly in the revised manuscript, and it will definitely be a source of confusion for readers. The authors should include a paraphrased version of their rebuttal explanation into the main body: “In our model, the self-propelled speed  $U$  is fixed for each swimmer. When hydrodynamic interaction is involved, each swimmer  $j$  is also advected by the flow field created by other swimmers with velocity  $U_{\perp}$ , thus, the speed of each swimmer is  $U(\cos \theta, \sin \theta) + U_{\perp}$ , which can be larger than  $U$ .”

Response: We thank the referee for this suggestion. We revised the manuscript to include an explanation of how  $U_j$  affects the group average velocity.

“According to Goldstone modes, the correlation function should cross zero, and the integration of correlation function over space should be zero...” – The other Reviewer pointed out an issue with this statement, which I agree with. I see that the correlation function should integrate to zero, and thus should cross zero at some point, but I do not see how this is mandated by Goldstone modes.

Response: Thank you for pointing this out. Indeed, as Referee 2 points out, the description of the Goldstone modes in the first response letter was not correct. Note that this erroneous language was only used in the response letter, not in the main manuscript.

“The tools that we present for analyzing the turning only, splitting and turning, or merging and turning, are generally applicable to any group size.” – I agree that the tools may be generalizable, but I don’t see how the conclusions obtained using smaller groups will be generalizable since, again as the authors state, the behaviour changes considerably for 10k swimmers. I would expect that generalizable conclusions for large groups can only be drawn using 10k swimmers since the behaviour does not change when going from 10k to 50k. This is a major point which the authors have not addressed convincingly and rigorously.

Response: We thank the reviewer for asking. We indeed analyze the school of 10k swimmers in most of our figures in the main text, which are listed as follows.

In Fig.2 C-G, we analyzed the time evolution of polar order parameter, school direction, and cluster number and size in a school of 10k fish.

In Fig. 3, we showed how the time-averaged polar order parameter changes as a function of the number of swimmers ranging from 100 to 10,000 swimmers.

Fig.4 E,F shows the time evolution of polar order parameter and correlation length for a school of 10k fish before they split. Fig.4G shows the correlation length for all clusters in the time evolution of a 10k fish school.

Fig.6 D-F, G-I shows a splitting event and a merging event of clusters within a school of 10k fish. Although on the x axis, the cluster sizes are less than 7500 swimmers, these clusters are extracted from simulations of 10k fish schools.

Fig.7 shows the information transfer speed in splitting and merging clusters within schools of 10k fish.

While we appreciate the referee's comment, we are somewhat puzzled by their statement that "generalizable conclusions for large groups can only be drawn using 10k swimmers since the behaviour does not change when going from 10k to 50k. This is a major point which the authors have not addressed convincingly and rigorously." The key point is that the splitting and merging phenomena, whether underlying the self-organization in the group of 10,000 fish, or whether occurring in a smaller group of 1000 fish, are the same: the mechanism for splitting (hydrodynamic interactions) is the same, and the signature of the splitting event (loss of scale-free correlation before splitting) is the same! In other words, when zooming-in on an individual splitting or merging event, qualitatively, it matters little that such event occurs in the context of a larger group of 10,000 fish or a smaller group of 1000 fish.

So, while in the manuscript, most of our analysis is based on the group of 10,000 fish, we also show analysis based on 1000 fish – both to highlight similarities and differences that arise with group size.

Scaling up to 10,000 fish primarily reveals the statistical characteristics of the self-reorganization but does not cause a change in the physical mechanisms causing the splitting and merging events. The consequences that these splitting / merging events have on the information propagation is qualitatively the same, irrespective of the size of the clusters that split or merge.

"...is to show our computational prowess..." – the authors should take care not to overemphasize the computational cost/prowess of their study in the manuscript, especially since it may be read by computational scientists if it is published in a multidisciplinary journal. The authors mention requiring three weeks of continuous run time on a 56-core desktop, which is approximately 28,000 core hours. This is relatively modest by modern HPC (High Performance Computing) standards.

Response: We thank the reviewer for clarifying this. This statement was made in the response letter, not in the manuscript. We make no such statement in the manuscript. Indeed, we agree with the reviewer that this is a moderate computation with 150,000 degrees of freedom in the case of 50,000 fish.

Siddhartha Verma.

Reviewer #1 (Remarks on code availability):

I still could not find any code uploaded with the manuscript (despite "Supporting code available as supplementary materials with the paper."), so I am unable to review it.

Response: Code is currently available at Github and will be made available publicly upon publication.

[https://github.com/ekanso/schooling\\_extreme/tree/main](https://github.com/ekanso/schooling_extreme/tree/main)

Reviewer #2 (Remarks to the Author):

The Authors have made several steps forward, although more is needed for me to recommend publication in Nature Communication. More specifically:

\* I am still completely baffled by the statement that the school swims faster than the individuals, and I see from Ref.1 report that I am not alone. In what reference frame this statement applies? Anyway, the current "clarification" in the amended version is not clear at all to me. I again suggest that this (old, by the way) result be removed from the paper.

Response: We thank the referee for bringing up this point again. The average velocity of the entire school is given by  $U(\cos \theta_j, \sin \theta_j) + U_j$ . The dipolar interactions, represented by  $U_j$ , destabilize side-by-side configurations, favoring in-line arrangements (drafting) that lead to higher swimming speeds in polarized group configurations; this dipolar flow field effect has been extensively documented in prior work: see, e.g., Tsang & Kanso PRE (2014) and Filella *et al.* PRL(2018). Because this effect has been clearly documented in prior literature, we revised the manuscript to briefly explain the mechanism, while pointing the reader to the literature that dives more deeply into the details. This result is independent of the choice of reference frame.

The novelty here is that, in a larger school (10K fish) undergoing self-organization, while individual clusters move at higher speeds, the entire school moves at much lower speeds, ensuring that the clusters "disperse" spatially, while the center of the entire group remains relatively in place.

Tsang, A. C. H. & E. Kanso (2014), Flagella-induced transitions in the collective behavior of confined microswimmers, Phys. Rev. E 90, 021001(R).

Kanso, E., & Tsang, A. C. H. (2015). Pursuit and synchronization in hydrodynamic dipoles. *Journal of Nonlinear Science*, 25(5), 1141-1152.

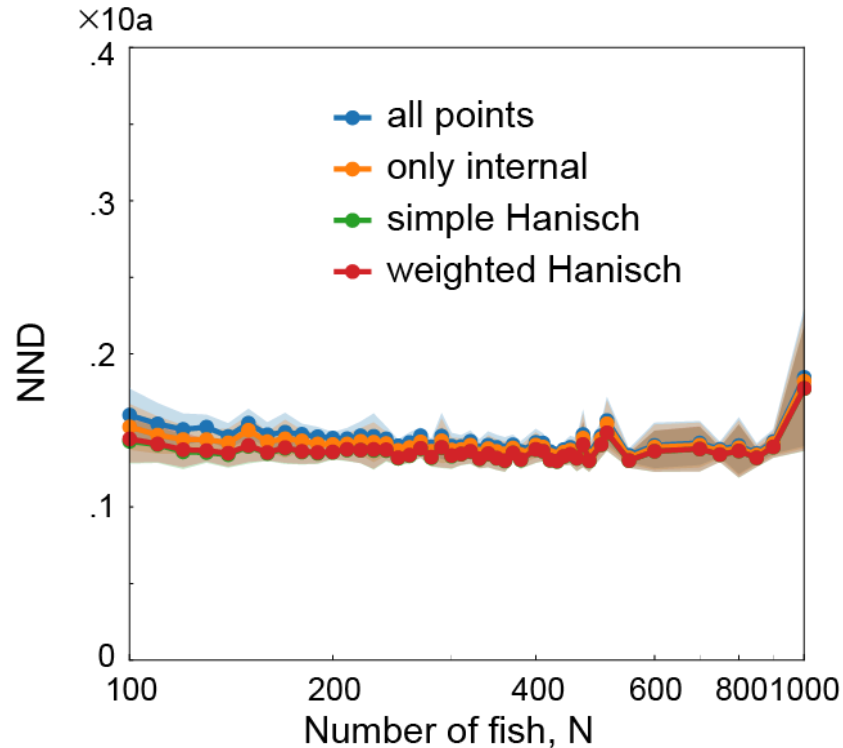
Filella, A., Nadal, F., Sire, C., Kanso, E., & Eloy, C. (2018). Model of collective fish behavior with hydrodynamic interactions. *Physical review letters*, 120(19), 198101.

\* The way the Authors take care of the boundary in the amended version of the manuscript is NOT the correct one: removing from the statistics points of the border is not the right way to go and not the one used in *Animal Behavior* 76 (1), 237-248 (2008), which clearly was not "carefully studied".

The correct way to cure the border bias is, for each point  $i$  to calculate its distance from the border, let call it  $R_i$ , and then - when counting all the pairs of points formed by  $i$  with its neighbours - to ignore all points beyond  $R_i$  from  $i$ .

Hence, either the Authors proceed with the correct procedure or - given the *very* weak decrease of NND with  $N$  and given the irrelevance of this result in the bigger picture of the paper - I suggest that this is removed.

Response: We thank the reviewer for pointing this out again. In the attached figure, we compared all three methods of removing the statistics of the border in *Animal Behavior* 76 (1), 237-248 (2008): only internal, simple Hanisch, and weighted Hanisch. They show no difference in the trend of the NND over  $N$ . And, following the referee's prior suggestion, we had already removed this figure from the main text of our paper in the first revision.



\* I appreciate the additional data to support that  $\lambda_i$  decreases before the loss of cohesion. As I said, this is very interesting.

Response: We thank the referee again for their support of this work – we appreciate their enthusiasm for these results and for finding them very interesting.

\* Regarding linear propagation, now that I see the equation in the main text, yes, I finally understand what is going on (see? equations helps after all!). Due to the anisotropy of perception, this is a \*first\* order equation in time and in space, hence, yes, there is a traveling solution. HOWEVER, this is not a wave equation at all and its unusual form means that propagation is exclusively in one direction, hence drastically anisotropic, and - most importantly - unlike anything recorded in real experiments, as disturbance waves are known to propagate in any direction. This must be explained more directly and explicitly than it is done at the moment.

Response: We thank the reviewer for their constructive feedback on the initial manuscript that led to this improvement. Indeed, we do not get a wave equation, we get a first-order transport equation. Our information transfer is anisotropic, in contrast to the isotropic information transfer in Attanasi *et al.* (2014). In the revised manuscript, we mention that the visually-mediated information transfer in our model only allows front-to-back information transfer, in contrast to the inertia-mediated information transfer introduced in Attanasi *et al.* (2014), which is certainly a more important theoretical contribution and allows information propagation in any direction.

In relation to experimental observations in animal groups, it seems that whether information transfer is isotropic or anisotropic depends on the animal of interest. In natural bird flocks (e.g. starlings), changes in travel direction propagate rapidly and coherently. Attanasi *et al.* (2014) recorded starling flocks performing collective turns and found that directional information spreads like a sound wave across the group. This propagation was effectively isotropic within the plane of the flock: once a turn starts, it fans out to all birds in the flock (no directional bias was reported in the plane of motion).

In contrast, observations in other animal groups, such as in the fish species known as rummy-nose tetra, show anisotropic information transfer because the interaction between individuals at microscopic level is anisotropic, much like in the model that we present in this work. Indeed, Lecheval *et al.* (2018) studied spontaneous U-turns in groups of rummy-nose tetra. They found that U-turns almost always start at the front of the group and then travel backward through the school like falling dominos. The new direction (and reduced speed) set by the first fish is passed to its immediate followers and so on, with each neighbor turning in succession. Notably, this propagation shows little amplification or damping: the timing of successive turns scales linearly with distance from the initiator, implying a nearly constant speed of information. In effect, information flows anisotropically along the school's length (front-to-back) – fish in front lead and those behind follow – with no significant sideways propagation reported.

Experiments on pigeon flocks also reveal a strong anisotropy in neighbor interactions. Pigeons have eyes on the sides of their head, giving them an almost 360° field of view but only a narrow frontal binocular zone. As a result, they're excellent at detecting motion around them but have limited straight-ahead depth perception. In Chen *et al.* (2017), individual pigeons tend to align with neighbors to their sides and rarely interact with birds directly ahead or behind. In other words, pigeon flocks exhibit directionally biased information flow: they interact more with lateral (side-to-side) neighbors compared to front/back neighbors.

Our work provides an alternative framework to capture such anisotropic flow of information, where the vision-based bias in the individual sensory and response behavior dominates information propagation in the group.

Attanasi, A., Cavagna, A., Del Castello, L., Giardina, I., Grigera, T. S., Jelić, A., ... & Viale, M. (2014). Information transfer and behavioural inertia in starling flocks. *Nature physics*, 10(9), 691-696.

Lecheval, V., Jiang, L., Tichit, P., Sire, C., Hemelrijk, C. K., & Theraulaz, G. (2018). Social conformity and propagation of information in collective U-turns of fish schools. *Proceedings of the Royal Society B: Biological Sciences*, 285(1877), 20180251.

Chen, D., Liu, X., Xu, B., & Zhang, H. T. (2017). Intermittence and connectivity of interactions in pigeon flock flights. *Scientific reports*, 7(1), 10452.

\* Regarding splitting in two the manuscript, I am all in favour of that, but - once my remarks are addresses - I would recommend publication in Nat Comm only of the first part on scale-free correlations.

Response: The handling editor at Nature Communications discouraged splitting the manuscript into two. We thank the referee for their willingness to support publication in Nature Communication based on our results regarding the loss of scale-free correlations as a precursor to a splitting event.

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A final remark regarding the reply to Ref.1 (if it can be forwarded to them).  
The Authors write:

"By construction, we are building our correlation function based on fluctuation of individual velocity, and thus, the average or mean of velocity fluctuation is exactly zero. According to Goldstone modes, the correlation function should cross zero, and the integration of correlation function over space should be zero."

There are two very wrong statements in this paragraph, which is worrying, because it suggests that the Authors do not have the physics of correlation functions fully under control. Here they are:

Response: We thank the reviewer so much for pointing out our oversight in the previous response letter. We are completely in agreement with the referee's analysis – the Goldstone modes are not due to the mean velocity fluctuations being zero, but reflect a broken symmetry that can sustain long-range perturbations at very small energetic cost – I'm very sorry that I did not catch this mistake in our previous response letter.

1. Goldstone Theorem (GT) by itself has nothing to do with the fact that the correlation function must cross zero. GT only states that the correlation must be long range, i.e. power law. If the correlation were calculated with a bona fide statistical ensemble (i.e. Boltzmann), then that GT power law correlation function would NOT cross the zero, as well as an exponential correlation function.

The fact that the correlation function computed here - with this particular experimental definition which lacks an ensemble - must cross the zero at some point is true for any kind of shape, power law (as in the case of GT), or exponential. And the reason why this correlation must cross the zero brings us to the second wrong statement:

2. It is true that the mean of the velocity fluctuation is by definition zero, but the integral of the

correlation function over  $r$  is NOT zero, just check the algebra. On the other hand, if we call NUM the numerator in the definition of the correlation function, then the integral of NUM over  $r$  IS zero, because one gets the square of the mean fluctuation. Because the integral of NUM is zero, this means that the function NUM must have a zero itself, so that the whole function  $C(r)$ , of which NUM is the numerator, must have a zero.

Whenever the ensemble correlation function is short-range (exponential), this zero is irrelevant and practically impossible to distinguish from the many zeros due to the noise/fluctuations of the correlation decayed to zero. On the other hand, when the ensemble correlation is scale-free (power law), then this zero becomes very evident, its position scales with  $L$ , which is the best indicator of scale free correlations.

Response: We thank the reviewer for taking the time to explain this – we appreciate it. We agree with all the statements made by the referee, and I apologize again for my oversight in reviewing the previous response letter, and not catching the erroneous statements about the Goldstone theorem.

**Review: “Self-reorganization and Information Transfer in Massive Schools of Fish”, by Hang et al.**

In this manuscript, the authors study the collective behaviour of a large number of point swimmers (on the order of  $\sim O(1k)$  to  $\sim O(10k)$  mostly) to better understand the behaviour of fish schools. The authors use a potential flow model combined with biased visual sensing and a set of empirical behavioural rules, to implement the motion of each individual point swimmer. The primary focus is to examine scale-free correlations of the motion, group cohesion, and information transfer among the swimmers.

I have the following questions and comments for the authors:

1. For the readers' benefit, the authors should clarify in the main body of the text (not supplementary) that the “*school of 50,000 fish*” is actually a collection of massless point particles, and that the ‘*flow interactions*’ or ‘*hydrodynamic interactions*’ specific to this study are based on simplified two-dimensional potential flow assumptions.
2. The mention of potential flow also brings another question to mind: how are the flow interactions damped in the simulations? Usually the influence decays with distance, but viscous damping is not allowed in potential flow. This would allow the flow-mediated disturbances to accumulate indefinitely over time, leading to unrealistic behaviour.
3. The authors make an important point when they state “...in the context of our model...” at one point in their manuscript. This should be clarified very early on in the main body, and maybe even in the abstract, to ensure that readers fully appreciate that the conclusions being drawn are dependent on the model parameters.
4. The primary model for point swimmer motion depends on the three free parameters “( $I_n, I_a, I_f$ )”. This brings about the question of having to manually tune these coefficients until the desired/expected behaviour is achieved. For example, Fig 3D shows that changing the value of  $I_f$  can change the behaviour substantially. So how is the generalizable ‘correct’ value of these parameters determined, besides tuning to desired behaviour? The authors mention using parameters that maintain polarity for small groups, but then why would the same parameters expected to be applicable in the 50k case, where the behaviour is very different?
5. Line 50: “*In physical models of flow-coupled ...*” – I am having some trouble understanding the meaning of ‘physical models’. I assume the authors are referring to fish-shaped models used for laboratory experiments? Also, I am a bit unclear on ‘...*perturbations get amplified as they propagate...*’ – perturbations die out due to viscous effects, them getting amplified would likely violate conservation of momentum.
6. Line 71: The authors liken message transmission to the game of telephone, and indicate that the message becomes distorted as it is passed among a large number of individuals. How does this happen in the authors’ model? Is there a stochastic component involved that leads to message distortion? Does the cumulative ‘noise’ grow with number of times the message is propagated?
7. Line 105: I am having some trouble understanding why the summation for  $P$  involves the complex exponential function (I assume ‘ $i$ ’ represents  $\sqrt{-1}$ ). Why is the imaginary part useful? Also, “ $\theta_j$  is the orientation of swimmer  $j$ ” with respect to what precisely, i.e., the group axis, the lab frame, or something else?

8. Lines 110 and 114: “*we found that, on average, schools swam faster than the individual swimming speed  $U$* ” – this is a bit puzzling to me, how can the average speed be faster than that of the individuals? Being slower would be understandable since not all individual velocity vectors may be parallel to each other, but I don’t fully understand the school being faster.
9. Line 138: “*the school turned frequently*” – what exactly induces a turning event in the authors’ model? Is this driven by an external catalyst, or is it based on an internal mechanism? Also, a brief description of why the lead swimmers turn instead of those in the middle of the group would be helpful – I assume it is due to the biased vision and the imposed rules to maintain alignment with neighbours?
10. Line 187: The calculation of  $C(r)$  is limited to group sizes of 1000 or smaller, and only to instantaneous snapshots of the data when the group is highly polarized. Doesn’t limiting the analysis to  $P > 0.9$  introduce a bias? It would be helpful if the authors clarify the rationale for doing so. Also, I think small group sizes are considered since they remain coherent and polarized, but then again, what is the benefit of selecting these? Wouldn’t it be more generalizable to consider 10k individuals, since the authors state that group behaviour changes minimally beyond this number?
11. At short distances, the correlation coefficient being close to 1 makes perfect sense since the point swimmers are instructed to maintain alignment using the motion model. But a correlation coefficient of -1 at extremely large distances is very surprising. What is the cause of this?
12. Line 211: “*...the slope of the best fit of  $\xi$  vs  $L$  is nearly one-third, similar to the slope...*” – What would happen if the authors consider the individual datasets shown in Fig 4D and get their corresponding slopes, i.e., separate slopes for dataset X, O, square, etc.? Do they show the same value of 1/3? Looking at the images, it seems to me the slopes would be very different, but a numerical value would be helpful to confirm. If they are not the same, then again the issue arises of what the ‘correct’ model parameter values are, since they can be selected arbitrarily.
13. Line 268: The analysis (this time for turning) is again limited to groups with a small number of individuals (<2000). As the authors state, the behaviour changes considerably for 10k swimmers, including fragmentation and merging. It is difficult for me to understand why the smaller groups were selected, especially since the conclusions are presented as if they should be generalizable to all schools.
14. Also, in that vein, the statement in Line 348 (and similar elsewhere) “*...massive schools of fish, consisting of up to 50,000 individuals...*” - while technically true due to the use of ‘up to’, could be tempered a bit, given that the majority of the analysis regarding correlation and information transfer is done using groups that are more than an order of magnitude smaller.
15. Line 296: The authors claim that “*our theory predicts an anisotropy in the information transfer*” – in my opinion it is not a prediction of theory, but rather a result of the sensing model imposed on the swimmers using biased vision.
16. Line 374: “*Here, we went beyond reporting the fragmentation-rejoining process to proposing a flow-based mechanism that drives...*” – Maybe the authors could provide some more discussion of the flow-based mechanism in the main text? I may have missed it, and I don’t remember the precise flow mechanism being discussed.

**Review: Revision of “Self-reorganization and Information Transfer in Massive Schools of Fish”, by Hang et al.**

The inclusion of a well-written ‘Mathematical Model’ section in the main body is an excellent decision by the authors, and it clears up several of the questions that I had previously.

Regarding perturbations/fluctuations, it is now clear to me that it is mentioned in the context of the stability of the group. The authors should clarify this very explicitly at least once in the manuscript. For instance, “...a perturbation, say, caused by an attacking predator...” leaves it open to interpretation whether the perturbations being mentioned are related to changes in velocity, pressure, vorticity (not applicable in this study), or some other quantity. Hence my original comment.

I also support the authors’ decision to remove references to the ‘telephone game’, it seemed a bit too informal to be included in a journal paper.

Regarding school speed being larger than individual speed, I now understand that the individual speed does not account for the background speed that the individual might be getting advected with. I feel that this is still not clarified explicitly in the revised manuscript, and it will definitely be a source of confusion for readers. The authors should include a paraphrased version of their rebuttal explanation into the main body: *“In our model, the self-propelled speed  $U$  is fixed for each swimmer. When hydrodynamic interaction is involved, each swimmer  $j$  is also advected by the flow field created by other swimmers with velocity  $U$  & , thus, the speed of each swimmer is  $JU(\cos \theta + \sin \theta) + U$  &  $J$ , which can be larger than  $U$ .”*

*“According to Goldstone modes, the correlation function should cross zero, and the integration of correlation function over space should be zero...”* – The other Reviewer pointed out an issue with this statement, which I agree with. I see that the correlation function should integrate to zero, and thus should cross zero at some point, but I do not see how this is mandated by Goldstone modes.

*“The tools that we present for analyzing the turning only, splitting and turning, or merging and turning, are generally applicable to any group size.”* – I agree that the tools may be generalizable, but I don’t see how the conclusions obtained using smaller groups will be generalizable since, again as the authors state, the behaviour changes considerably for 10k swimmers. I would expect that generalizable conclusions for large groups can only be drawn using 10k swimmers since the behaviour does not change when going from 10k to 50k. This is a major point which the authors have not addressed convincingly and rigorously.

*“...is to show our computational prowess...”* – the authors should take care not to overemphasize the computational cost/prowess of their study in the manuscript, especially since it may be read by computational scientists if it is published in a multidisciplinary journal. The authors mention requiring three weeks of continuous run time on a 56-core desktop, which is approximately 28,000 core hours. This is relatively modest by modern HPC (High Performance Computing) standards.

Siddhartha Verma.