Research

CrossMark
click for updates

Author for correspondence:
Giancarlo De Luca
e-mail: giancarlo.de-luca@inserm.fr

†Present address: IPLESP—Institut Pierre Louis d'Épidémiologie et de Santé Publique, UMR-S 1136, INSERM, Paris, France.

Royal Society Publishing

Fishing out collective memory of migratory schools

Giancarlo De Luca[1,†], Patrizio Mariani[2], Brian R. MacKenzie[2,3] and Matteo Marsili[4]

[1]SISSA, International School for Advanced Studies, Trieste, Italy
[2]Centre for Ocean Life, and [3]Centre for Macroecology, Evolution and Climate, National Institute for Aquatic Resources, Technical University of Denmark, Charlottenlund, Denmark
[4]ICTP, The Abdus Salam International Centre For Theoretical Physics, Trieste, Italy

Animals form groups for many reasons, but there are costs and benefits associated with group formation. One of the benefits is collective memory. In groups on the move, social interactions play a crucial role in the cohesion and the ability to make consensus decisions. When migrating from spawning to feeding areas, fish schools need to retain a collective memory of the destination site over thousands of kilometres, and changes in group formation or individual preference can produce sudden changes in migration pathways. We propose a modelling framework, based on stochastic adaptive networks, that can reproduce this collective behaviour. We assume that three factors control group formation and school migration behaviour: the intensity of social interaction, the relative number of informed individuals and the strength of preference that informed individuals have for a particular migration area. We treat these factors independently and relate the individuals' preferences to the experience and memory for certain migration sites. We demonstrate that removal of knowledgeable individuals or alteration of individual preference can produce rapid changes in group formation and collective behaviour. For example, intensive fishing targeting the migratory species and also their preferred prey can reduce both terms to a point at which migration to the destination sites is suddenly stopped. The conceptual approaches represented by our modelling framework may therefore be able to explain large-scale changes in fish migration and spatial distribution.

1. Introduction

Grouping behaviour is a widespread phenomenon in animal ecology and is thought to be an emerging property of the self-organization of individual organisms [1]. While living in groups, social animals benefit from several advantages, among which is a more efficient capacity in problem solving [2–4]. Of particular interest is the ability of the group to make collective decisions also when it is composed of individuals with contrasting preferences and information [5,6]. How groups reach a consensus decision has recently received much attention [7–10], and several mechanisms to pool the information in the group have been proposed [1,6].

Often no obvious reason can be adduced to explain the social behaviour of certain species except the fact that those groups are more efficient than single individuals in retrieving information from the environment [9,11,12]. For groups on the move, such as fish schooling, bird flocking or mammal herding, it has been shown that information transfer and social interactions are important factors of group cohesion and can promote the ability of making consensus decisions [10,13,14].

An example of such a collective decision-making problem is the structure of migration routes in some fish species. Migration between widely separated, but geographically stable locations of spawning and feeding sites raises several questions about how these animals manage to learn and *remember* the migration route between feeding and spawning sites. Where is the information on the path stored? How is it retrieved, shared and elaborated by a migrating

group? Are these tasks performed significantly better by the group with respect to the individuals? Shedding light on the functioning of these mechanisms is a fundamental issue in ecology but may also be relevant to fields such as sociology and economy where it is common to deal with large systems of competitive agents that share information [4,11]. We hypothesize that *collective memory* might play an important role in the migration process of fish populations [13] and model its effects on schooling behaviour and migration efficiency. We tackle these questions by assuming that individuals have different amounts of information about migration routes and that only a fraction of them possess some information, whereas the rest only exhibit a social behaviour. Those assumptions are consistent with numerical simulations of the evolution of leader and social traits in migratory populations [15,16] but are introduced in our model in a different way. In fact, previous approaches mainly fall in a class of agent-based models with spatial interaction [1,15,17–19] where 'social' individuals tend to align and to follow the individuals that are nearby, in a finite spatial range. This reproduces a realistic dynamics, but it gives little insight into the mechanisms by which the collective behaviour emerges from individual interactions. Indeed, due to their complexity, spatial dynamics models can be studied only with extensive numerical simulations.

Here, instead, we take a stochastic adaptive network approach. Network approaches have already been successfully applied to address collective behaviour in animal groups [8,20,21]: adaptive network models provide, in fact, a simpler mathematical structure that can be analysed more easily than real space models (i.e. without relying on simulations). In all these models, as in ours, spatial dynamics is implicitly taken into account through link creation and destruction processes: changes in the neighbourhood of the individuals due to spatial dynamics are reproduced by link dynamics between nodes (figure 1).

Capitalizing on previous models [22,23], we build a model introducing the key ingredient of memory for preferred route directions in a fraction of the individuals (the informed ones). This is introduced as an *a priori* bias for a particular route in the choice behaviour of the informed individuals, that is, based on their experience in that particular habitat: their *memory*. Therefore, the collective choice of the route direction is a function of individual and social processes. We are able to find an exact solution for the model that provides a clear picture of how information is elaborated, stored and shared in the group and allows us to describe an observed switch of migratory path in fish populations as a result of a loss of group-level information.

2. Theoretical framework

Most studies about swarming phenomena in animal groups have relied on real space dynamical models [1]. Here, we address the issue of group formation using a network dynamical model [22,23]. Neighbouring nodes in the graph correspond to neighbouring individuals in space (figure 1).

Let us consider a group with N individuals. In our network model, each individual is represented by a node (thus N is the total number of nodes), and each node, i, has an internal dynamical variable, a_i, that can take integer values ranging from 1 to q. Although the mathematical solution
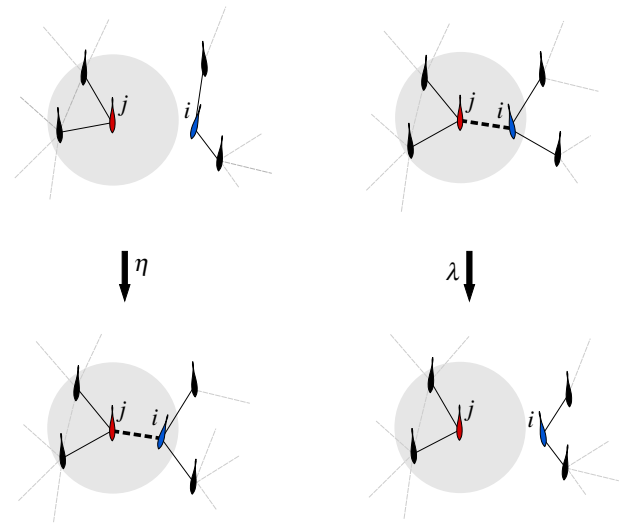
Figure 1. Connection between the link creation and destruction process and real space models where η is the link creation rate and λ is the link destruction rate. (Online version in colour.)

does not depend on the specific interpretation of the variable a_i, in the context of migrating groups, a_i might be considered as the direction taken by a single individual to reach the destination site. Links between nodes represent interactions among individuals by which they influence each other in their choice of the destination. While space is not explicitly resolved, we assume that neighbouring nodes in the graph correspond to neighbouring individuals in space (figure 1). Yet, nearby individuals need not necessarily influence each other (see below).

More precisely, a state of the system is defined by the adjacency matrix of the system g_{ij} and by the set of the internal dynamical states variables a_i. In our model, links are *mutual* and, thus, the adjacency matrix is a symmetric matrix (i.e. for all i, j, we have that $g_{ij} = g_{ji}$), such that $g_{ij} = 1$ if there is a link between the nodes i and j, and $g_{ij} = 0$ otherwise. The evolution of the system is governed by stochastic dynamics in which both the neighbourhood and the values of the internal dynamical state may vary, according to stochastic Poissonian processes. These are discussed in the following (we refer the reader to the electronic supplementary material for a detailed mathematical definition).

2.1. Network dynamics

The network evolves by creation and destruction of links that mimic the spatial interaction between individuals. Link creation is quantified by the rate η at which individuals form new links with other individuals. This rate encodes both evolutionarily selected traits for pro-social behaviour and environmental factors, notably the average distance between individuals. In our model, we assume that the interactions between individuals heading towards different directions decay much faster than interactions between close individuals heading towards the same direction. This is in agreement with the real space dynamical model and is achieved in the network by assuming that link creation can occur only when individuals have the same internal state $a_i = a_j$. This is equivalent to saying that if $a_i \neq a_j$, then the link between nodes i and j decays immediately.

Finally, individuals linked and moving in the same direction can also move further apart from each other, which is

formally encoded by assuming that links between nodes decay with a constant rate λ. These two processes provide a *mean field* description of the real space dynamics. Indeed, link creation and decay depend on the geometry of the neighbourhood in spatially explicit models, which is averaged out within the mean field description. Mean field approximations such as this one work very well to capture the qualitative behaviour of complex systems. To set an analogy, in a gas, one does not need to trace the trajectory of each molecule. It is enough to provide a 'collision integral' that loosely speaking gives the probability that a particle moving in a certain direction will interact with a particle moving in a different direction. Here, we are taking the same approach.

2.2. Internal state dynamics

The change of the internal state is a Poissonian process that occurs with rate ν for each individual. The choice of the destination a_i is influenced by two factors: (i) pro-social behaviour, by which an individual keeps the same destination of their neighbours, and (ii) memory, by which an isolated individual preferentially heads towards a destination α_i that is encoded in its memory.

More precisely, when an individual updates its internal state, (i) if it is linked to other individuals, then it will update its internal state conforming to the state of the majority in its neighbourhood, i.e. the new state a_i' is

$$a_i' = \underset{x}{\mathrm{argmax}} \left(\sum_j g_{ij} \delta_{xa_j} \right). \qquad (2.1)$$

In formula (2.1), δ_{xy} is Kronecker delta function, i.e. if $x = y$, $\delta_{xy} = 1$, otherwise $\delta_{xy} = 0$. Again, this rule is necessary within our mean field description of spatial interaction, because if an individual were to choose a direction which is different from that of the (majority of the) group it is in, then it would quickly move far apart and its links would decay.

On the other hand, (ii) if an individual is isolated (not linked), then its choice of the internal state is influenced by its preference for a destination that is encoded in its memory. More precisely, we assume that each individual has a preferred value of the internal variable, let us call it α_i. In the case of an internal state update event, an unlinked individual will pick up a state according to the following probability distribution:

$$\mathrm{Prob}(a_i = a) = \frac{e^{h_{\alpha_i} \delta_{a\alpha_i}}}{q - 1 + e^{h_{\alpha_i}}}, \qquad (2.2)$$

where h_{α_i} is a parameter that measures the intensity of the preference. This also encodes, besides information processing and storage capabilities, environmental factors related to the properties of a given feeding site, such as quantity of prey, water temperature, water quality, etc.

The fraction of individuals with a preferred destination α is n^α, but we also contemplate a fraction n^0 of 'uninformed' individuals who have no *a priori* preference for any memorized destination. We use the convention that uninformed individuals have $\alpha_i = 0$ and $h_{\alpha_i} = 0$. Therefore, uninformed individuals update their direction at random, which is described by equation (2.2) with $h_{\alpha=0} = 0$.

Previous network approaches used a voter model update rule, instead of a majority rule [8,20,21]; this choice makes no qualitative difference in the stationary case, because our main results are based on a state space decomposition (see the electronic supplementary material) that remains valid as long as the update rule promotes local uniformity. However, we expect detectable differences in the transient behaviour of these systems. Biologically, a majority rule captures the nonlinearity of group behaviour.

As in spatially explicit models, in our description, individuals compromise about directional choices. The majority rule does not prohibit that an individual i heading towards a given destination may change its route upon encountering another individual j. While this is not an elementary event described by the processes above, it can clearly occur as a composite event that entails the decay of all the links of i, an update of its choice and the formation of a link with j. The probability of this event is non-zero and it decreases with the number of individuals i is interacting with, as one expects.

In some cases, individuals in groups need to compromise between information gathering from the environment and social cohesion of the group [9,24], and thus some previous modelling approaches have assumed a trade-off between information capabilities and pro-social behaviour, in that informed individuals have a reduced tendency to follow their peers. The present modelling framework may be extended to encompass this situation also by making, for example, η take different values for informed and uninformed individuals. This generalization of the model leads to the same conclusions as those discussed below, but it comes at the cost of more complex mathematics. In addition, there is no conclusive evidence, as far as we are aware of, that such trade-offs really exist in populations of fishes [10]. We have, however, checked that adding these trade-offs to the model is inconsequential as far as the main results of the model discussed here are concerned, which is why we discuss these aspects in the electronic supplementary material.

2.3. Invariant distribution

Given the above transition rates, we can write down the master equation (see the electronic supplementary material) and derive the invariant distribution that describes the stationary state. One key observation in this is that, because only links between nodes with the same internal state can be established, the process will converge to states where all links (i, j) are between nodes with $a_i = a_j$. Any state with links (i, j) connecting nodes with $a_i \neq a_j$ is transient, i.e. it is not going to occur in the long run. This allows us to partition the states of the system into a transient class and a closed ergodic class. This ensures that the invariant distribution is *unique*. It can be shown (see the electronic supplementary material for details) that the process satisfies the detailed balance and the probability to observe a state with a given network $\{g_{ij}\}$ and profile of choices $\{a_i\}$ in the stationary state is given by

$$\pi(\{g_{ij}\}, \{a_i\}) = \frac{1}{\mathscr{Z}} \prod_{j<i} e^{\sum_i h_{\alpha_i} \delta_{a_i \alpha_i}} \left(\frac{2\eta \delta_{a_i a_j}}{\lambda(N-1)} \right)^{g_{ij}}, \qquad (2.3)$$

where $\mathscr{Z}$ is the normalization constant. In particular, when, for some i and j, we have that $a_i \neq a_j$ and $g_{ij} = 1$, the invariant distribution is zero. We are also assuming the convention that $0^0 = 1$.

Let $N_a^\alpha = \sum_j \delta_{a_j a} \delta_{\alpha_j \alpha}$ be the number of individuals that are in state a, but would like to be in state α, and let $n_a^\alpha = (N_a^\alpha / N)$.

If, in equation (2.3), we call

$$z = 2\frac{\eta}{\lambda} \qquad (2.4)$$

the non-dimensional parameter that accounts for the effective creation of links in the network, thus measuring the *sociality* of the group, then with standard mathematical manipulations (see the electronic supplementary material) we can easily write the stationary state distribution in terms of the densities $\mathbf{n} = \{n_a^\alpha\}$ as follows:

$$p(\mathbf{n}) = \frac{1}{\mathscr{Z}} e^{-N[F(\mathbf{n};z,\mathbf{h})+O(1/N)]}, \tag{2.5}$$

where

$$F(\mathbf{n};z,\mathbf{h}) = \sum_a n_a^0 \log(n_a^0) + \sum_{a\alpha} n_a^\alpha \log(n_a^\alpha) \\ - \sum_{a\alpha} h_\alpha n_a^\alpha \delta_{\alpha a} - \frac{z}{2}\sum_a (n_a)^2, \tag{2.6}$$

and $\mathscr{Z}$ is the normalization constant. In the large population limit ($N \to \infty$), this distribution peaks exponentially in N around the minima of F.

The stationary points of $F(\mathbf{n};z,\mathbf{h})$ satisfy the following system of equations:

$$n_a^\alpha = e^{h_\alpha \delta_{\alpha a} + z n_a} \frac{n^\alpha}{(e^{h_\alpha}-1)e^{z n_\alpha} + \sum_a e^{z n_a}}, \tag{2.7}$$

where $n_a = \sum_i n_a^i$ is the total density of individuals whose internal state is a (see the electronic supplementary material for the detailed calculation).

Therefore, with a large number of individuals and in the stationary state of the system, we are able to use equation (2.7) to analytically describe the fraction of individuals with *a priori* preference α that end up heading towards destination a.

This set of nonlinear equations has many solutions in principle. Those corresponding to stationary states can be fully characterized in terms of the average degree of the network $\langle k \rangle$ (i.e. the average number of neighbours of individuals) that is a proxy for the school density. It can be shown that one measure of the network degree is $\langle k \rangle = z(1 - (1/q))\sigma + (z/q)$, where the quantity

$$\sigma = \frac{q \sum_i (n_i)^2 - 1}{q - 1} \tag{2.8}$$

is a direct measure of the school efficiency and it takes values between $\sigma = 1$, when all individuals belong to a group that migrates towards the same destination, and $\sigma = 0$, when individuals distribute equally between different destinations. Hence, the solution with high coordination ($\sigma \simeq 1$) also corresponds to high network densities $\langle k \rangle \simeq z$.
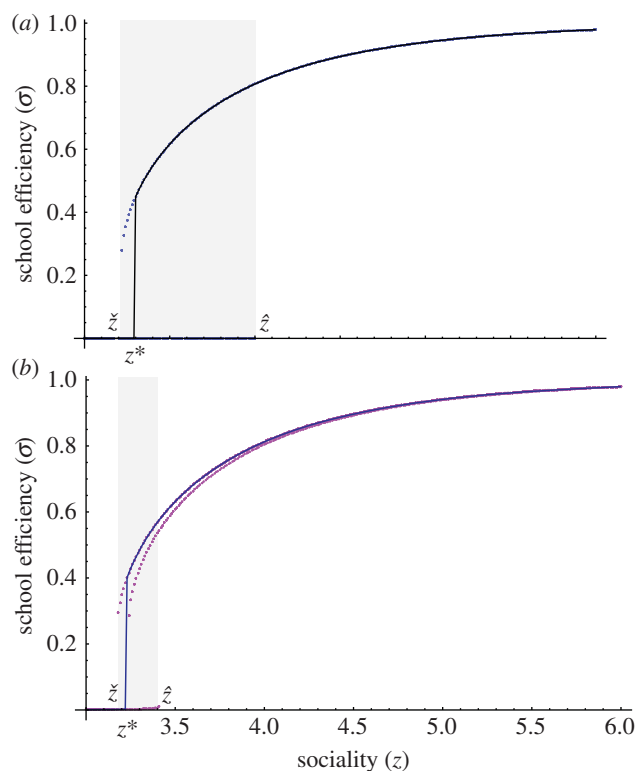
Among all the solutions of equation (2.7), we shall focus on those corresponding to the global minimum of $F(\mathbf{n};z,\mathbf{h})$ that determine the behaviour of the system, because they correspond to the values around which the stationary distribution shall peak.

3. Results

We shall analyse two cases: (1) the case of a population without informed individuals, $n^0 = 1$, and (2) the case where a fraction $n^1 = 1 - n^0$ of the individuals have a preferred migratory destination, whereas the rest are not informed.

3.1. Migration without information

When no information is available in the group, the system reduces to an adaptive network model in which group

Figure 2. Critical group dynamics: school efficiency σ as a function of the social parameter z in (*a*) non-informed group $n^1 = 0$ and (*b*) informed group $n^1 = 0.05$, $h = 0.5$. The dotted lines correspond to all the stable solutions of equation (2.7), the shadowed areas identify the coexistence region, whereas the solid lines correspond to the equilibrium solution.

coordination depends only on the rates at which links are created or destroyed [22,23].

Below a certain threshold $\check{z}$, only one local minimum exists that corresponds to a symmetric solution $\sigma = 0$ (figure 2*a*); there the network is sparse, $\langle k \rangle < 1$, and the group does not migrate. At $\check{z}$, a new bundle of q local minima appear at which $\sigma > 0$. There the network is dense, $\langle k \rangle > 1$, and a fraction of the individuals comparable to N (called in graph theory the *giant component*) are connected with one another and coordinated on the same destination choice.

The analysis also produces the full probability distribution of different states that allows ranking the solutions in terms of their probability (see the electronic supplementary material). Between $\check{z}$ and $\hat{z}$, both solutions coexist, and individuals can migrate in a coordinated manner or not. Above $\hat{z}$, the only local minima are for $\sigma > 0$, whereas the sparse solution $\sigma = 0$ becomes unstable. There is an intermediate point z^* below which the sparse solution is the most likely outcome whereas, above it, the high-density solution will prevail.

3.2. Informed migration

In order to analyse the role of information in the model, we study the simplest possible case, with q destinations, a density of informed individuals $n^1 = 1 - n^0$ and a preference h about a single destination.

Equation (2.7) again can be solved numerically to obtain a prediction on schooling behaviour. Information has two main effects on the system (figure 2*b*). First, it breaks the symmetry between the q high-density solutions found in the $n_0 = 1$ case, by selecting the solution with the preferred destination $\alpha = 1$ as the most likely. The $q - 1$ solutions corresponding
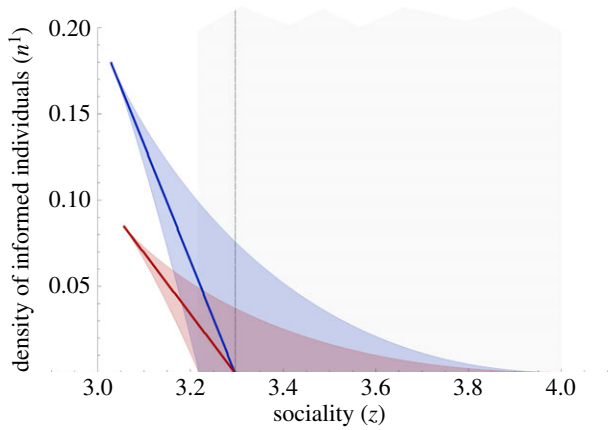
Figure 3. Phase diagram of the system with $q = 4$ possible directions. The grey area corresponds to a preference parameter $h = 0$ (no preferences), and the dashed line is the critical line. The blue area corresponds to $h = 0.5$, and the thick blue line represents the corresponding critical line. The red area corresponds to $h = 1$, and the thick red line also represents the corresponding critical line.

to migration towards other destinations remain stable, but are much less likely to be selected by the population.

Second, the coexistence region between high- and low-density solutions $[\check{z}, \hat{z}]$ is reduced in the case of informed migration (figure 2). In fact, this region becomes smaller as the number of informed individuals increases (figure 3).

Eventually, there exists a critical value of n^1 at which the region collapses into a point. This change in the behaviour of the system is equivalent to a second-order phase transition in physics. For values of n^1 greater than this critical point, the system has a smooth transition between low- and high-density states, as z increases, and a single solution is found. Moreover, the coexistence region and the critical value change with h. The thick line in figure 3 marks the point, in the coexistence region, where the two solutions are equally probable; on the right (left) of this line, we expect to see the high (low) density solution.

The behaviour of the solution as the parameters h and $n^1 = 1 - n_0$ vary, at fixed z, is depicted in figure 4. For low values of z (figure 4a), we observe a smooth crossover from low- to high-density solutions as h and/or n_1 increase, whereas when z is larger the system exhibits a sharp transition between the two solutions (figure 4b). The presence of a sharp transition with coexistence in a broad range of parameters is a robust feature of this model.

For more complicated settings using competing groups with different preferred migratory destinations, it can be shown that, for large z, the population coordinates towards the migratory destination that provides the largest product $n^\alpha h_\alpha$ (see the electronic supplementary material). This quantity can be interpreted as the strength of the group's collective memory towards a given migration site, α.

This provides us with a vivid picture of how we expect the collective behaviour of the population to change when the parameters z, h and n_0 change. Adapting this picture to the observed behaviour of populations provides hints on the likely underlying causal effects. In brief, when z is large, i.e. for individuals with a marked pro-social behaviour, we expect abrupt transitions when either the density n^α of individuals with a given preference or the intensity h_α of that preference varies in such a way as to cross the boundaries in the phase diagram (figure 3).
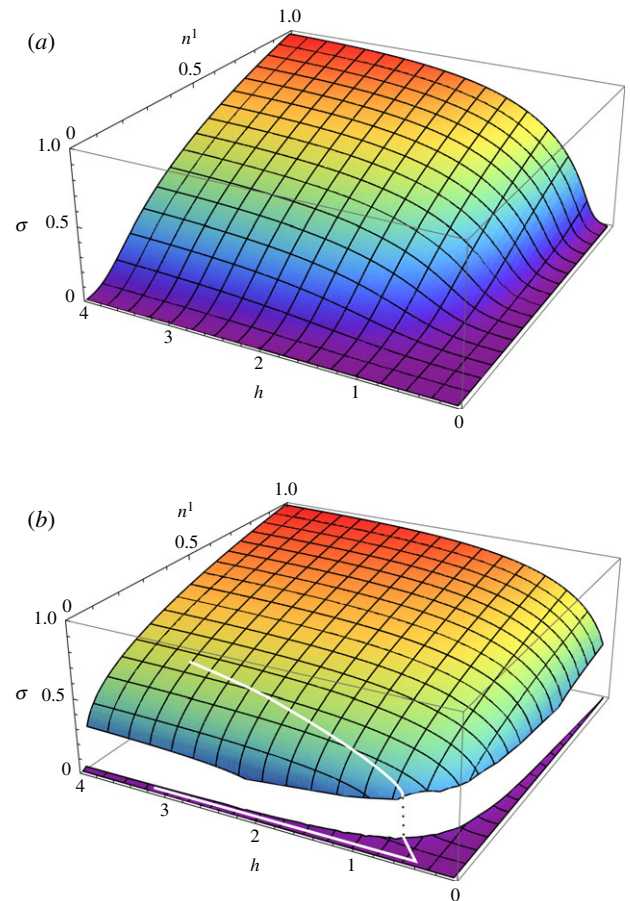
Figure 4. School efficiency σ as a function of the fraction of informed individuals n^1 and strength of the preference h when the social parameter z is (a) in a non-critical region $z = 2.5$ and (b) in a critical region $z = 3.1$. The white line in (b) is a schematic of the hysteresis mechanism for a fish population starting with high n^1 and h, then decreasing n^1 and h (e.g. overfishing of both migratory species and its prey) and subsequently increasing h (increase of prey population).

When both the density of informed individuals and the intensity of preference h_α decrease, abrupt transition from efficient group formation to collapse of migration efficiency is visible. We note that this hysteresis cycle is consistent with observed stock collapses of migratory fish populations [25]. When the migratory population is described using a social parameter z close to the critical point, then the interplay between the memory for a given destination, h, and the fraction of the individuals informed, n^1, about this destination can produce an abrupt transition in the migration of the species.

In the case of a school migrating in direction 1, a decrease of the value of h and n^1 over the years, due, for example, to overfishing of both individuals and prey in the migration site, can force the system to cross the critical line reaching eventually low values of both h and n^1. When in this condition, an increase in the value of h might occur due, for example, to better habitat conditions or food availability, for those few vagrant fish that might still be present in the area. However, this increase alone cannot bring the system back to the original state, because the system may not cross again the critical line. Thus, the group may not migrate in direction 1, even though previous habitat conditions are re-established.

4. Discussion

We show that abrupt changes in migratory patterns of animal groups can be caused by removal of knowledgeable individuals from the group or by decreasing preference of the individuals towards a particular migratory destination. We demonstrate this with a robust analytical approach that allows us to clearly identify the factors regulating group formation processes. Our results are consistent with previous models suggesting that a small number of informed individual can lead to large group migrations [14,26]. Additionally, we demonstrate that diminishing individual preference for a given migration site can preclude group formation and break the migration process.

4.1. The migration game

The migration process can be described as an emergent property of the population undertaking a group formation game: when the spatial density of fish is locally low, each individual moves independently, and the system is in a sparse network configuration with a value of z below the lower edge of the coexistence region. In this state, uninformed individuals cannot migrate, whereas informed individuals can undertake a *solitary* migration towards their preferred destination. Owing to external stimuli (water temperature, local currents, topography, etc.), the density may increase and so does the value of z, driving the system towards the coexistence region. In this region, even though the local density of fish is high, a sparse network configuration with fish moving independently is still stable, but an alternative and stable dense network configuration also appears. When the system reaches the upper edge of this region, further increasing the density, the sparse network state becomes unstable, whereas the dense network state prevails, and the school starts a migration towards the preferred destination. On the other hand, a *hysteretic* cycle is present in this system and when the local density of fish decreases in the school, the sociality, z, decreases and the system is driven back to the coexistence region. A similar effect can be reproduced in the system by lowering the preference factor, h. The schooling configuration remains stable until the system reaches the lower edge of the coexistence region: at this point, fish stop schooling, and the system switches back into the sparse configuration (solitary fish).

The group formation game described above can be repeated each year naturally driving changes in the preference term h, hence in the memory of migratory fish. Likewise, changes in this or in the other term of the model can occur when the migratory population is affected by external stimuli, for example overfishing, habitat degradation, demographic fluctuations. Because of the hysteretic cycle, such variations may then result in *abrupt* changes in the migratory patterns.

4.2. Conflicting preferences

From the asymptotic analysis (electronic supplementary material), we demonstrate that, for large value of z, the group shall migrate towards the direction α for which the product $n^\alpha h_\alpha$ is maximal, whereas in the limit of small z the sparse configuration is the only stable one. This suggests that our results might be extended to groups with conflicting preferences. It is relevant to note that in our model *all individuals* have a social component. For example, in groups with conflicting preferences, our model suggests that, for some range of the parameters, an informed individual can follow the group and

migrate towards a site different from its preferred destination. This approach makes our definition of leaders dependent not only on the amount of information stored, but also on the social context in which they live. Therefore, the interaction between personal information and social effects is explicitly resolved in our model and—we note—it has been suggested to operate in living groups [10,27].

4.3. Collective memory and breakdown of social traditions

Breakdown of social traditions, due to selected fishing on older informed individuals, has been hypothesized to have contributed to stock collapses in several large commercially important fish populations [13,25].

Our sketch of the migration game suggests that social dynamics may lead to such collapses and that the integrity of migration pathways and spatial distributions of migratory predators might be particularly vulnerable to perturbations such as fishing or habitat degradation. Fishing out informed individuals and their prey can exacerbate the loss of collective memory up to the point where a migratory pathway is suddenly interrupted. We can assume that each year young individuals join the group: among them a fraction are able to gather information and remember a migratory route, whereas the rest have a purely social behaviour. The 'information-gathering-able' individuals behave as uninformed individuals ($h = 0$), but *learn* a new migratory route during the first migration(s). If the group does not succeed in starting migration, or migrates towards a different location, the young 'information-gathering-able' individuals will not learn the traditional migration route of the group and the social traditions of the group will not be transmitted to the new generations. The loss of collective memory in the group will then force the system to cross the critical line, and the migration towards the destination site will stop.

An example of a prey–predator collapse and subsequent abrupt disappearance of migratory route is provided by Atlantic bluefin tuna (*Thunnus thynnus* Linnaeus, 1758) and its main prey, herring (*Clupea harengus* Linnaeus, 1758) in the Norwegian and the North Seas. During the 1950s to 1970s, both species were heavily exploited in these regions, resulting in the disappearance of both species [28–30]. Since then, the herring populations in both regions have recovered to moderate to high levels [28,29], but bluefin tuna have been extremely rare during the 1980s to 2000s and apparently have not migrated to these areas in large numbers since their disappearance several decades ago [30]. These hysteretic dynamics are consistent with a fishing-induced removal of predators having preference for migration to these regions and a fishing-induced decline in habitat quality which then leads to the collapse of group formation and a sudden change in migratory path (cf. figure 4).

5. Conclusion

We have presented a model that offers and elucidates a plausible mechanism for migration dynamics. By extending and generalizing previous approaches, our model shows that group formation dynamics have a critical dependence on sociality, number of informed individuals and strength of the preference in informed individuals. For example, partial

removal of knowledgeable individuals may be sufficient to interrupt the transmission of social traditions in groups of animals. Such critical dependence is consistent with abrupt transitions that are commonly observed in migration patterns of social animals such as Atlantic bluefin tuna as well as other fish populations [25].

Our findings offer deep insights into migration dynamics and suggest interesting directions both for data analysis (e.g. new interpretations of spatial temporal dynamics of migratory populations) and for further theoretical development (e.g. accounting for conflicting preferences, continuous directions, different segregation policies, topological interaction).

Contrary to previous agent-based approaches [1,15,17–19], our model has the advantage of being analytically soluble, and thus it provides a powerful theoretical bench test for hypotheses on collective animal behaviour.

References

1. Sumpter DJT. 2010 *Collective animal behavior*. Princeton, NJ: Princeton University Press.

2. Krause J, Ruxton GD. 2002 *Living in groups*. Oxford, UK: Oxford University Press.

3. Krause J, Ruxton GD, Krause S. 2010 Swarm intelligence in animals and humans. *Trends Ecol. Evol.* **25**, 28–34. (doi:10.1016/j.tree.2009.06.016)

4. Surowiecki J. 2005 *The wisdom of crowds*. New York, NY: Anchor.

5. Lachlan R, Crooks L, Laland K. 1998 Who follows whom? Shoaling preferences and social learning of foraging information in guppies. *Anim. Behav.* **56**, 181–190. (doi:10.1006/anbe.1998.0760)

6. Conradt L. 2011 Models in animal collective decision-making: information uncertainty and conflicting preferences. *Interface Focus* **2**, 226–240. (doi:10.1098/rsfs.2011.0090)

7. Sumpter DJT, Krause J, James R, Couzin ID, Ward AJW. 2008 Consensus decision making by fish. *Curr. Biol.* **18**, 1773–1777. (doi:10.1016/j.cub.2008.09.064)

8. Couzin ID *et al.* 2011 Uninformed individuals promote democratic consensus in animal groups. *Science* **334**, 1578–1580. (doi:10.1126/science. 1210280)

9. Ward AJW, Herbert-Read JE, Sumpter DJT, Krause J. 2011 Fast and accurate decisions through collective vigilance in fish shoals. *Proc. Natl Acad. Sci. USA* **108**, 2312–2315. (doi:10.1073/pnas. 1007102108)

10. Miller N, Garnier S, Hartnett AT, Couzin ID. 2013 Both information and social cohesion determine collective decisions in animal groups. *Proc. Natl Acad. Sci. USA* **110**, 5263–5268. (doi:10.1073/pnas.1217513110)

11. Conradt L. 2011 Collective behaviour: when it pays to share decisions. *Nature* **471**, 40–41. (doi:10. 1038/471040a)

12. Berdahl A, Torney CJ, Ioannou CC, Faria JJ, Couzin ID. 2013 Emergent sensing of complex environments by mobile animal groups. *Science* **339**, 574–576. (doi:10.1126/science.1225883)

13. Brown C, Laland KN. 2003 Social learning in fishes: a review. *Fish Fish.* **4**, 280–288. (doi:10.1046/j. 1467-2979.2003.00122.x)

14. Couzin ID, Krause J, Franks NR, Levin SA. 2005 Effective leadership and decision-making in animal groups on the move. *Nature* **433**, 513–516. (doi:10.1038/nature03236)

15. Guttal V, Couzin ID. 2010 Social interactions, information use, and the evolution of collective migration. *Proc. Natl Acad. Sci. USA* **107**, 16 172–16 177. (doi:10.1073/pnas.1006874107)

16. Guttal V, Couzin ID. 2011 Leadership, collective motion and the evolution of migratory strategies. *Commun. Integr. Biol.* **4**, 294–298. (doi:10.4161/cib.4.3.14887)

17. Katz Y, Tunstrøm K, Ioannou CC, Huepe C, Couzin ID. 2011 Inferring the structure and dynamics of interactions in schooling fish. *Proc. Natl Acad. Sci. USA* **108**, 18 720–18 725. (doi:10.1073/pnas.1107583108)

18. Vicsek T, Zafeiris A. 2012 Collective motion. *Phys. Rep.* **517**, 71–140. (doi:10.1016/j.physrep.2012.03.004)

19. Chaté H, Ginelli F, Grégoire G, Peruani F, Raynaud F. 2008 Modeling collective motion: variations on the Vicsek model. *Eur. Phys. J. B* **64**, 451–456. (doi:10. 1140/epjb/e2008-00275-9)

20. Huepe C, Zschaler G, Do AL, Gross T. 2011 Adaptive-network models of swarm dynamics. *New J. Phys.* **13**, 073022. (doi:10.1088/1367-2630/13/7/073022)

21. Gross T, Blasius B. 2008 Adaptive coevolutionary networks: a review. *J. R. Soc. Interface* **5**, 259–271. (doi:10.1098/rsif.2007.1229)

22. Marsili M, Vega-Redondo F, Ehrhardt G. 2008 Networks emerging in a volatile world. EUI Working Paper ECO. European University Institute, San Domenico di Fiesole, Italy.

23. Ehrhardt G, Marsili M, Vega-Redondo F. 2006 Phenomenological models of socioeconomic network dynamics. *Phys. Rev. E* **74**, 36106. (doi:10. 1103/PhysRevE.74.036106)

24. Krause J, Bumann D, Todt D. 1992 Relationship between the position preference and nutritional state of individuals in schools of juvenile roach (Rutilus rutilus). *Behav. Ecol. Sociobiol.* **30**, 177–180. (doi:10.1007/BF00166700)

25. Petitgas P, Secor DH, McQuinn I, Huse G, Lo N. 2010 Stock collapses and their recovery: mechanisms that establish and maintain life-cycle closure in space and time. *ICES J. Mar. Sci.* **67**, 1841–1848. (doi:10. 1093/icesjms/fsq082)

26. Huse G, Railsback S, Fernö A. 2002 Modelling changes in migration pattern of herring: collective behaviour and numerical domination. *J. Fish Biol.* **60**, 571–582. (doi:10.1111/j.1095-8649.2002. tb01685.x)

27. Herbert-Read JE, Krause S, Morrell LJ, Schaerf TM, Krause J, Ward AJW. 2013 The role of individuality in collective group movement. *Proc. R. Soc. B* **280**, 20122564. (doi:10.1098/rspb. 2012.2564)

28. International Council for the Exploration of the Sea. 2011 *Report of the herring assessment working group for the area south of 62 deg N.* Copenhagen, Denmark: ICES.

29. International Council for the Exploration of the Sea. 2012 *ICES Advice. Book 6.* Copenhagen, Denmark: ICES.

30. International Commission for the Conservation of Atlantic Tunas. 2012 *Report of the 2012 Atlantic Bluefin Tuna stock assessment session.* Madrid, Spain: ICCAT. See http://www.iccat.int/Documents/ Meetings/SCRS2012/SCI-003_ENG.pdf.