Chapter 9
Discussion and Further Open Problems

9.1 Summary

For the past 30 years, hyperbolic and kinetic models have been used to investigate the growth, movement and self-organisation of cells, animals, and even human pedestrians. One of the main reasons for employing such models—as opposed to the classical parabolic models—is their finite propagation speed that makes them more biologically realistic. Another reason is that these models do seem to exhibit a richer pattern dynamics compared to the parabolic models.

In this study, we reviewed some of the local and nonlocal hyperbolic and kinetics models derived to investigate various biological aggregations and traffic-like movement. We presented models that investigated the movement and aggregation of various bacteria (e.g., *Myxobacteria*, *Escherichia Coli*), cells (e.g., tumour cells), and animal populations (e.g., flocks of birds or herds of ungulates). Moreover, since traffic-like collective movement is such a common behaviour in biology (from intracellular transport, to ant traffic and pedestrian self-organised movement [1–3]), we also discussed some traffic flow models. (Although it may seem unusual to discuss car-traffic models in a monograph focused on biological phenomena, we chose to do so at the beginning of Chap. 3 since the same car-traffic models have been applied to describe pedestrian traffic and collective behaviours, and further generalised to biological traffic, such as cellular, bacterial and ants traffic.)

Our goal was not to provide a very comprehensive review of these hyperbolic and kinetic models. Rather, we wanted to present the complexity of the biological and mathematical problems, and to summarise the patterns exhibited by the models. Moreover, since this study is intended for researchers not familiar with these types of models (and the analytical and numerical approaches derived to investigate them), we took a step-by-step approach to present a clearer view of the motivations and the costs associated with increased model complexity. We started with the simplest one-dimensional models described by advection or advection-reaction equations. Then,

we investigated systems of local and non-local hyperbolic models that have constant or density-dependent speeds and turning rates. Finally, we discussed a couple of kinetic models in higher dimensions, and their hydrodynamic limits (and in some cases their parabolic limits). By choosing this structural approach to review the hyperbolic and kinetic models, we were able to highlight the contribution of these models to the investigation of group patterns in various communities of organisms. We also stressed the difficulties that these complex models are confronted with, such as the absence of analytical approaches to investigate some of the resulting spatial and spatio-temporal patterns, and/or the absence of numerical approaches to illustrate the behaviour of the more complex kinetic models.

The mathematical models reviewed in this study were mainly deterministic (even if they were shown to exhibit also chaotic dynamics; see, for example, Fig. 5.23). Even so, the kinetic models contained a stochastic component in the velocity, since the turning events were usually governed by Poisson processes. However, recent studies started to focus on models that incorporate stochasticity in an explicit manner, either additively or multiplicatively, and thus we reviewed a few such models at the end of Chaps. 5 and 6. Another way to incorporate stochasticity into the models was to start with the Langevin equations for the motion of particles (where external noise was added explicitly to particles' velocity), and then derive the corresponding stochastic kinetic and hyperbolic equations [4–6]. Note that this Langevin approach (as well as the stochastic Ornstein-Uhlenbeck processes [7]) lead to distribution functions that satisfied equations which were hyperbolic with respect to the space variable and parabolic with respect to the velocity variable. For this reason, we chose not to describe them here in more detail.

The majority of models discussed here incorporated spatial dynamics. The few exceptions were: (i) the kinetic models for active particles, where the population could also change over an "activity" space; and (ii) the age-structured models, that could describe the formation of human pairs [8], predator-prey dynamics [9], tumour growth [10], or the epidemic spread of diseases [11] in age-structured populations.

9.2 Biological Relevance of Models' Assumptions and Generated Numerical Patterns

The numerical investigation of the patterns exhibited by the kinetic and hyperbolic models reviewed in this study allows for a visual comparison of these theoretical models with the patterns observed in nature, with the final goal of determining whether the assumptions incorporated into the models can explain the reality. In regard to *animal behaviours*, these assumptions usually refer to: (i) the necessity of having repulsive-attractive-alignment interactions versus only alignment interactions, or only attractive-repulsive interactions; (ii) the nature of spatial interactions as determined by the various nonlocal kernels; (iii) the nature of inter-individual communication mechanisms. In regard to *cell behaviours*, these assumptions usually

refer to (i') the strength of cell-cell adhesion versus the strength of cell-matrix adhesion; (ii') the appropriate incorporation of specific signalling pathways that control cell macroscopic behaviours (e.g., movement, turning).

The mathematical models reviewed here were shown to exhibit a large variety of spatial and spatio-temporal patterns. Many of these patterns can be connected to empirically observed animal group behaviours: zigzagging flocks of birds, rippling behaviours observed in Myxobacteria colonies, travelling pulses and stationary pulses corresponding to moving (e.g., travelling schools of fish) and resting aggregations, respectively. The expanding and contracting group behaviours that characterise the breather patterns have been observed for example in flocks of birds [12]. Vortices or mills (i.e., rotating groups) are group patterns observed quite frequently in schools of fish (e.g., barracuda, bluefin tuna, or sharks [13, 14]) or groups of ants [15]. The formation of shock waves (i.e., gradient blow-up patterns) is a well known pedestrian behaviour observed during mass events which result in panic stampede [16]. The travelling trains could describe the propagation of density waves through the aggregation (a behaviour observed in schools of herring [17]).

While many of the mathematical patterns can be traced back to empirical observations, there are also some biologically unrealistic patterns, such as the density blow-ups. These patterns are mathematical artefacts caused by the particular assumptions incorporated into the models (e.g., interaction kernels discontinuous at the origin [18], or nonlinear production of an external signal [19]). When such blow-up solutions occur, it is an indication that the model is no longer appropriate to describe the behaviour of the biological system. We note here that these solutions were displayed by both local and nonlocal hyperbolic models (see also Table 9.1 for a summary of the patterns discussed here).

In regard to inter-individual communication, it was shown that some patterns seem to be connected with specific communication mechanisms. For example, mechanism M5—describing interactions with neighbours moving towards the reference individual—seems to generate the observed ripples in Myxobacteria colonies (irrespective of how this mechanism is incorporated into local or nonlocal continuum models [20–22], or into individual-based models [23]). However, the most common pattern observed in every biological aggregation, namely the stationary pulses, is associated with the majority of communication mechanisms (see also Table 5.2). Moreover, when multiple communication mechanisms are used in a combined manner by one group of individuals, it can lead to behaviours (patterns) not predicted by the use of one communication mechanisms, including chaotic behaviours; see the discussion in Sect. 5.6.

A recent review by Bellomo and Dogbé [24] discussed the derivation and use of empirical data to validate models for traffic and crowds dynamics. Available data usually refers to the speed and movement direction of cars and pedestrians [25–27], as well as cells [28], bacteria [29, 30], fish [31], birds [32] or ungulates [33]. However, the incorporation of this data into kinetic and hyperbolic models is still an open research area, with very few studies combining modelling with data analysis.

Another open research area is related to the translation of results obtained with animal crowd models to the understanding of human behaviours [34, 35].

When ethical concerns do not allow to experiment with human subjects, one could focus on non-human subjects (e.g., ants, mice, sheep) to gain some understanding on collective human behaviour (and movement) under specific conditions (e.g., extreme escape from various built environments). However, as recently discussed in [36], there is the need to have a more systematic connection between animal and human experiments, to be able to understand better the context in which reliable inferences can be drawn from experiments with non-human crowds.

9.3   Directions for Future Research

We conclude the discussion of pattern formation in this monograph by summarising some possible directions of future research. To this end, we focus on modelling, numerical and analytical aspects.

Modelling Multiscale models have been developed intensively over the past years in the context of cell dynamics, to connect macroscopic processes related to cell movement and turning behaviours, to microscopic processes that occur inside cells and control cell movement/turning. The majority of kinetic models in the literature consider simplifications of the molecular-level processes (i.e., cell signalling pathways) involved in cell movement and turning. In the future it is expected that more detailed signalling pathways will be incorporated into the multiscale models for collective cell movement (e.g., the Erk/MAPK pathway, the JNK pathway or the p38 signalling pathway that all have roles in cell migration [37]). Moreover, not many multiscale models have been developed in the context of ecological collective movement (among the very few we mentioned for human crowds [38, 39]). It is expected that in the future, research in animal communication, animal psychology and physiology will be combined with mathematical modelling of animal movement, to increase our understanding regarding the collective behaviour of animals [40].

Another aspect related to modelling that will develop further in the next years is the incorporation of stochastic events in these hyperbolic/kinetic models. More and more studies recognise the importance of environmental and demographic stochasticity in animal/cell movement [41–43]. Until now the majority of models for the collective movement of cells/bacteria/animals that incorporated stochasticity have been of discrete type, with stochasticity affecting the individual level (see the IBMs discussed briefly in Chap. 1). However, we expect that the upcoming decades will see a significant increase in the development of stochastic transport models for animal/cell dynamics, where noise will have an impact at the population level. This will lead to the further development of analytical and numerical methods to investigate the patterns generated by these new models.

Numerical Investigation of Patterns One of the most interesting (and most difficult to investigate) aspects of patterns formation focuses on connecting the

observed biological patterns to specific mathematical and biological mechanisms. Intensive numerical investigations could provide some understanding of the biological mechanisms behind specific patterns. We mentioned before the connection between the communication mechanism M5 and ripples [20, 21, 44, 45]. Stationary pulses, on the other hand, are one of the most common patterns, being observed in almost every model discussed here (see Tables 5.2 and 9.1, and the majority of models discussed throughout this monograph). Hence, we cannot associate this pattern with a specific biological mechanism. However, since many of the models presented here have not been the subject of very thorough numerical and analytical investigations, it is possible that they could exhibit even more (possible exotic) patterns. The discovery of new spatial and spatio-temporal patterns (especially for multi-dimensional nonlocal kinetic and hyperbolic models) requires the development of fast numerical schemes, to be able to run multiple simulations that would span large parameter spaces. This is particularly relevant for the multi-dimensional (nonlocal) kinetic models. Intensive simulations are also required for the numerical investigation of the bifurcation dynamics of these models, and the tracking of various solution branches that can bifurcate at specific points in the parameter space. In particular, new continuation algorithms need to be developed to take into account the characteristics of these local/nonlocal hyperbolic and kinetic models. One first step was recently made in [46], where the authors described a continuation algorithm that considers the symmetry structure of the nonlocal hyperbolic models presented in Chap. 5; see Eqs. (5.14), (5.18) and (5.19).

Analytical Investigation of Patterns While numerical simulations can offer some insight into the mechanisms behind these patterns, analytical investigations (using, for example, existence results, linear and nonlinear stability, bifurcation and symmetry theory) are necessary to: (i) explain the role of model parameters on the formation (or not) of the patterns, (ii) reduce the size of the parameter space where we look for specific patterns, (iii) rigorously identify and classify all patterns that could be exhibited by a mathematical model, (iv) decide whether the model is biologically realistic (e.g., exhibits finite or blow-up patterns, and if so in which biologically realistic/unrealistic parameter spaces?). As discussed throughout this review, many hyperbolic and kinetic models have not been subjected to detailed analytical investigation of pattern formation (and this could explain the lack of patterns in columns 2, 3, 4 and 6 of Table 9.1). Moreover, apart form classifying these patterns based on their symmetry subgroups (as discussed in Chap. 8), it is unclear how else one could classify them. This classification approach raises another question: how to classify the (similarly-looking) patterns generated by the corresponding stochastic models (see Fig. 5.26), which have lost the initial symmetry. It is likely that further analytical investigations would reveal that these complex hyperbolic and kinetic models might generate new patterns and bifurcations, whose investigation could be very challenging.

Table 9.1 Summary of some of the patterns exhibited by the hyperbolic and kinetic models presented throughout this monograph

Spatio-temporal patterns	Local 1-eq. models (1D)	Non-local 1-eq. models (1D)	hyperbolic systems (1D)	Nonlocal hyperbolic systems (1D)	2D (or 3D) models (mesoscopic, macroscopic)
Stationary pulse		✓	✓	✓	✓
Travelling pulse	✓			✓	✓
Travelling front	✓			✓	
Travelling train				✓	
Ripples (standing waves)			✓	✓	
Feather				✓	
Travelling feather				✓	
Breather				✓	
Travelling breather				✓	
Zigzags (Vortices (2D))				✓	✓
Semi-zigzags (stop and go waves)				✓	
Density blow-up				✓	✓
Shocks	✓	✓			✓
Lanes					✓
Chaos				✓	✓

The list is not very comprehensive, since we focused mainly on nonlocal (1D) hyperbolic systems for which detailed numerical and analytical investigations have been performed to identify and classify the exhibited patterns

Combining analytical and numerical approaches will lead to the further development of the area of pattern formation in nonlocal kinetic and hyperbolic models. Some of the questions that could be answered in the future are:

- Can the patterns observed in nonlocal models (especially the more exotic ones, such as the feathers, breathers, zigzags) be exhibited also by the local models? If not, why?
- Are the complex (exotic) patterns discussed throughout this monograph specific only to the hyperbolic/kinetic models? In other words, if we develop parabolic or individual-based models that incorporate communication mechanisms similar to the ones discussed in nonlocal hyperbolic systems, can we obtain similar patterns?
- Can the complex 1D patterns exhibited by the 1D nonlocal hyperbolic and kinetic models be generalised to 2D models? If so, what are the mathematical/biological assumptions that need to be incorporated into these 2D models, to generate the appropriate patterns?
- How could one incorporate various 2D communication mechanisms into the existent mesoscopic and macroscopic models for the collective behaviours of cells/bacteria/animals? In this case, could the corresponding 2D patterns be associated with particular communication mechanisms (or combination of mechanisms)?
- How do we connect the 1D and 2D models for collective spatial movement of cells/bacteria/animals to the available data? What kind of data is necessary to be collected to parametrise these models, to allow for quantitative predictions?
- Could the assumption of "pairwise interactions", which is incorporated into the Boltzmann-type kinetic models, impede our understanding of the contribution of other particles/cells to these interactions? This is a valid question since the in vivo dynamics of cells is not always determined by pairwise interactions, but by interactions with a variety of other cells via communication molecules (cytokines, chemokines) produced by these cells. Similarly, it is less likely that animals in group interact with their neighbours via "binary collisions", and is more likely that these interactions involve more than two individuals (if the community comprises multiple individuals). Moreover the derivation of the Boltzmann equation in the limit $N \rightarrow \infty$ also requires that collisions involve only uncorrelated particles, in the sense that particles that have collided already will not collide again. This assumption does not seem to carry great biological realism, since animals in a group will likely interact again.
- Can we understand the bifurcation structure of the stochastic PDE models for the collective movement of cells/bacteria/animals? How can we extend the current stochastic bifurcation theory [47–50] (mainly developed for ODEs) to the nonlocal and local transport models discussed in this study (as well as many more other models in the literature)? How can we adapt the (dynamical) D-bifurcation and (phenomenological) P-bifurcation theory to the realities of the chaotic and deterministic patterns generated by the nonlocal hyperbolic models presented briefly in Chap. 5?

To conclude, we remark that the use of hyperbolic and kinetic models to answer biological questions is far from having reached its full potential. On the contrary, they seem to be used more and more to investigate various problems in ecology and medicine. Moreover, in the last few years these models have been applied to new research areas, such as social dynamics [51], economy [52] or human psychology [53]. Furthermore, the authors in [54, 55] suggested that these kinetic models could be the start of a biological mathematical theory for complex systems. In particular, Bellomo and Forni [55] argued that these models can incorporate two of the most important aspects of living matter: the notion of function or purpose for biological organisms, and the multi-scale aspect of biological interactions. While some first steps have been taken in this direction, we note that these are very complex aspects that require further extensive investigations.

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