Super-individual based model for fish migration

Petro Babak

One of the most remarkable characteristics of collective motion of fish is the emergence of complex migration patterns in which swimming fish are synchronised by remaining together and moving in the same direction. These migration patterns, referred to as fish schools, are often explained using individual based models (IBM's) that focus on interactions between single individuals. The IBM's appear to be realistic and robust; however, they are computationally unable to efficiently describe migration of large groups of fish. Here, an approach for developing computationally efficient super-individual based models from simple individual based models for fish migration is proposed. This approach accentuates on ecological mechanisms underlying collective motion of fish, and interaction between them; it explicitly incorporates such important mechanisms in collective motion of fish as fish school splitting and merging.

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SUPER-INDIVIDUAL BASED MODEL FOR FISH MIGRATION

Petro Babak

Calgary, Alberta, Canada

Email: *petro@ualberta.ca*

Abstract

One of the most remarkable characteristics of collective motion of fish is the emergence of complex migration patterns in which swimming fish are synchronised by remaining together and moving in the same direction. These migration patterns, referred to as fish schools, are often explained using individual based models (IBM's) that focus on interactions between single individuals. The IBM's appear to be realistic and robust; however, they are computationally unable to efficiently describe migration of large groups of fish. Here, an approach for developing computationally efficient super-individual based models from simple individual based models for fish migration is proposed. This approach accentuates on ecological mechanisms underlying collective motion of fish, and interaction between them; it explicitly incorporates such important mechanisms in collective motion of fish as fish school splitting and merging.

Keywords: Fish migration; collective motion; individual based model; super-individual based model.

1. Introduction

Individual based models (IBM's), also called agent-based models, for fish migration seek to capture effects of individual organisms and interactions between them on population migration. The IBM's have many advantages, including ability to explain complex population phenomena from common knowledge about individual behaviour (Giardina, 2008;

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Grimm and Railsback, 2005). However, a major problem with these models is their computational inability to describe efficiently migration of typically large groups of pelagic fish.

Contrary to individual based models, super individual based models (SIBM’s) assess effects of groups or classes of organisms on population dynamics (Scheffer *et al.*, 1995). The basic unit of SIBM’s is a super-individual that is understood as a class of similar organisms according to one or many ecological criteria (Hughes and Thomas, 1971). Since each super-individual is usually associated with a large number of individuals, all population of organisms can be divided into a relatively small number of super-individuals. Therefore, super-individual based models are much more computationally efficient for studying very large fish populations.

SIBM’s for migration of marine organisms are traditionally developed based on one or another individual based model by associating each individual with a fixed number of individuals (Malchow, Petrovskii and Medvinsky, 2002; Hellweger, 2008). Then, they implicitly assume that mechanisms driving movement of individuals and their interactions are the same as mechanisms of group motion and group interactions. While these conventional super-individual based models allow considering the movement of numerous groups of marine organisms at a low computational cost; they lack clear argumentation at the level of fish groups.

The main objective of this work is to develop a framework for constructing ecologically sound SIBM’s for fish migration. The new SIBM’s would directly account for mechanisms underlying collective motion of fish, rather than extend individual based model by replacing an individual with a group of individuals. These models for fish migration would be as robust as IBM’s but much more computationally efficient and would explicitly account for fish school merging and splitting.

2. Methods

In our framework, each super-individual based migration model is derived based on a particular IBM that mimics the motion of real fish (Aoki, 1980; Breder, 1954; Czirok & Vicsek, 2001; Huth & Wissel, 1992; Reynolds, 1987; Vicsek *et al.*, 1995). For illustration purposes in this work for derivation of SIBM we will use popular discrete individual based model proposed by Vicsek *et al.* (1995). This model describes collective motion of a group of self-propelled particles (e.g., fish, birds, insects) based on the dynamical equations for position $x_i(t)$ and velocity $v_i(t)$ of the *i*-th particle

$$x_i(t+\Delta t) = x_i(t) + v_i(t)\Delta t. \qquad (1)$$

The self-propelled nature of particles is achieved by keeping a constant magnitude for the velocity $|v_i(t)| = v_0$ pointing in direction $\theta_i(t)$. At each time step the Vicsek et. al. (1995) model assumes that a given particle moves in the average direction of particle motion in its local neighbourhood $S(i)$ (a circle of radius Δ centred at the particle location) with some uncertainty, as described by

$$\theta_i(t+\Delta t) = \langle \theta_i(t) \rangle_{S(i)} + \varepsilon_i^t, \qquad (2)$$

where ε_i^t is a stochastic noise drawn from some distribution with zero mean and standard deviation σ.

The individual interactions between particles defined by Equations (1)-(2) are able to create very complex behavioural patterns for these particles. This is due to interplay between randomness and alignment for the angle of particle velocity. Specifically, when the randomness effect is dominant, dynamics of particles is disordered, and particles do not tie to each other. On the other hand, when the alignment effect is dominant, particles form strong bonds for long time periods. In this case clusters of particles can be observed (Fig. 1).

In our analysis each particle represents a single fish, then a cluster of particles can be interpreted as a fish school. To distinguish different fish schools we introduce *interaction domains* of fish. An interaction domain of one single fish is defined as a circle of diameter Δ. If one fish belongs to the local neighbourhood of another fish (i.e., distance between these fish is not larger than Δ), then the interaction domains for these two fish have nonzero intersection, or, equivalently, their union is a connected set. An interaction domain for a group of fish is a union of interaction domains for all individual fish from this group. Then, *a fish school is defined as a maximal group of fish such that their (school) interaction domain is a connected set*, see Fig. 1.

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To further understand fish migration patterns described by the IBM of Vicsek *et. al.* (1995) a simulation study was conducted. From this simulation study the following characteristic features of fish motion were observed: (a) school size, i.e., the number of fish in a school, varies with time and changes from school to school; (b) school interaction domain depends on the school size and varies with time; (c) school velocity is not the same as the velocity of any individual fish; (d) noise of the school velocity is smaller than the noise of individual particle velocity; (e) after some time interval a school can split into smaller parts or merge with some other school or schools. Moreover, it was also noted that the distribution of school splitting time can be approximated by an exponential distribution, and the size of smaller school part after school splitting is approximately truncated exponentially distributed on the interval $[0, N/2]$.

Let us now proceed with formulation of a new super-individual based model for fish migration consistent with the individual based model by Vicsek *et al*. (1995). A foundation of this SIBM is, of course, a concept of super-individual. Each super-individual is defined as a fish school. So, each super-individual is formed by a group of fish that remains together, and possesses a similar velocity for a long time period. The velocity of a super-individual is defined as the average velocity of all fish in this super-individual. Of course, the velocity of different fish within any super-individual varies; however, these variations are small, and do not lead to immediate fracturing of super-individuals into parts. The time evolution of each super-individual is described using merging and splitting processes.

The detailed description of the SIBM follows. Let us denote the size (i.e., the number of fish) of the *i*-th super-individual by N_i. An interaction domain of the *i*-th super-individual is denoted by $A_i = A(N_i)$. The location X_i of the *i*-th super-individual is the centre of mass of its interaction domain. The velocity V_i of the *i*-th super-individual is the average velocity of all fish that belong to this super-individual. We assume that the magnitude of velocity depends only on the size of the super-individual $|V_i(t)| = V_{0,i} = V_0(N_i)$.

The movement of the *i*-th super-individual is described by the following equation

$$X_i(t+\Delta t) = X_i(t) + V_i(t)\Delta t, \qquad (3)$$

where at each time step the angle Θ_i of the velocity V_i is equal to a perturbed angle of the velocity from the previous step, that is,

$$\Theta_i(t+\Delta t) = \Theta_i(t) + \mathrm{E}_i^t, \qquad (4)$$

where a perturbation E_i^t has zero mean and standard deviation $\Sigma_i = \Sigma(N_i)$.

With respect to merging and splitting processes for super-individuals the following is assumed. In accordance with fish schools merging in the IBM of Vicsek *et al.* (1995), in the super-individual based model two super-individuals merge into one super-individual if the interaction domains for these two super-individuals overlap. The size of the merged super-individual is equal to the sum of the sizes of both super-individuals. The location of the newly merged super-individual is defined as a centre of mass of both super-individuals. The angle of velocity of the merged super-individual is equal to the weighted average of the angles of velocities of both super-individuals before merging (Fig. 2). Such weighted averaging of the angles was observed in (Pitcher and Wyche, 1983).

Moreover, each super-individual splits into two independent super-individuals after time τ_i; this time is referred to as a splitting time. The splitting time is assumed to satisfy the exponential distribution with the mean $<\tau_i>=<\tau(N_i)>$. The size of a smaller super-individual after splitting, denoted by $N_i^{\min}$, is distributed according to the truncated exponential distribution on the interval $[0, N_i/2]$ with mean $<N_i^{\min}>=<N^{\min}(N_i)>$. The direction of movement of the newly splitted super-individuals is the same as the direction of the super-individual before splitting. The new super-individuals are located on the orthogonal line to their velocity on the distance larger than the distance necessary for their merging. The location of the super-individual immediately before splitting is a centre of mass of the new super-individuals (Fig. 2).

3. Results

When comparing the individual based model of Vicsek *et al.* (1995) and the super-individual based model for fish migration developed based on it we can clearly note that these two models are structurally different; however, they are indeed consistent. To show the consistency between the IBM and SIBM, the following comparison study is carried out. Firstly, a statistical analysis of the IBM of Vicsek *et al.* (1995) is performed. Model parameters for this analysis are chosen in such way that the simulated fish would form fish

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schools that are relatively stable. In particular, the noise for the distribution of velocity angle is chosen from the normal distribution centred at zero with standard deviation $\sigma = 0.2$; the magnitude of the velocity $v_0 = 0.01$; the radius of the local neighbourhood $\Delta = 0.05$ and the time step $\Delta t = 1$. In total, 200 particles in a square domain of size 2 by 2 with periodic boundary conditions are chosen.

If we denote the fish school size by N, then the results of our statistical analysis of the Vicsek et al. (1995) IBM can be summarized as follows: (a) the average school interaction domain is $A(N) = 0.005 + 0.0008 \cdot N$; see Fig. 3(a), (b) the average school velocity is $V_0(N) = 0.009 + 0.00113 \cdot (N+1)^{-1/4}$; see Fig. 3(b), (c) the standard deviation of the school velocity angle is $\Sigma(N) = 0.0014 + 0.2082 \cdot N^{-1/2} \approx \sigma \cdot N^{-1/2}$; see Fig. 3(c), (d) the average time to school splitting is $<\tau(N)>= 66.3501 \cdot N^{-1/2}$; see Fig. 3(d), and (e) the average size of the smaller school part after school splitting is $< N^{\min}(N) >= 0.591 \cdot N/(1+N)^{1/2}$; see Fig. 3(e). School interaction domains in the Vicsek et al. IBM can take on different shapes; these shapes change from simulation to simulation. However, it was not observed any preferential direction of school anisotropy for interaction domains, and any particular fish distribution within interaction domain. Therefore, a fish school in Vicsek *et al.* (1995) model can be viewed as a circle of uniform density with the area $A(N)$.

The parameter values for the super-individual based model are chosen in accordance with the IBM of Vicsek *et al.* (1995). Specifically, in simulations of the SIBM, 20 super-individuals of random size are selected in a square domain of size 2 by 2 with periodic boundary conditions. The total size of all super-individuals is set to be the same as the number of fish in the IBM. The values for functions $A(N)$, $V_0(N)$, $\Sigma(N)$, $<\tau(N)>$ and $< N^{\min}(N) >$ are taken from the results of the above described statistical analysis.

When comparing results of simulations for the individual based model and super-individual based model, it can be observed that fish schools for the IBM and super-individuals for the SIBM have virtually the same spatial distribution and interaction domains (Figs. 4(a, b)). Moreover, it can be also noted that the distribution of fish school sizes and the distribution of super-individual sizes are very close; the deviation between these two distributions is very small (Fig. 4(c)). Thus, a consistency between both models with respect to the structure of fish schools vs. super-individuals is established.

4. Discussion

Many mechanisms explicitly underlying individual fish migration are different from mechanisms of fish school migration. For example, fish individuals within one school intend to avoid collisions to their neighbours, but still remain close to each other (Barbaro *et al*., 2009). On the other hand fish schools may experience merging in a collision, or splitting when the distance between fish school parts becomes too large. In terms of scales, the mechanisms for individual fish migration can be considered as microscopic mechanisms and those for fish schools as mesoscopic mechanisms. However, regardless of the differences in mechanisms and scales, fish migration models based on individual mechanisms and on school mechanisms must consistently describe the same migration scenarios. Therefore, there should be apparent relationship between migration mechanisms for individual fish and fish schools.

Presently, there exist several individual based models (also called IBM’s, agent-based models or Lagrangian models) for migration of fish (Giardina, 2008). All these models describe motion of each individual fish separately and can be considered as migration models at the microscopic level. In the case of migration of very large groups of fish such as fish schools, realistic applications of individual based models become difficult due to extremely large number of variables or degrees of freedom. A possible methodology to resolve this problem relies on upscaling using principles of coarse graining (Levitt, 1976; Tolman, 1979). Application of coarse graining methodology allows reduction in the degrees of freedom and elimination of fine interaction details in fish systems. Therefore, the simulation of a coarse-grained model requires fewer resources and goes faster than that for the same individual based model.

In this paper we demonstrate how to derive a model for fish school migration applying coarse-graining principles to an individual fish migration model. The object of the new fish school migration model is no longer an individual fish as in individual based models (IBM’s). It is a super-individual which can be understood as a fish school, a large group of fish staying together and moving in the same direction in a coordinated manner. To create new a model for fish schools migration, that is, a super-individual based model (SIBM), more

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precise definition of a super-individual is needed. This definition can be obtained from the analysis of a chosen IBM for individual fish migration, or, alternatively, from real observations. In this paper the IBM of Vicsek *et al.* (1995) was selected as a basis for construction of the super-individual based model. This IBM was chosen due to its simplicity and possibility of realistic simulations of fish motion patterns. Analyzing Vicsek's *et al.* (1995) model we observed that the motion of any two fish is dependent if these the locations of these fish can be connected using a broken line with vertices at the other fish locations in such way that the maximal segment will not exceed the radius of the fish interaction domain. In such case we could say that these two fish belong to the same fish school - a group of fish such that the motion of any two fish in this group is dependent, see Fig. 1. Note that in the percolation theory similar definition was used for determination of off-lattice percolation clusters (Stoll, Stern and Stucki, 1996; Stoll, 1998).

The analysis of the model of Vicsek *et al.* (1995) allowed us to observe fish school merging and splitting. Note that these two mechanisms could be related to fusion-fission in nuclear physics (Bodansky, 1996). We also investigated the structure of fish schools generated by the model of Vicsek *et al.*, as well as dynamical characteristics of fish schools, see Figs. 3. This allowed us to construct a super-individual as a group of fish uniformly occupying a circular area and moving with the same speed. Each super-individual could split into smaller super-individuals, and any two super-individuals could merge into one larger super-individual. Therefore, the most important difference between the super-individual based model (SIBM) proposed in this paper and individual based models, in general, is that it explicitly incorporates such important mechanisms in fish school migration as fish school splitting and merging. Moreover, although the developed SIBM is structurally different from its underlying IBM, the models were shown to be consistent, see Figs. 4. Thus, the super-individual based model can be thought of as an upscaled individual based model it relies on. Furthermore, this model is much more computationally attractive for studying typically large populations of pelagic fish than the corresponding IBM.

Finally, when adopting the SIBM's approach for practical applications external factors affecting fish migration such as food availability, water temperature, salinity and other environmental conditions can be incorporated. Because the nature of these effects is density independent, they can be easily implemented in SIBM's by analogy to IBM's (Hubbard *et al.*, 2004). However, the "summed up" nature of the density independent external factors on fish schools has to be taken in account. Since a single fish has to do many turns to detect a

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gradient of the external factors, a fish school could follow the external gradient more effectively than a single fish (Huth and Wissel, 1993).

In conclusion, it is not intended for the SIBM proposed here to be thought of as a replacement for existing models of fish migration such as IBM's and continuous models. Rather, it is intended to provoke discussion and thought about how to enhance or extend such models using super-individual mechanisms.

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Figures

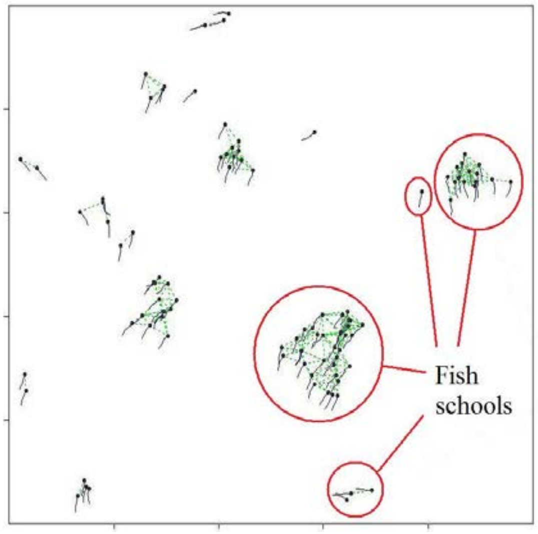

Figure 1. Clusters of particles, that is, fish schools. Fish schools are formed when the alignment force dominates the effect of randomness; fish remain together for a long time interval, contain different number of particles, and occupy different areas.

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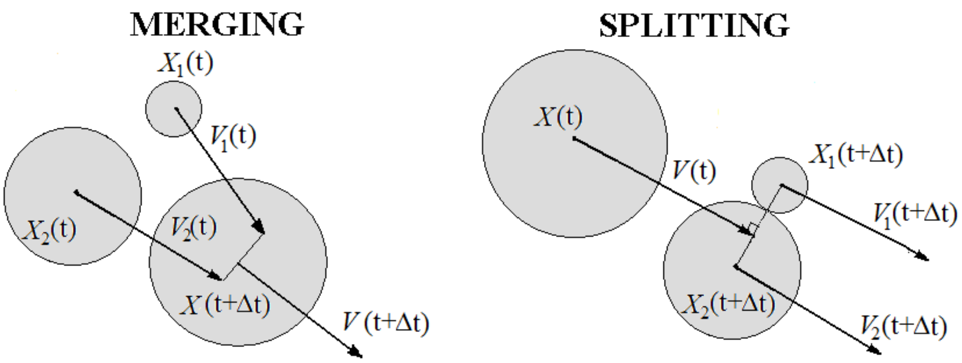

Figure 2. Illustration of merging and splitting processes for super-individuals.

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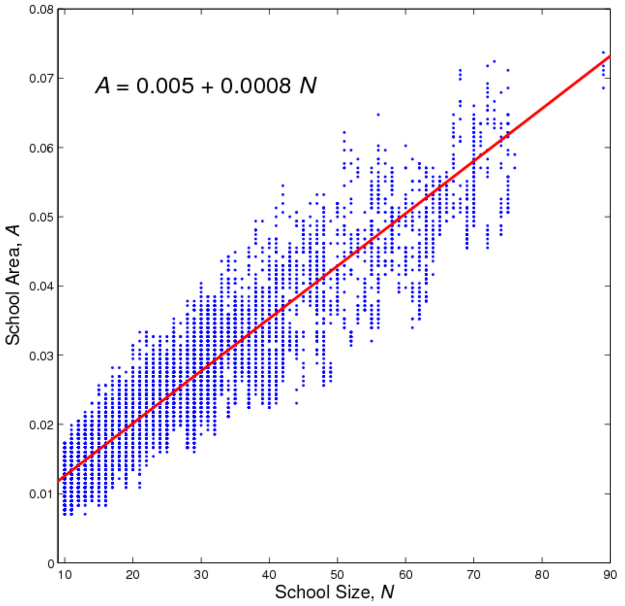
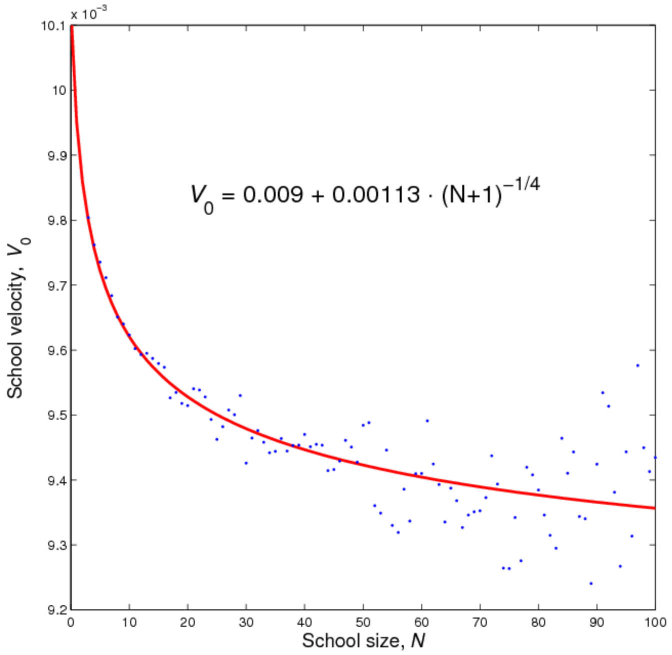


(a)



(b)

Figure 3. Results of statistical analysis of the Vicsek et al. IBM for 200 particles in a square domain of size 2 by 2 with periodic boundary conditions, $\sigma = 0.2$, $v_0 = 0.01$, $\Delta = 0.05$, $\Delta t = 1$. (a) the average school interaction domain, (b) the average school velocity, (c) the standard deviation of the school velocity angle, (d) the average time to school splitting, and (e) the average size of the smaller school part after school splitting.

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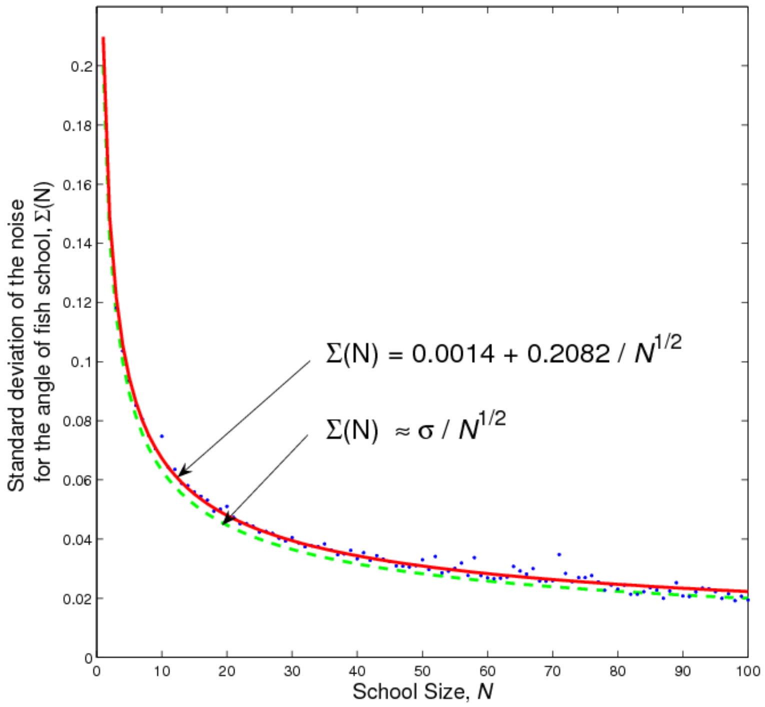
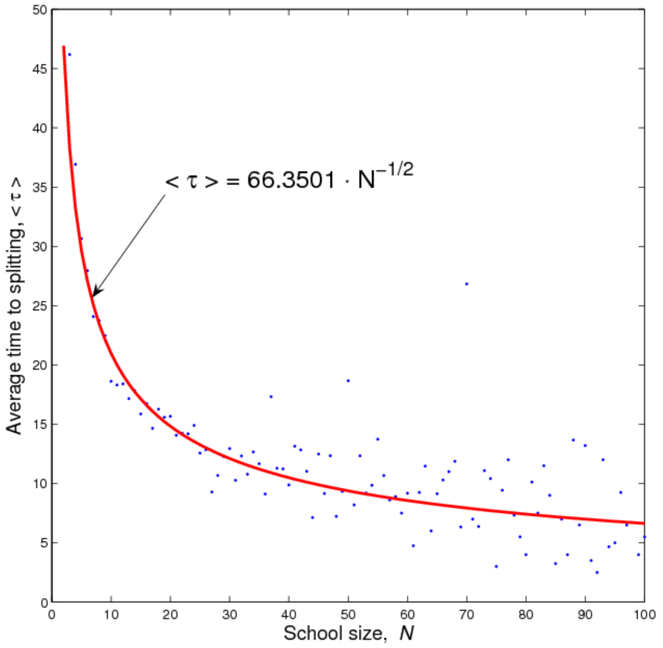


(c)



(d)

Figure 3. Cont.

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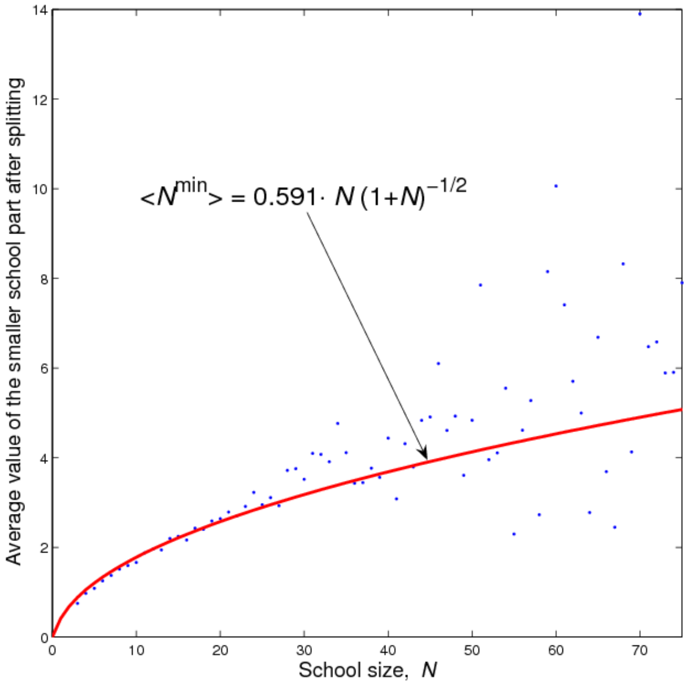
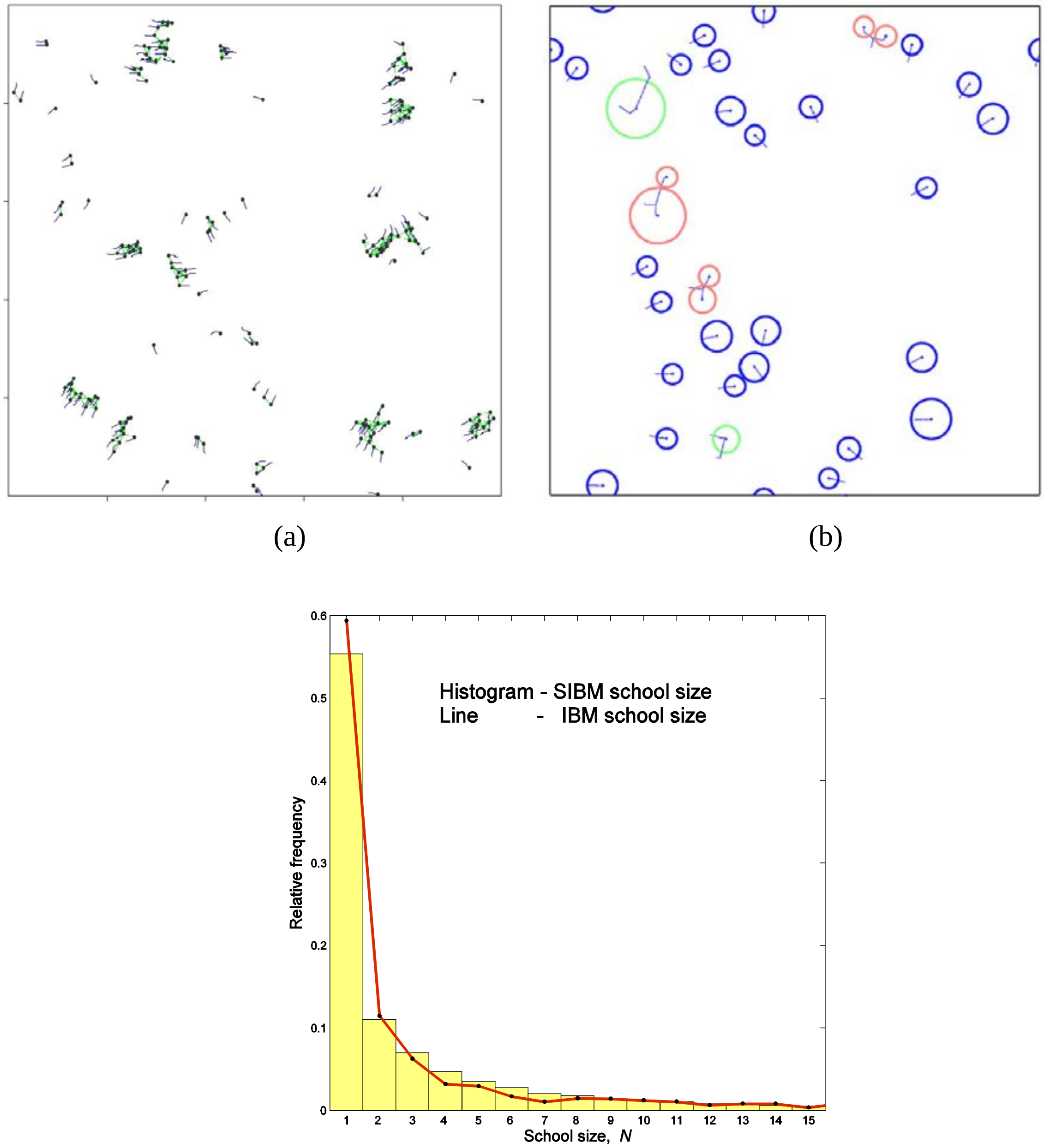


(e)

Figure 3. Cont.



(a) (b)

(c)

Figure 4. Snapshots from simulations of the Vicsek et.al. (1995) IBM (a), and the SIBM [splitted super-individuals shown with red colour and merged super-individuals shown with green colour] (b). The comparison between the school size distribution in the IBM [line plot] and the super-individual distribution in the SIBM [bar plot] (c).