Self-Organized Fish Schools: An Examination of Emergent Properties

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Abstract. Heterogeneous, “aggregated” patterns in the spatial distributions of individuals are almost universal across living organisms, from bacteria to higher vertebrates. Whereas specific features of aggregations are often visually striking to human eyes, a heuristic analysis based on human vision is usually not sufficient to answer fundamental questions about how and why organisms aggregate. What are the individual-level behavioral traits that give rise to these features? When qualitatively similar spatial patterns arise from purely physical mechanisms, are these patterns in organisms biologically significant, or are they simply epi-phenomena that are likely characteristics of any set of interacting autonomous individuals? If specific features of spatial aggregations do confer advantages or disadvantages in the fitness of group members, how has evolution operated to shape individual behavior in balancing costs and benefits at the individual and group levels? Mathematical models of social behaviors such as schooling in fishes provide a promising avenue to address some of these questions. However, the literature on schooling models has lacked a common framework to objectively and quantitatively characterize relationships between individual-level behaviors and group-level patterns. In this paper, we briefly survey similarities and differences in behavioral algorithms and aggregation statistics among existing schooling models. We present preliminary results of our efforts to develop a modeling framework that synthesizes much of this previous work, and to identify relationships between behavioral parameters and group-level statistics.

Types of Aggregations

Aggregation occurs in the smallest organisms—bacteria—and the largest—whales—and spans virtually the entire extant diversity of taxon, habitat, trophic level, life-history strategy, degree of mobility, and many other biological characteristics (Parrish and Edelstein-Keshet, 1999; Camazine et al., 2001). Physical aggregation can be regarded as part of a continuum in group integration. At one end of this continuum are territorial animals with little need to engage in information transfer and no need for group structure. At the other end are highly integrated, long-term associations between individuals that know—and perhaps are even related to—other members of the group, and in which members can potentially have high rates of direct and indirect information exchange. Honeybee hives, cetacean pods, and human communities are examples of these highly integrated groups (Wilson, 1975). In these systems, established pathways of long-term communication between known individuals (clones, siblings, reciprocating group members), or at predetermined locations (the hive, the calving grounds, the dinner table), may supplement immediate sensory contact. Thus, the members remain part of the “group” even while they range widely in space. In these dispersed groups, coordinated function can be maintained as long as the necessary information is transferred between group members (e.g., the sensory integration systems of Norris and Schilt, 1988; Schilt and Norris, 1997), though distance between interacting components inevitably affects the evolution and stability of emergent group properties (Hillier and Hanson, 1990; Latané et al., 1995).
Between these extremes of group integration are what could be considered “prototypical” animal aggregations—herds, swarms, flocks, and schools. Within the fishes, over 50% of species school—that is, display synchronous and coordinated movement—at some point in their life histories (Shaw, 1978), and an unknown additional number aggregate more coarsely. Prototypical aggregations exhibit coordinated motion, but group members are generally unrelated and never develop lasting relationships (in the game-theoretic, “tit-for-tat” sense) with other members. Many of these groups are extremely large (e.g., a school of a billion herring). Individuals in such groups interact with a neighborhood of other members, but those may represent a vanishingly small fraction of the group as a whole. This suggests that mechanisms which maximize information transfer among individuals could be evolutionarily beneficial. One example of this is a repeated arrangement within the group, reminiscent of crystal lattices, in which individuals assume preferred positions and orientations relative to their neighbors. Such arrangements could, for example, maximize sensory contact between members in such a way as to reflect ambient conditions, and the organisms’ predominant sensory systems, morphology, etc. (Parrish, 1992; Parrish and Edelstein-Keshet, 2000).

We can characterize possible behavioral adaptations in members of these groups on at least two levels: (1) short-term reactions to modify position with respect to immediate neighbors; and (2) behavioral responses that do not necessarily improve position relative to immediate neighbors but that contribute to group-level characteristics that ultimately benefit the individual by benefiting the group. These group-level adaptations are among the most fascinating—and the most difficult to assess—aspects of animal aggregations.

**Pattern versus Function**

Human perception tends to recognize attributes of the whole: an even density profile, polarity, distinct edges, or specific shape. While it is tempting to assume that conspicuous features of biological aggregations are somehow beneficial, the existence of qualitatively similar patterns that arise from physical phenomena shows that this need not be the case. For example, some shapes found in three-dimensional schools (e.g., torus and funnel) are echoed in two-dimensional insect configurations (e.g., wheel), suggesting that such shapes may be adaptive for group members (Fig. 1). However, these patterns could be evolutionarily neutral, or even pathological. Virtually identical shapes can be found in a wide range of inanimate aggregations, from water vapor to planets, in which these patterns arise from simple abiotic interactions between individual components, in the absence of evolutionary dynamics. Key steps in understanding biological aggregations in nature must be to distinguish biologically relevant features from nonadaptive epiphenomena, and to more explicitly and mechanistically describe the links between individual behaviors and group pattern.

Dynamic patterns and movement are necessary characteristics of many biological aggregations, and are perhaps better criteria to distinguish adaptive responses from epiphenomena. For example, fish schools display complex emergent properties such as coordinated motion and directed activity. Compression, hourglass, vacuole, fountain, and flash expansion (Fig. 2; Pitcher and Parrish, 1993) are all maneuvers that minimize predatory risk only if all members perform them correctly (e.g., Parrish, 1989). Parabolic formations in tuna schools may allow cooperative hunting advantages (Partridge et al., 1983). These emergent group properties appear to have readily apparent biological interpretations, and physical analogs may be harder to find. However, these dynamic group properties clearly confer more evolutionary advantages under some circumstances than others (e.g., evading small predators that target individuals while becoming targets for large predators that target groups; Parrish, 1993). Furthermore, the key evolutionary question remains: do these behaviors involve trade-offs between short-term gain for the individual and long-term functioning of the group? If so, what is the evolutionary context in which selection for these behaviors occurs?

**Traffic Rules**

Assuming structure is advantageous, how is it maintained? Laboratory and field attempts to address this question in fish schools have been limited (Partridge and Pitcher, 1980; Aoki et al., 1986; Parrish and Turchin, 1997), in part because obtaining three-dimensional trajectories on specific individuals for a relevant period of time is difficult. Data that do exist are typically from highly artificial conditions (e.g., relatively small schools in highly lit still-water tanks; Parrish and Turchin, 1997). Three-dimensional tracking techniques have not yet advanced to the stage where it is feasible to observe large schools (i.e., over 10), in three dimensions, over long times (i.e., for more than seconds). Despite these difficulties, quantitatively accurate observations of fish behavior within schools will undoubtedly become available in the next few years. However, while those data will provide a means of assessing short-term behavioral responses by fish to neighbors within a group, they will not by themselves provide the strong linkage between individual and group characteristics that we require to understand the mechanics and evolution of schooling behaviors.

Making this linkage requires an additional approach, namely, mathematical or computational models of schooling behavior. These models posit a specific, quantitative set of behavioral interactions—essentially, they create a set of traffic rules—and quantitatively assess the emergent properties of the resulting schools. Ideally, both the inputs (i.e.,
individuals’ responses to neighbors) and model output (group-level characteristics) can be compared to data from real aggregations.

A key purpose of modeling is to distinguish behavioral cause from organizational effect by studying the consequences of various hypothetical social interaction rules. Most simulation models of animal aggregations in the literature assign a set of forces that act on the speed and direction of each individual and are modulated in response to other individuals or the local environment. Typical force components include locomotory (e.g., biomechanical forces such as drag), aggregative (e.g., long-range attraction, short-range repulsion), arrayal (e.g., velocity matching), and random (e.g., individual stochasticity; Grünbaum and Okubo, 1994). The detailed biomechanics of locomotory forces are usually not considered in fish schooling simulations. Instead, most simulations simply associate behavioral movement “decisions” with the movements that result. However, there are exceptions, notably a few modeling studies that specifically address hydrodynamic interactions between members of a school (e.g., Weihs, 1973).

Published modeling studies have for the most part addressed a relatively restricted range of behavioral algorithms. Most analyses focus on variation in one of three categories: behavioral matching, positional preference, and numerical preference.

Behavioral matching (aka allelomimesis: Deneubourg and Goss, 1989) occurs when the individual agents try to match their behavior with other nearby agents. Most often, behavioral matching is modeled by having each agent explicitly match its orientation with that of its nearby neighbors (e.g., a zone of parallel orientation: Aoki, 1982; Huth and Wissel, 1992; Dill et al., 1997; Table 1, Fig. 3). Less often, fish match their speed, either to that of their companions, or to some arbitrarily decided value (e.g., Romey, 1996; Vabø and Nøttestad, 1997).

Positional preference refers to each fish having a preferred position relative to one or more of its companions.
Usually, positional preference is formulated as a preferred distance to one or more nearest neighbor(s). Variations on positional preference include assigned distance zones (e.g., repulsion, parallel orientation, attraction, searching) within which neighbors are treated equally (Huth and Wissel, 1992; Stöcker, 1999) or continuous distance weighting (Warburton and Lazarus, 1991; Reuter and Breckling, 1994; Romey, 1996). In some models, other positional parameters influence responses, such as bearing angle to neighbors, or estimated collision time (Dill et al., 1997). The biological underpinning is obvious: that individual group members do not collide, that groups do not dissolve, and that stragglers join. Taken together, behavioral matching and positional preference describe what a fish should do, e.g., move towards or away from neighbors, align with neighbors, search for neighbors (Fig. 3; RPOA dependence, Table 1), and how much consideration it should give any neighbor in the perception field (neighbor scaling rule, Table 1).

Numerical preference refers to the number of neighbors to which a fish pays attention, which we generically refer to as the rule size. Variations include an a priori value (e.g., 4: Warburton and Lazarus, 1991) or a conditional value (e.g., choose up to 4 in the nearest zone: Aoki, 1982; choose up to 4, front prioritized: Huth and Wissel, 1992). Many simply have each fish average over all other fish (e.g., all visible: Reuter and Breckling, 1994; Vabø and Nøttestad, 1997; all fish: Romey, 1996).

In general, modeling studies of schooling have been limited in several important respects, which future studies should aim to improve upon. Most models have used a relatively small population (e.g., 8 to 20 fish; Table 1), despite the fact that several studies point out that small numbers of fish may produce artificial results (e.g., Romey, 1996). Most models have operated in two dimensions. Although this may be justified on the basis of computational resources, generalizing from two to three dimensions may not be straightforward. Many models include some stochastic or chaotic elements; however, the degree of replication in modeling studies is generally lower than ideal to characterize the frequency distributions of possible outcomes.

Most simulation studies also assume that all individuals are identical. Romey (1996) has shown that the inclusion of a single fish with different traffic rules will alter schooling (measured as group speed and turning rate). Furthermore, the inclusion of multiple agents with one of two rule sets produces sorting (Romey, 1996), which may translate into emergent properties (e.g., horizontal bands versus extended columns of ungulates, Gueron et al., 1996). The possibility that variability within the group may not only affect emergent properties such as coordinated movement and spatial pattern, but may also itself be an emergent property, clearly deserves further consideration in modeling studies.

The parameter space explored by each model is typically only a small subset of possible variations, which ideally would include variations in (at least): initial position and velocity; the strength and type of stochastic components; spatial distribution of repulsion, parallel orientation, and attraction; and degree of variation between individuals in a group (Table 1). Because most studies are not consistent in
Table 1

Summary of fish school simulation parameters and output variables. R/PO/A-sequential zones of repulsion, parallel orientation (variably used), and attraction where “zone” implies equal force within a proscribed area (see Figure 3). Direction matching implies the use of a zone of parallel orientation. All other definitions as in the text. Numbers in parentheses refer to footnotes.

| Reference | Population Size | Starting Orientation | Velocity | R/PO/A Dependence | Direction Matching? | Neighbor Scaling | Rule Size |
|-----------|-----------------|----------------------|----------|-------------------|---------------------|-----------------|-----------|
| Aoki (1982, 1984) | 8, 32 | Random position & orientation within bounded area | Random | Zone (1, 2) | Yes | Position, weighted by front priority | Up to 4 |
| Warburton & Lazarus (1991) | 2–9 | Regular square lattice | Not specified | Linear distance | No | Constant | 1–8 |
| Huth & Wissel (1990, 1992, 1994) | 8 | Random position & orientation in fixed area | Random | Zone (1) | Yes | Constant; Single choice (4) | Up to 4, front prioritized |
| Reuter & Breckling (1994) | 10, 20, 30, 40, 50 | Random position, orientation & speed within bounded area | Not clear | Linear distance | Yes | Distance-weighted average (1/D; 1/D²) | All visible |
| Romey (1996) | 2–10 | Random position & orientation within bounded area (5) | Constant | Linear distance | No | Constant | All |
| Vabø & Nøttestad (1997) | 900 | Random position & orientation within bounded & fixed areas | Constant | Discrete distance | No | Single choice (7) | All visible |
| Stöcker (1999) | 12, 64 | Random position & orientation within bounded area | Constant | Zone (1) | Yes | Constant | Variable (8) |

| Reference | Random Component (distribution) | Aggregation Indices Individual | Aggregation Indices Group | Aggregation Indices Group Population |
|-----------|---------------------------------|-------------------------------|---------------------------|----------------------------------|
| Aoki (1982, 1984) | Gamma (speed); Normal (direction; 3) | Net Individual Displacement | Compactness (1/SD of x, y coordinates) | Group Center Displacement; Group Shape (max IID²)/area |
| Warburton & Lazarus (1991) | Circular normal (direction) | Inter-Individual Distance | Group Center Displacement; Group Shape (max IID²)/area | Polarization; Expanse (rms distance to center) |
| Huth & Wissel (1990, 1992, 1994) | Gamma (speed); Normal (direction) | Nearest Neighbor Distance (neighbors 1–3) | Polarization; Expanse (mean distance to center) | Group Speed; Group Turning Rate |
| Reuter & Breckling (1994) | Normal (direction, speed) | Nearest Neighbor Distance | Polarization; Expanse (mean distance to center) | Group Speed; Group Turning Rate |
| Romey (1996) | Uniform (direction; 6) | Instability (maximum individual distance traveled) | Group Speed; Group Turning Rate | Number of Schools |
| Vabø & Nøttestad (1997) | Discrete probabilities of choosing less than optimal direction | Number of Schools; School Size | Number of Schools; School Size | Number of Schools; School Size |
| Stöcker (1999) | Uniform (direction; 9) | Instability (maximum individual distance traveled) | Number of Schools; School Size | Number of Schools; School Size |

Note that random components selected from a normal distribution are centered on calculated means as per Figure 3.

(1) Distance-specific zones of repulsion, parallel orientation, attraction, and searching. A blind spot (30–60 deg.) behind.
(2) Beyond the zone of attraction, but within the visual angle (270 deg), attraction based on linear distance.
(3) Outside the sensed area, direction was chosen from a uniform circular distribution (i.e., random walk).
(4) Single Choice = choose only one neighbor with a weighted probability N1, 1/2N2, 1/4N3, 1/8N4.
(5) Individuals can sense entire area (~100 BL).
(6) Every 15 or 30 time steps.
(7) Highest (optimal) attraction value direction (of eight 45 deg increments) chosen.
(8) All neighbors within the parallel orientation zone considered equally. Only closest neighbor within attraction zone considered.
(9) Only applied to single fish with no neighbors (i.e., random walk searching).
various authors to simulate schooling in fish (see also Table 1). Repulsion is always negative on the y-axis, whereas attraction is positive. Zones of no repulsion or attraction (e.g., parallel orientation) are at zero. The x-axis is distance from fish of interest, displayed in arbitrary units. (a) Aoki (1982); (b) Warburton and Lazarus (1991); (c) Huth and Wissel (1990, 1992, 1994); (d) Curves showing the relative strengths of repulsion (left), parallel orientation (center), and attraction (right) in Reuter and Breckling (1994). Note that total social force always sums to 1.0. (e) Romey (1996). (f) The attraction strength used by Vabø and Nøttestad (1997) and Stöcker (1999); see also Flierl et al. (1999).

Inconsistencies between modeling approaches and aggregation indices have led different authors to draw seemingly contradictory conclusions about how individual behaviors affect group-level characteristics. For example, Aoki (1982; 1984) reports that removing the repulsion zone causes school disintegration, whereas Huth and Wissel (1990, 1992, 1994) assert it has little effect on schooling. Huth and Wissel (1990, 1992, 1994) maintain that only a low number of influential neighbors (≤ 3) are needed, whereas Warburton and Lazarus (1991) state that increasing the rule size is essential for school stability. Reuter and Breckling (1994) and Romey (1996) found that adding random or individual movement had little effect on schooling, but Warburton and Lazarus (1991) concluded that the incorporation of random movements destroyed schooling. Because these studies lack a common framework for specifying behaviors and summarizing spatial patterns, it is not possible to resolve whether these reflect true biological differences or simply comparisons between apples and oranges.

A Synthetic Simulation Study

We are currently working on a simulation model of fish schooling that explores much of the parameter space covered in previous models. Our model operates in three dimensions, and does not (as yet) include any rules that, a priori, program emergent property (i.e., no behavior matching or zone of parallel orientation). Following Grünbaum and Okubo (1994) and others, we model the movement decisions of each fish as a sum of locomotory, social, and random forces. Model fish are based on our quantitative observations of schooling giant danios (Danio aequipinatus; unpub. data), with a mass of 1.7 g, a length of 5.3 cm, a maximum speed of 11.2 body lengths [BL]/s, and a maximum acceleration of 11.2 BL/s². Locomotory force consists of drag, specified as a drag coefficient (C_D) of 0, 0.01, or 0.02 (based on a range of estimated drag coefficients for streamlined bodies = 0.01–0.001; Videler, 1993). Details of the methodology are presented elsewhere (Viscido et al., unpub. data).

We have thus far used this model to study a range of population from 2 to 128 fish, but report here only results for 128 fish. We examined variation in three aspects of the social force: the attraction/repulsion function, the neighbor scaling rule, and the rule size. Attraction/repulsion was modeled as a linear, piecewise linear, or convex (sensu

![Figure 3. Caricatures of the attraction-repulsion functions used by various authors to simulate schooling in fish (see also Table 1).](image-url)
Warburton and Lazarus, 1991) function with $F = 0$ centered at 1.9 BL (Fig. 3h). We based this preferred nearest neighbor distance on schooling experiments with real fish from a previous study (Parrish and Turchin, 1997). We used a perception distance of 180 BL (i.e., so individuals could detect neighbors to which they choose not to respond). A neighbor scaling rule weighted the attraction/repulsion force by the distance to each influential neighbor. Weighting was constant (i.e., equal weighting), negative linear, or negative sigmoid. Finally, the number of influential neighbors (rule size) was set at 4, 8, 16, or 24 fish.

Random force was chosen for each timestep from a normal distribution with mean $F = 0$ and standard deviation equivalent to 1/3, 1/6, and 1/18 of the maximum social force an individual fish could experience from another fish. The amount of random force experienced by any individual was a function of the distribution of nearby neighbors. Individuals within a school experienced relatively little social force because most neighbors are at or near the equilibrium (i.e., $F = 0$), thus random forces can be proportionately large. Individuals divorced from the group but close enough to sense it experienced maximum social force (i.e., attraction), and proportionately little random force. In our simulations, median random force as a function of total force ranged from 8%–18% depending on rule size. We computed fish movement as acceleration resulting from the sum of random and social forces, minus drag.

Each parameter combination in our simulations were replicated 15 times, for 1800 time steps (of 1 s) each. We examined our model output with a suite of 11 aggregation indices that encompass individual- to population-level characteristics (Table 2). Statistics were based on time averages taken over the second half of each simulation (900 time steps), to avoid undue influence from initial conditions. We report here the results of systematic comparison within a single rule (e.g., drag off versus high drag) where the default conditions were medium random force, no drag, piecewise linear attraction/repulsion, constant neighbor scaling, and a rule size of 16. All numbers in text are means, and all statistics are one-way ANOVAs.

In general, over the range of parameter values we used, asocial forces (drag, randomness) had a less drastic effect on fish schooling behavior than did the various functions composing the social force (Fig. 4). Within the range of random force examined, there was no significant effect on any index of aggregation (Fig. 4). The addition of drag slowed fish down and increased the tortuosity of their paths, with a resulting increase in group size (without drag—46 fish/group, with drag—104 fish/group) and cohesion (without drag—1.5BL, with drag—1.1BL). These larger, slower groups milled rather than moving forward (net to gross displacement ratio [NGDR] dropped from 0.5 to 0.1), which decreased polarization. However, once added, there was no difference between the low and high drag condition (Fig. 4).

Social forces had a significant effect on most measures of schooling. Fish with convex attraction-repulsion (A/R) responses stayed closer together and had more tortuous paths than fish with piecewise linear A/R responses. The result was an increase in collisions (convex—720 collisions; piecewise linear—270 collisions; Fig. 4). Polarization was unaffected; it was equally low (83 deg.) for both functions.

Numerical preference had strong effects, both in terms of the number of influential neighbors and how that influence was scaled. Changing the neighbor scaling rule from equal weighting to a negative sigmoid function effectively increased the influence of close neighbors. Fish moved faster and in straighter paths. Schools became smaller (sigmoid—33 fish/group; constant—104 fish/group) and slightly more polarized (sigmoid—70 deg.; constant—83 deg.), but also more diffuse (sigmoid—1.9BL; constant—1.1BL). As a result, collisions decreased (sigmoid—5 collisions; constant—270 collisions). Using a smaller rule size (4 fish) produced equivalent results to negative sigmoid neighbor scaling. Thus a higher number of influential neighbors increases school size at the expense of internal structure (measured as polarization). Paying attention to more neighbors leads to large groups because it causes a

| Index                        | Computation                                      | Level            |
|------------------------------|--------------------------------------------------|------------------|
| Curvature                    | Mean turning angle per cm traveled               | Individual       |
| Fractal Dimension            | How “dimensional” the path is                    | Individual       |
| NGDR                         | Net displacement divided by gross displacement   | Individual       |
| NND                          | Mean linear distance to nearest neighbor         | Individual       |
| Group Size                   | Number of fish within 5 body lengths of each other | Group           |
| Expanse                      | Mean quadratic distance to center for each group | Group           |
| Polarization                  | Mean angle deviation between individual and group heading | Group           |
| Groups                       | Number of groups in the universe, including stragglers | Population     |
| Stragglers                   | Number of fish more than 5 body lengths from any other fish | Population     |
| Collisions                   | Number of collisions per fish per minute (reported as total collisions) | Population     |
| Clark and Evans (1954) Index | Observed NND vs. expected NND for a randomly spaced population | Population     |
network of overlapping influences (Warburton and Lazarus, 1991): each group member “pulls on” a different set of companions, causing groups to remain cohesive. Over the range of rule size (RS) examined,

\[ \text{Group Size} = 3 \times \text{RS} - 7 \quad (\text{df} = 59, r^2 = 0.85). \]

Several other higher order properties emerged during our modeling. There was a clear linear relationship between group speed and polarization, across all rule sizes. Faster groups are more polarized (Fig. 5a). We note that there is no preferred speed, so that this is not an inevitable result of a polarized group, but probably reflects the fact that slower groups are composed of individuals with more tortuous paths. We also have begun to examine substructure within groups. At the level of an individual’s immediate neighbors (here defined as N1–6), nearest neighbor distance is virtually identical (Fig. 5b), indicating that at this scale, spacing is quite regular. However, when rule size is very large (24 influential neighbors), this relationship breaks down (Fig. 5b), perhaps indicating an upper limit for rule size.

Although our results are preliminary, they highlight some interesting patterns. First, school cohesion and coordinated movement can be partially achieved by positional and numerical preferences, without the need for behavioral matching. This shows that schools might indeed arise by large numbers of simple, overlapping interactions (Warburton and Lazarus, 1991; Romey, 1996). Our preliminary results also indicate that the shapes of the functions used to characterize both positional and numerical preferences are clearly very important (Fig. 4), and worthy of careful investigation in the future. Finally, our results demonstrate the need to consider many different quantitative indices of aggregation when assessing model results (Fig. 4).

**Emergent Evolution**

A central issue in modeling studies of aggregation is distinguishing between group- and population-level characteristics that are direct, inevitable consequences of the assumptions built into the model, and those that are truly “emergent properties.” In an evolutionary context, the im-

**Figure 5.** Higher-order index comparisons. (A) Group speed versus polarization for rule sizes 4, 8, 16, and 24. (B) Mean variance in the six nearest neighbor distances for individuals in the center of the school, over four rule sizes. Individuals were considered “central” if they were closer to the group center than the median distance to center for the whole group.
portance of this distinction is that emergent properties may be closely tied to indirect behavioral adaptations, which benefit individuals by benefiting the group. To satisfy the definition of emergent properties, the larger system (the group) must possess them, while its components (the individual members) do not (Clark et al., 1997). To a large extent, designating a group characteristic as "emergent" or not is a matter of degree. For instance, models in which individuals actively align their directions to those of neighbors typically produce polarized groups (Huth and Wissel, 1992, 1994; Reuter and Breckling, 1994; Stöcker, 1999), but this is probably too direct an outcome of the assumptions to be considered an emergent property. Dill et al. (1997) pose a model in which each fish estimates its time to impact with other fish. In such a system, agents implicitly consider their neighbors’ orientation, velocity, and position, rather than explicitly doing so. Collision avoidance would therefore seem to be a direct outcome and not an emergent property of this model. However, what about the converse: is polarization an emergent property of collision-avoidance behavior?

From a biological perspective, an operational distinction might be to consider whether the group behavior benefits the members because of their membership. For example, Grünbaum (1998) used model results to suggest that when individuals simultaneously display gradient-climbing and alignment behaviors in a noisy environment, groups to which they belong more accurately climb environmental gradients, whereas loners can not. If displaying both behaviors is costly to an individual, but it nonetheless benefits by being part of a group in a better environment, this would qualify as emergent under this criterion.

Given the relatively underdeveloped state of schooling behavior models and observations that unify individual, group, and population characteristics, it is unavoidable that studies of the evolutionary "hows and whys" of schooling remain somewhat speculative and oversimplified. Nonetheless, several studies have attempted to incorporate evolutionary ideas into schooling models by allowing iterative improvement of parameters, using an objective function as an analog to "fitness" in the evolutionary sense (Huse and Gjøsæt, 1999; Bonabeau et al., 2000). For instance, Hiramoto et al. (2000) link a standard simulation of schooling (à la Huth and Wissel, 1992) to a genetic algorithm that selects the width of the parallel orientation zone, the size of the blind angle, the number of influential neighbors, and the neighbor scaling rule (front, side, or distance priority, random choice) to maximize fitness. In this case, fitness is modeled as the minimization of four output variables: nearest neighbor distance, polarization, expanse, and fractal dimension. As a result, parallel orientation zone is maximized and blind angle is minimized. A larger question is whether this definition of most fit—that is, least variable—is correct?

Simulation studies like these hinge directly on two questions: (1) what is optimal, and (2) what is the relationship between individual and group optimality? Such questions are certain not to have simple or universal answers. It is unlikely that we will soon attain complete, realistic models of an aggregating organism’s life history that would allow us to truly represent “fitness” in a population with evolving behaviors. However, we are optimistic about the role of schooling simulations in addressing two central issues raised in this paper. First, we believe model studies will be successful in elucidating the mechanistic relationships between individual-level behavior and the group-level spatial patterns they produce. Second, we expect that the combination of explicit observations of schooling fish, improved simulations of the observed behaviors, and expanded use of statistical indices of aggregation on real and model aggregations will prove sufficient to identify the true behavioral algorithms used by fish.

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