

Self-Organized Fish Schools: An Examination of Emergent Properties

JULIA K. PARRISH^{1,2,*}, STEVEN V. VISCIDO², AND DANIEL GRÜNBAUM³

¹ *School of Aquatic and Fishery Sciences, Box 355020, University of Washington, Seattle, Washington 98195-5020;* ² *Zoology Department, University of Washington; and* ³ *School of Oceanography, University of Washington*

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 epiphenomena 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).

* To whom correspondence should be addressed. E-mail: jparrish@u.washington.edu

This paper was originally presented at a workshop titled *The Limits to Self-Organization in Biological Systems*. The workshop, which was held at the J. Erik Jonsson Center of the National Academy of Sciences, Woods Hole, Massachusetts, from 11–13 May 2001, was sponsored by the Center for Advanced Studies in the Space Life Sciences at the Marine Biological Laboratory, and funded by the National Aeronautics and Space Administration under Cooperative Agreement NCC 2-896.

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 epiphenom-

ena, 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.*,

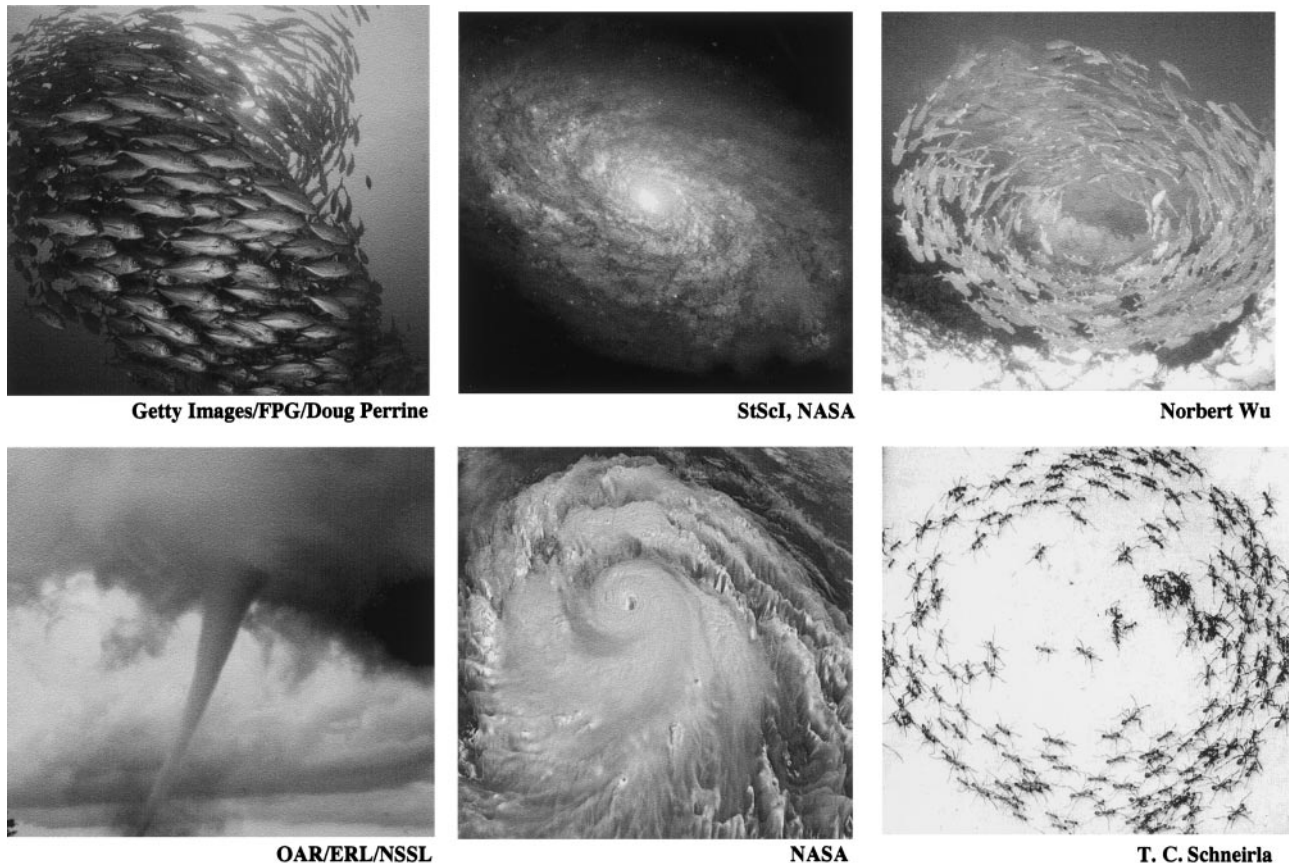


Figure 1. Three- and two-dimensional expressions of emergent structure in animate and inanimate aggregations—whorl patterns. Left: tornado structure in fish (top) and water vapor (bottom). Middle and right: whorl and toroid in planets, fish, ants, and water vapor, clockwise from top left. Top left reprinted with permission by FPG; bottom left courtesy of National Severe Storm Laboratory; middle top and bottom courtesy of National Aeronautic Space Administration; top right taken by Norbert Wu, www.norbertwu.com © 1999; bottom right taken by T. Schneirla and reprinted with permission by W. H. Freeman & Company.

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.

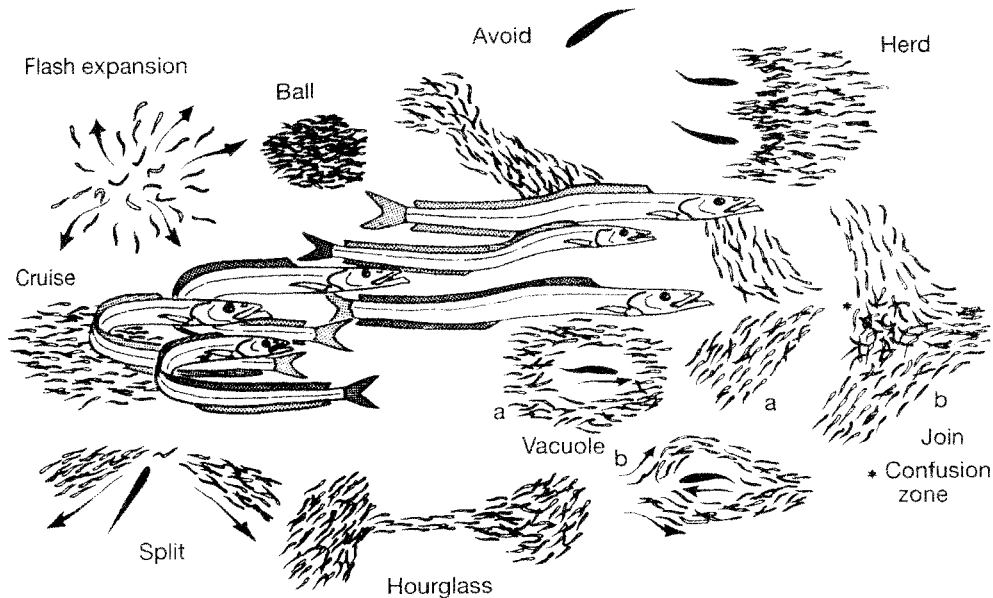


Figure 2. Examples of coordinated movement and directed activity, both emergent properties of fish schools, which are also commonly cited defense tactics against predatory attack. Fig. 12.8. from Pitcher and Parrish 1993. Reprinted with permission from the author and Kluwer Academic Publishers.

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/D ²)	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 Population
Aoki (1982, 1984)	Gamma (speed); Normal (direction; 3)	Net Individual Displacement	Compactness (1/SD of x, y coordinates)	
Warburton & Lazarus (1991)	Circular normal (direction)	Inter-Individual Distance	Group Center Displacement; Group Shape (max IID ²)/area	
Huth & Wissel (1990, 1992, 1994)	Gamma (speed); Normal (direction)	Nearest Neighbor Distance (neighbors 1–3)	Polarization; Expanse (rms distance to center)	
Reuter & Breckling (1994)	Normal (direction, speed)	Nearest Neighbor Distance	Polarization; Expanse (mean distance to center)	
Romey (1996)	Uniform (direction; 6)		Group Speed; Group Turning Rate	
Vabø & Nøttestad (1997)	Discrete probabilities of choosing less than optimal direction	Instability (maximum individual distance traveled)		Number of Schools
Stöcker (1999)	Uniform (direction; 9)		Polarization; School Direction	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 $N_1, 1/2N_2, 1/4N_3, 1/8N_4$.
- (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).

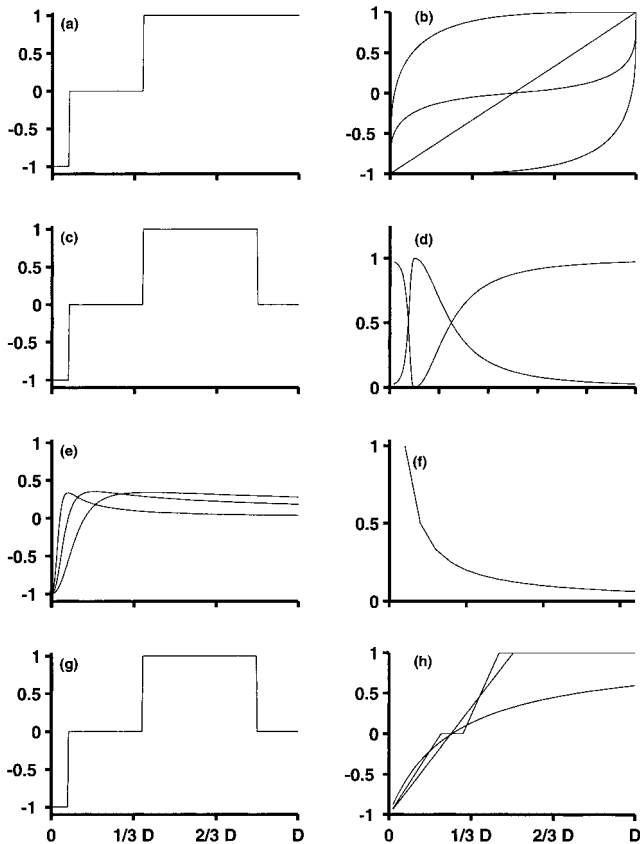


Figure 3. Caricatures of the attraction-repulsion functions used by various authors to simulate schooling in fish (see also Table 1). Repulsion is always negative on the y-axis, whereas attraction is positive. Zones of no repulsion or attraction (e.g., parallel orientation) are at zero. The x-axis is 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). (g) Stöcker (1999). (h) Our simulation.

these aspects (among others), direct comparisons of their results are not possible.

Finally, although most authors quantified school characteristics in their simulations with one or more index of aggregation, there is little or no consensus on which indices are most biologically relevant. Consequently, different studies tend to cite different statistics, again making comparisons difficult. For example, it is difficult to determine whether Romey's (1996) model provides the same amount of polarization as Huth and Wissel's (1992), because the former did not report that particular emergent property. A related but more subtle problem is that no single paper has simultaneously presented indices at the individual, group, and population levels (Table 1). In part this is because the distinction between group and population is meaningless in some models (*i.e.*, all individuals always interact and there-

fore the entire population is always part of the same group, *e.g.*, Aoki, 1982; Reuter and Breckling, 1994). Even when this is not the case, most studies use initial conditions or behaviors that predispose individuals to start and remain within a single large group. However, there are again notable exceptions, for example, the cellular automata models of 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*

Table 2

Aggregation indices at the individual, group, or population level used to evaluate traffic rules in our simulation

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

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	RandomForce Low (High)	Drag High (Low)	A/R function Convex (Piecewise linear)	Neighbor Scaling Logistic (Constant)	Rule Size 4 (16)
Curvature	◇	↑	↑	↑	◇
Fractal D	◇	◇	↑	↓	◇
NGDR	◇	◇	↓	↑	↑
NND	◇	◇	↓	↑	↑
Grp Size	◇	◇	◇	↓	↓
Expanse	◇	◇	↓	↑	↓
Polar	◇	◇	◇	↑	↑
# groups	◇	◇	◇	↑	↑
# strag	◇	◇	◇	◇	↑
# crashes	◇	↓	↑	↓	↓
IoA	◇	◇	↓	↑	◇

Figure 4. Results of one-way ANOVAs systematically comparing parameter values within a given traffic rule listed as column headings. Within each traffic rule, arrows indicate a significant difference in the index between the listed condition (e.g., rule size, “4” nearest neighbors) to that of the default set in parentheses (one-way ANOVA, $n = 15$, $P < 0.001$). White diamonds indicate no significant difference. Rows are 11 indices of aggregation. Individual level: path curvature, fractal dimension (higher is more tortuous), net to gross displacement ratio (NGDR; higher is straighter), nearest neighbor distance (NND). Group level: group size (in fish), mean distance to group center (or expanse, in body lengths), polarization (lower is more aligned). Population level: number of groups, number of stragglers, and the Clark and Evans (1954) index. See Table 2 for details on how each index was computed.

“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,

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

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 virtu-

ally 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-

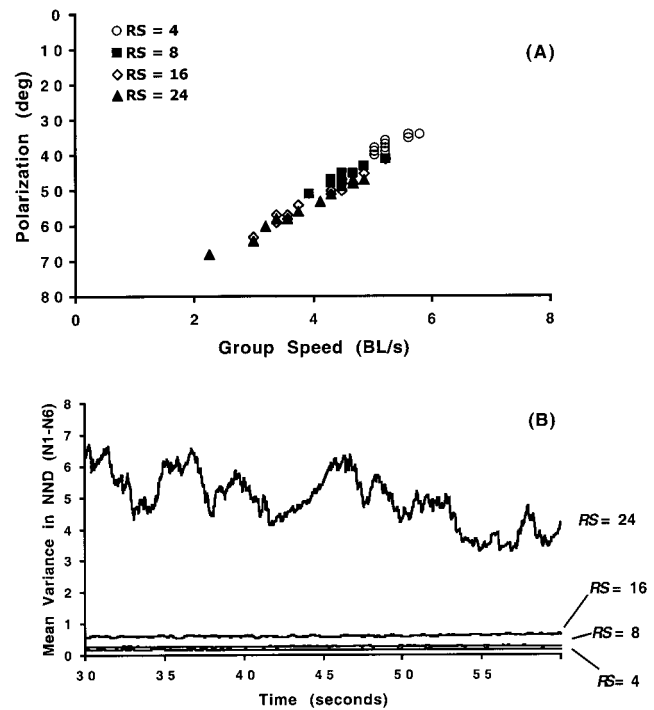


Figure 5. Higher-order index comparisons. (A) Group speed versus polarization for rule sizes 4, 8, 16, and 24. (B) Mean variance in the six nearest neighbor distances for individuals in the center of the school, over four rule sizes. Individuals were considered “central” if they were closer to the group 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 Gjoesaete, 1999; Bonabeau *et al.*, 2000). For instance, Hiramatsu *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.

Acknowledgments

This paper is the result of fruitful interactions with the participants of the CASSLS workshop (*The Limits to Self Organization in Biological Systems*) and the International Ethological Conference symposium (*The Many Facets of Gregariousness*), in particular Jean-Louis Deneubourg, Guy Theraulaz, Charlotte Hemelrijk, and Laurent Dagorn. Kate Litle and Jennifer Weitzman provided invaluable last-minute help. The original manuscript was greatly improved by two anonymous reviewers. This research was supported in part by a National Science Foundation grant to JKP and DG, CCR-9980058.

Literature Cited

- Aoki, I. 1982. A simulation study on the schooling mechanism in fish. *Bull. Jpn. Soc. Sci. Fish.* **48**: 1081–1088.
- Aoki, I. 1984. Internal dynamics of fish schools in relation to inter-fish distance. *Bull. Jpn. Soc. Sci. Fish.* **50**: 751–758.
- Aoki, I., T. Inagaki, and L. van Long. 1986. Measurements of the three-dimensional structure of free-swimming pelagic fish schools in a natural environment. *Bull. Jpn. Soc. Sci. Fish.* **52**: 69–77.
- Bonabeau, E., G. Sylvain, D. Snyers, P. Kuntz, and G. Theraulaz. 2000. Three-dimensional architectures grown by simple ‘stigmergic’ agents. *Biosystems* **56**: 13–32.
- Camazine, S., J.-L. Deneubourg, N. R. Franks, J. Sneyd, G. Theraulaz, and E. Bonabeau. 2001. *Self-Organization in Biological Systems*. Princeton University Press, Princeton, NJ.
- Clark, P. J., and F. C. Evans. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* **35**: 445–453.
- Clark, M., K. Irwig, and W. Wobke. 1997. Emergent properties of teams of agents in the Tileworld. *Lect. Notes Comput. Sci.* **1209**: 164–176.
- Deneubourg, J. L., and S. Goss. 1989. Collective patterns and decision-making. *Ethol. Ecol. Evol.* **1**: 295–311.
- Dill, L. M., C. S. Holling, and L. H. Palmer. 1997. Predicting the three-dimensional structure of animal aggregations from functional considerations: the role of information. Pp. 207–224 in *Animal Groups*

- in *Three Dimensions*, J. K. Parrish and W. M. Hamner, eds. Cambridge University Press, New York.
- Flierl, G., D. Grünbaum, S. Levin, and D. Olson. 1999.** From individuals to aggregations: the interplay between behavior and physics. *J. Theor. Biol.* **196**: 397–454.
- Grünbaum, D. 1998.** Schooling as a strategy for taxis in a noisy environment. *Evol. Ecol.* **12**: 503–522.
- Grünbaum, D., and A. Okubo. 1994.** Modelling social animal aggregations. Pp. 296–325 in *Frontiers in Theoretical Biology: Lecture Notes in Biomathematics*, Vol. 100, S. A. Levin, ed. Springer-Verlag, New York.
- Gueron, S., S. A. Levin, and D. I. Rubenstein. 1996.** The dynamics of herds: from individuals to aggregations. *J. Theor. Biol.* **182**: 85–98.
- Hillier, B., and J. Hanson. 1990.** *The Social Logic of Space*. Cambridge University Press, New York.
- Hiramatsu, K., S. Shikasho, and K. Mori. 2000.** Mathematical modeling of fish schooling of Japanese medaka using basic behavioral patterns. *J. Fac. Agric. Kyushu Univ.* **45**: 237–253.
- Huse, G., and H. Gjoesæte. 1999.** A neural network approach for predicting stock abundance of the Barents Sea capelin. *Sarsia* **84**: 457–464.
- Huth, A., and C. Wissel. 1990.** The movement of fish schools: a simulation model. Pp. 578–590 in *Biological Motion: Lecture Notes in Biomathematics*, Vol. 89, W. Alt and G. Hoffman, eds. Springer, Berlin.
- Huth, A., and C. Wissel. 1992.** The simulation of the movement of fish schools. *J. Theor. Biol.* **156**: 365–385.
- Huth, A., and C. Wissel. 1994.** The simulation of fish schools in comparison with experimental data. *Ecol. Model.* **75**: 135–145.
- Latané, B., J. Liu, A. Nowak, M. Bonaventura, and L. Zheng. 1995.** Distance matters: physical space and social influence. *Pers. Soc. Psych. Bull.* **21**: 795–805.
- Norris, K. S., and C. R. Schilt. 1988.** Cooperative societies in three-dimensional space: on the origins of aggregations, flocks, and schools, with special reference to dolphins and fish. *Ethol. Sociobiol.* **9**: 149–179.
- Parrish, J. K. 1989.** Re-examining the selfish herd: are central fish safer? *Anim. Behav.* **38**: 1048–1053.
- Parrish, J. K. 1992.** Do predators ‘shape’ fish schools: interactions between predators and their schooling prey. *Neth. J. Zool.* **42**: 358–370.
- Parrish, J. K. 1993.** Comparison of the hunting behavior of four piscine predators attacking schooling prey. *Ethology* **95**: 233–246.
- Parrish, J. K., and L. Edelstein-Keshet. 1999.** Complexity, pattern, and evolutionary trade-offs in animal aggregation. *Science* **284**: 99–101.
- Parrish, J. K., and L. Edelstein-Keshet. 2000.** Reply to Danchin and Wagner. *Science* **287**: 804–805.
- Parrish, J. K., and P. Turchin. 1997.** Individual decisions, traffic rules, and emergent pattern in schooling fish. Pp. 126–142 in *Animal Groups in Three Dimensions*, J. K. Parrish and W. M. Hamner, eds. Cambridge University Press, New York.
- Partridge, B. L., and T. J. Pitcher. 1980.** The sensory basis of fish schools: relative roles of lateral line and vision. *J. Comp. Physiol.* **135**: 315–325.
- Partridge, B. L., J. Johansson, and J. Kalisk. 1983.** Structure of schools of giant bluefin tuna in Cape Cod Bay. *Environ. Biol. Fishes* **9**: 253–262.
- Pitcher, T. J., and J. K. Parrish. 1993.** Functions of shoaling behavior in teleosts. Pp. 363–439 in *Behaviour of Teleost Fishes*, 2nd ed. Chapman and Hall, London.
- Reuter, H., and B. Breckling. 1994.** Self-organization of fish schools: an object-oriented model. *Ecol. Model.* **75**: 147–159.
- Romey, W. L. 1996.** Individual differences make a difference in the trajectories of simulated schools. *Ecol. Model.* **92**: 65–77.
- Schilt, C. R., and K. S. Norris. 1997.** Perspectives on sensory integration systems: problems, opportunities, and predictions. Pp. 225–244 in *Animal Groups in Three Dimensions*, J. K. Parrish and W. M. Hamner, eds. Cambridge University Press, Cambridge, UK.
- Shaw, E. 1978.** Schooling fishes. *Am. Sci.* **66**: 166–175.
- Stöcker, S. 1999.** Models for tuna school formation. *Math. Biosci.* **156**: 157–190.
- Vabø, R., and L. Nøttestad. 1997.** An individual-based model of fish school reactions: predicting antipredator behaviour as observed in nature. *Fish. Oceanogr.* **6**: 155–171.
- Videler, J. J. 1993.** *Fish Swimming*. Chapman & Hall, London. 260p.
- Warburton, K., and J. Lazarus. 1991.** Tendency-distance models of social cohesion in animal groups. *J. Theor. Biol.* **150**: 473–488.
- Weihs, D. 1973.** Hydromechanics of fish schooling. *Nature* **241**: 290–291.
- Wilson, E. O. 1975.** *Sociobiology: The New Synthesis*. Harvard University Press, Cambridge. 672p.