Extracting Interactive Control Algorithms from Group Dynamics of Schooling Fish

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1 Introduction

Biological groups such as schools of fish, flocks of birds, and herds of ungulates are remarkable for the effectiveness with which they maintain group structure, detect and avoid obstacles and predators, locate resources and migration routes, and perform other coordinated tasks (Parrish and Hamner, 1997). The precise choreography of collective motion frequently displayed by these groups belies the fact that the underlying behavioral mechanisms operate at the level of the individual (Camazine et al., 2001). That is, individuals within these groups respond independently to their own sensory inputs, physiological and cognitive states, and locomotory contraints. Over evolutionary time scales, the genetic basis of social behaviors that lead to effective grouping is the result of selection on individuals' DNA, with the fitness value of each potential behavior mediated through how an individual exhibiting that behavior benefits, relative to its competitors inside and outside the group. The interesting interplay between organizational levels, coupled with the high prevalence of social groups across a wide range of animal taxa, and the strong impacts animal groups have on ecological dynamics, have provided a strong motivation for biologists to better understand the behavioral bases of social aggregation behaviors. From the engineering perspective, the high level of coordination achieved by these groups, and the idea that they are the result of a lengthy optimization process (natural selection) makes social grouping behaviors interesting candidates for biomimetic, or at least biologically inspired, algorithms that confer on robotic systems some desirable traits of natural groups.

Despite this high level of interest, and a great number of observational and theoretical studies, the mechanics underlying animal groups are still poorly understood. This is true for a number of reasons. The relevant behaviors are difficult to observe experimentally under representative conditions with the necessary precision and duration. Also, while there exist mathematical meth-

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ods for characterizing the movements of biotic or engineered agents given a hypothetical behavioral algorithm, the converse is usually not possible: There are few tools to deduce the behavioral algorithms that were responsible for any specific set of observed movements. A further complication is that a high degree of variability exists between different species, between different individuals within a single species, and frequently also within the same individual observed at different times. Thus, there is not a single type of grouping behavior, but a whole range of alternative behaviors that may be expressed in different situations, and that have different costs and benefits to the individuals that employ them.

In the biological literature, schooling behaviors are frequently simulated in individual-based models as a set of Newtonian forces acting on individuals (e.g. Okubo, 1986; Warburton and Lazarus, 1991; Huth and Wissel, 1992; Grünbaum, 1994; Romey, 1992; Grünbaum, 1998b; Flierl et al., 1999; Couzin et al., 2002; Parrish et al., 2002). The forces on an individual in these models typically include "social" forces that are modulated by the individual's position relative to other individuals. The social forces in these models typically undergo changes in direction and magnitude as functions of distances to neighbors, such as an attraction to relatively distant neighbors coupled with a repulsion from neighbors that are too close, and in some cases a tendency to match velocity or heading with neighbors at an intermediate distance. In addition, other forces are usually included that reflect stochastic elements of behavior; environmental stimuli such as boundaries, predators, and food; and physical effects, such as hydrodynamic drag (Parrish and Viscido, 2003).

There are many variations of these behavioral rules in the literature, and many are successful in the sense that they generate simulated groups that share some key characteristics with biological groups. However, there remain important deficiencies in these models. One of these is that some elements of natural groups, such as the ability to form and maintain very large groups (much larger than the typical number of neighbors that any given individual can interact with simultaneously), are not well replicated by existing models. The fact that biological systems show behaviors not replicated by any existing models suggests that some essential components of real schooling behavior are lacking in the models. Another difficulty is that algorithms based on very different behavioral rules can generate simulated schools that appear intuitively realistic to the human eye. This suggests that either these different algorithms produce groups that are functionally indistinguishable, or (more probably) that human intuition is not sufficiently discerning to discriminate between alternative hypothetical grouping behaviors. Clearly, quantitative comparisons between simulated outcomes of hypothetical rules and the real movements of organisms in natural groups are needed to determine the characteristics of social behaviors in real biological groups.

To provide these comparisons, we developed motion analysis hardware and software to track the precise 3-dimensional positions of fish in small schools as they moved and interacted in experimental tanks. The focal fish in these

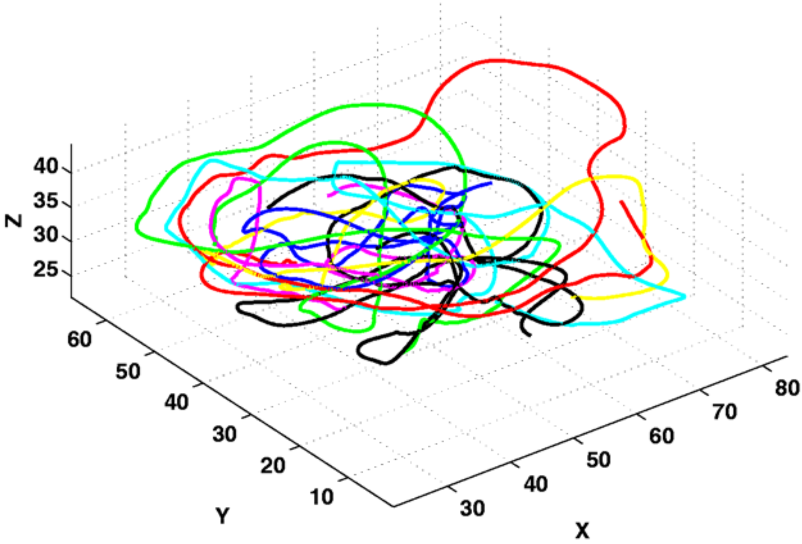

Fig. 1. Trajectories of eight individual Giant Danios, a facultatively schooling fish, within a 1 meter cubed observation tank. These data represent 30 seconds of position data, with each individual's 3-dimensional position determined by computerized video analysis every thirtieth of a second. Units are centimeters. The graphic represents one-twentieth of the data collected in each ten minute experiment; the analysis presented here is based on six such experiments.

studies were giant danios, *Danio aequipinnatus*. Preliminary observations, results of which are reported here, were carried out in a 1 meter cubed acrylic observation tank. In a typical experiment, a small group, usually of eight fish, was transferred from a culturing facility and into the observation tank. After an acclimation period of six hours, the fish were video-taped using two digital camcorders, which had been positioned and calibrated prior to the introduction of fish. The resulting video sequences were captured onto a computer, and public-domain software used to identify fish within the two camera views. A motion analysis software package developed by us, *Tracker3D*, was used to analyze the raw pixel position files from the two cameras and reconstruct the positions of each fish throughout a ten-minute sequence of interactions with other group members. This software is written in Matlab 6.5 and can be downloaded for noncommercial scientific use from the authors' website. An example of the trajectories of fish in our studies is shown in Figure 1. An animated version of these data is also available at the authors' website. See Parrish et al. (2002) and Viscido et al. (2004) for additional details on experimental methods.

2 Statistics of individual positions within schools

To partially characterize the behavioral interactions in our fish experiments, we identified the nearest neighbor of each fish in our movement sequences at each frame (approximately 18000 observations for each of 44 fish, over five independent 8-fish experiments and one 4-fish experiment). For each focal fish at each frame, we calculated the relative angle and distance of the nearest neighbor in the frame of reference of the focal fish Parrish and Turchin (1997). Despite the obvious 3-dimensional motion of the school as a whole, fish tended to be at a relatively small elevation angle relative to their nearest neighbor. Therefore, our initial analysis aimed at understanding the behavioral responses governing the horizontal positions of fish relative to their nearest neighbors.

We quantified the schooling interactions of our fish in our experiments by generating *probability density functions* (*PDF*s) of relative horizontal positions. Using the *PDF*s of the 44 fish as separate samples, we calculated the mean *PDF* and the *empirical orthogonal functions* (*EOF*s), which are the "modes" that most efficiently describe the variance in the whole ensemble. *EOF* modes are the eigenvectors of the correlation matrix calculated from the data, in a procedure known as a *proper orthogonal expansion* (Papoulis, 1984). We used *EOF* codes written in Matlab by Hooimeijer (2000). The mean *PDF* of relative nearest neighbor position, and the first five *EOF* modes, are plotted in Figure 2.

*EOF*s have a number of useful statistical characteristics. The *EOF* modes are orthogonal; each sample in the ensemble used to generate the *EOF*s can be reconstructed exactly as a linear combination of *EOF* modes. If we define $p_i(x, y)$ to be the observed *PDF* for the ith fish, then

$$p_i(x, y) = \bar{p}(x, y) + c_{i,1}E_1(x, y) + c_{i,2}E_2(x, y) + c_{i,3}E_3(x, y) + \ldots, \tag{1}$$

where $\bar{p}(x, y)$ is the mean *PDF* for all fish; $E_j(x, y), j = 1, 2, \ldots$ are the *EOF* modes; and $c_{i,j}$ are the coefficients of the jth mode in the *EOF* expansion. The variance represented by each mode is the maximum possible (that is, the first mode is the most "energetic" possible; of the remaining variance, the second mode is the most energetic possible, and so on), and is given by the eigenvalues associated with the each *EOF* mode. The variance represented by each mode, and the histograms of the coefficients $c_{i,j}$, and shown in Figure 3.

3 Behavioral switches in schooling fish

The *EOF* modes extracted from our data have a number of features that are biologically significant. One is that the first mode, which represents over 75% of the ensemble variance, is conspicuously similar to the mean *PDF*. This

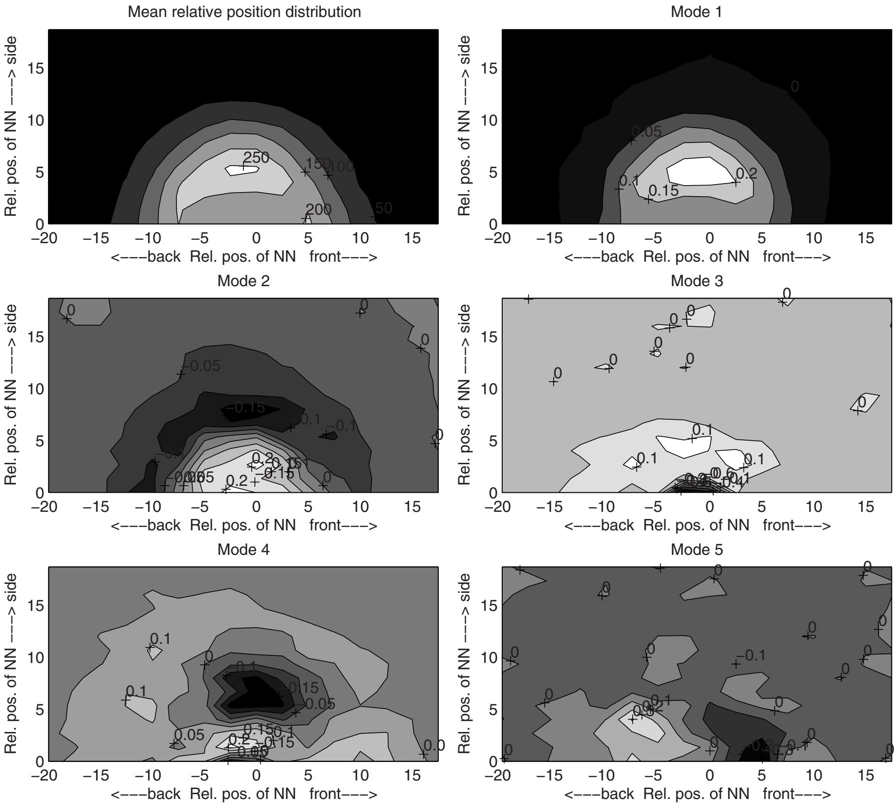

Fig. 2. Probability density functions of nearest neighbor positions for schooling fish. The mean distribution from the 44 fish observed in the six experiments (top left panel) suggests that nearest neighbors are commonly found in a lateral position at a distance of approximately 5 centimeters. The remaining panels show the first five empirical orthogonal functions (*EOF*s) representing deviations from the mean distribution in the individual fish, in order of decreasing contribution to the variance. The first mode is quite similiar to the mean, suggesting that a large component of the variability between individual fish consisted of up- and down-regulation of the preference for lateral neighbors. Note that these data include nearest neighbors from both right and left sides.

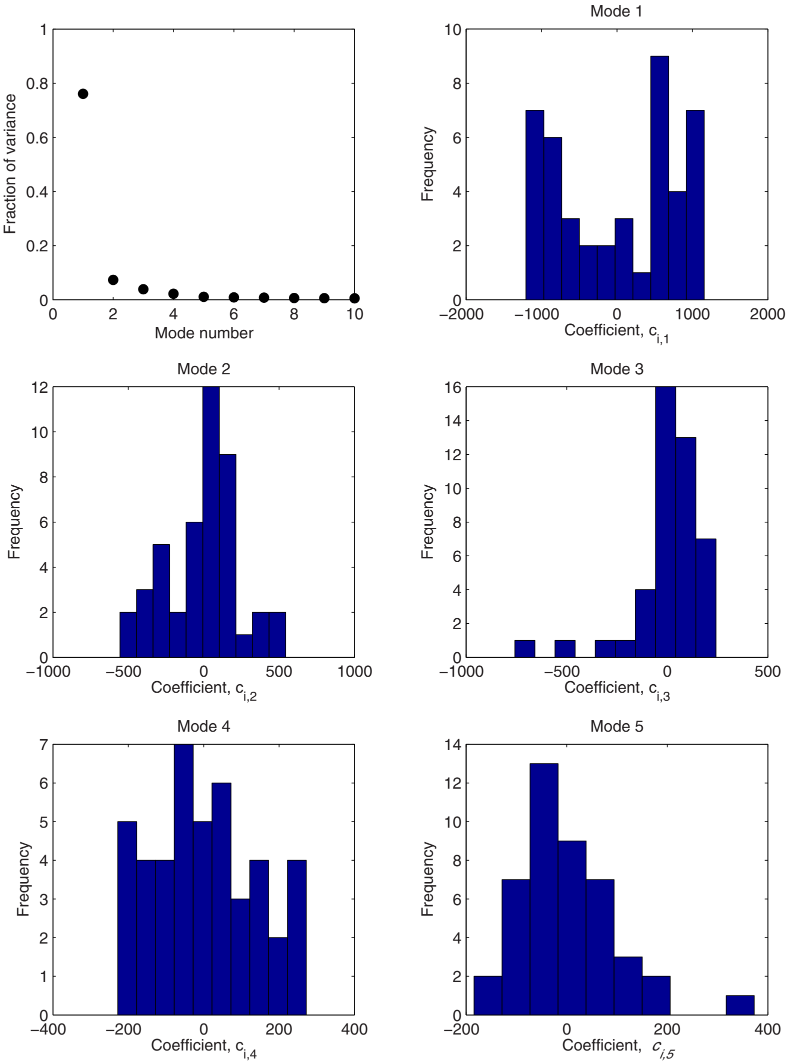

Fig. 3. Convergence and distributions of the coefficients $(c_{i,j})$ of the *EOF* modes in Figure 2. The top left panel shows the variance captured by the first ten modes. Convergence is rapid: the first mode alone contains over 75% of the total variance, and the first ten modes contain nearly 95% of the total variance. The remaining panels show histograms of the *EOF* coefficients in the expansions for the individual fish (see Equation 1). The histogram for the first mode is biomodal. This suggests that, in different individuals, the first mode either reinforces or cancels the preference for lateral nearest neighbors.

implies that, depending on whether the coefficient $c_{i,1}$ is positive or negative for the i*th* fish, this mode will either reinforce or cancel the spatial pattern of nearest neighbor positions represented by the mean *PDF*.

Another interesting feature of the *EOF*s for nearest neighbor position is that the coefficient of the first mode, $c_{i,1}$, is bimodally distributed (Figure 3). That is, individual fish tend either to have strongly negative first modes, which effectively cancel the spatial pattern evident in the mean, or strongly positive first modes, which reinforce the mean pattern. Relatively few individuals have intermediate values of $c_{i,1}$. This bimodality suggests an examination of whether differences exist primarily among fish within experiments, or among fish across different experiments. A plot of $c_{i,1}$ coefficients grouped by experiment (Figure 4) makes it clear that fish within an experiment behave very similarly to each other, at least in the aspects of social behavior that determine the relative horizontal positions. Even in Experiment 2 – the only experiment in which coefficient values near zero were observed – all fish behaved similarly, such that variation within this experiment was low.

Because all experiments were conducted under identical conditions, and individuals were chosen at random from a larger population in culture, there is no reason to believe that individuals in one group of fish were systematically different from those in any other group. Thus, differences between experiments likely reflect facultative changes – that is, a behavioral switch – in schooling behavior, rather than intrinsic differences in the individuals between experiments. Furthermore, the two types of social interaction appeared to be typified by strongly positive or strongly negative values, with corresponding differences in nearest neighbor distributions. There appeared to be a "consensus" among neighboring fish at any given time about which behavioral mode to exhibit, and different experiments resulted in different consensus behaviors.

To understand what these modes may represent in biological terms, we constructed a "typical positive coefficient", from the mean of all positive instances of $c_{i,1}$,

$$c_1^+ \equiv \text{mean}(c_{i,1} > 0) \ , \tag{2}$$

and a "typical negative coefficient" from the mean of all negative instances of $c_{i,1}$,

$$c_1^- \equiv \text{mean}(c_{i,1} < 0). \tag{3}$$

In our data, we found these values to be $c_1^+ = 671.9$ and $c_1^- = -806.2$.

We then assembled two "prototypical" nearest neighbor distributions, using only the mean and the first *EOF* mode with these positive and negative coefficients,

$$\begin{aligned} p^+(x,y) &= \bar{p}(x,y) + c_1^+ E_1(x,y), \\ p^-(x,y) &= \bar{p}(x,y) + c_1^- E_1(x,y). \end{aligned} \tag{4}$$

The prototypical distributions (Figures 5 and 6) show that groups of fish adopted two very different behavioral modes, both of which have biologically

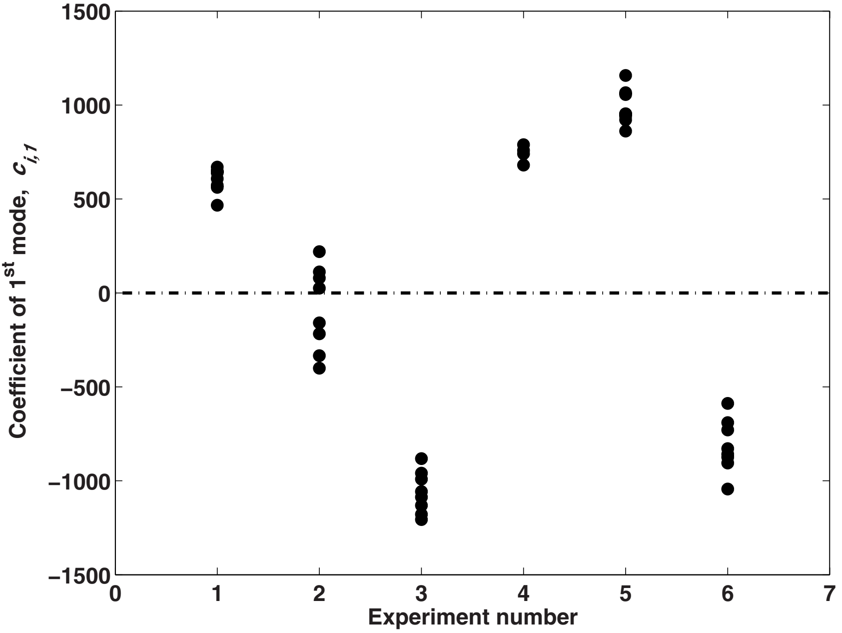

Fig. 4. Coefficients of the first *EOF* mode ($c_{i,1}$), grouped by the experiment in which they were observed. All experiments had eight fish, except experiment 4 which had four fish. This figure shows the high degree of consistency between the individuals within each experiment: Nearly all of the total variation in nearest neighbor position preference is between fish in different experiments, and almost none of it is between fish in the same experiment. This suggests that there is a "consensus" preferred nearest neighbor position among individuals in a group at any given time.

reasonable interpretations. In one behavior, represented by the positive distribution, nearest neighbors were usually in a lateral position, at a distance of between 5 and 10 centimeters. In the other behavior, represented by the negative distribution, the nearest neighbor was usually either directly in front of or behind the focal individual.

Using the values of $c_{i,1}$ to assign fish to one of these behavioral types, we found the following generalizations to hold:

- Fish with positive coefficients formed cohesive, milling groups. In contrast, fish with negative coefficients formed loose, disorganized aggregations, dominated by intermittent pairwise interactions (i.e., leader-follower or pursuit-escape behaviors).
- Fish with positive coefficients had relatively low speeds and accelerations, particularly the along-track component of acceleration. In contrast, fish with negative coefficients swam faster and accelerated more rapidly.

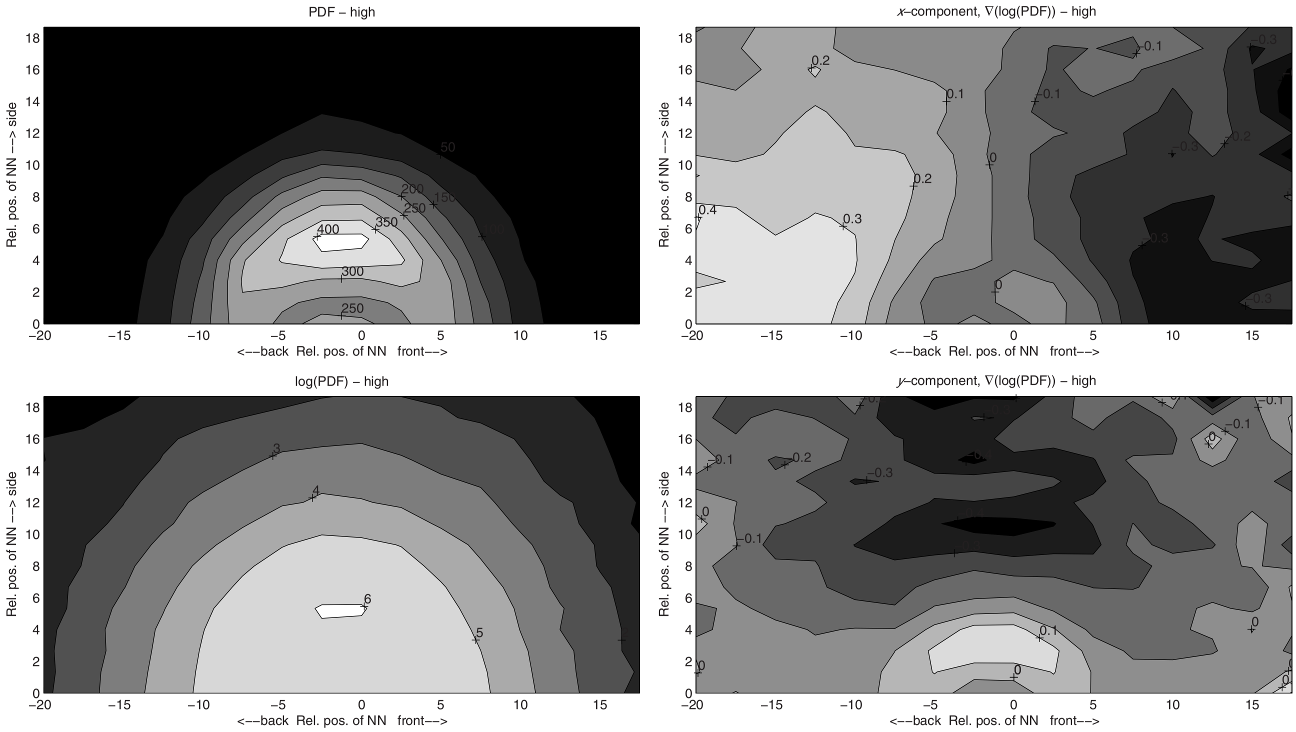

Fig. 5. PDF's and related distributions for the prototypical "high" coefficient c_1^+ (see Equations 2, 3), reflecting the lateral nearest neighbor preference. The top left panel shows the prototypical distribution from Equation 4. The bottom left shows the natural logarithm of this distribution, and the two right panels show the x- and y-components of the gradient of the logged distribution. These gradient components represent experimentally-derived advective fluxes in an *ADE* model of nearest neighbor position (see Equations 5, 6).

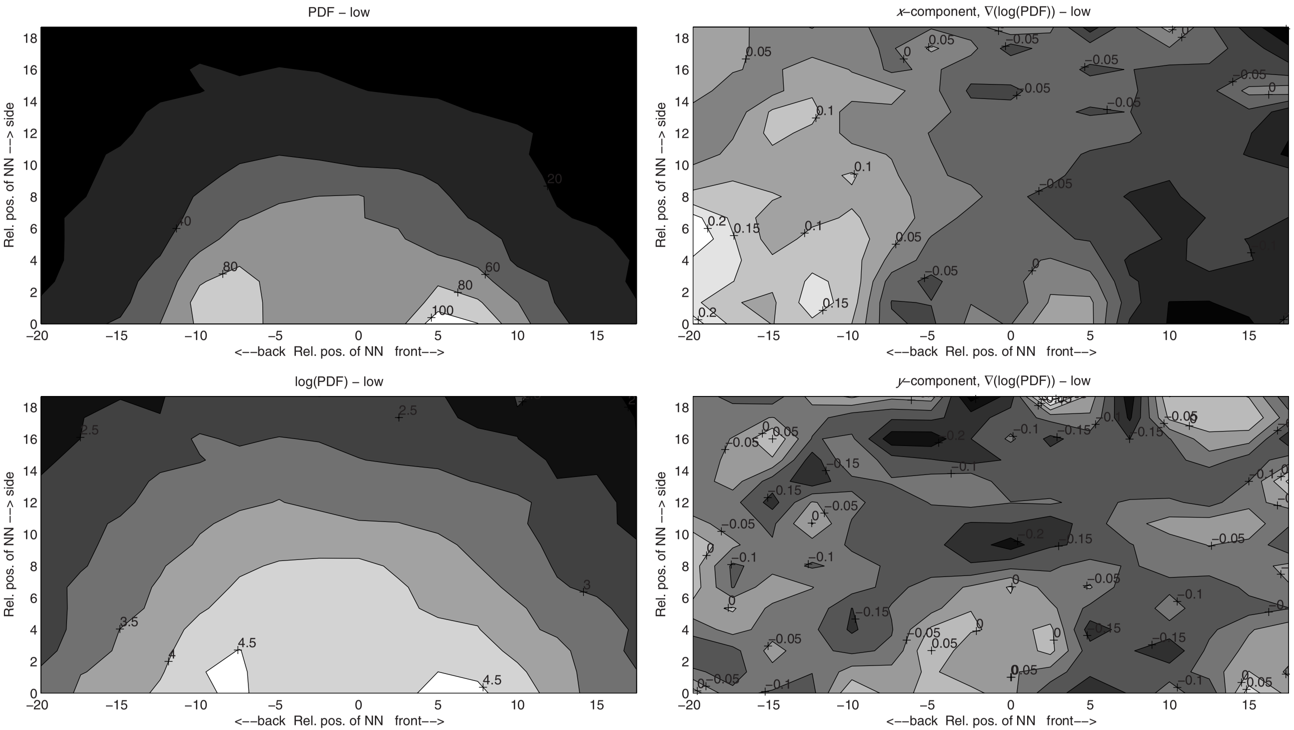

Fig. 6. PDF's and related distributions for the prototypical "low" coefficient c_1^- (see Equations 2, 3), reflecting the lateral nearest neighbor preference. Other details similar to Figure 5.

- Fish with positive coefficients spent equal amounts of time nearest to each other fish in the group, and all were similar to each other. In contrast, fish with negative coefficients differed from each other, both in which other individuals were most frequent nearest neighbors, and in whether they were more frequently in front of or behind their nearest neighbor.

In the context of these general trends, it is interesting to consider Experiment 2, the only experiment in which coefficient values did not fall into either the positive or negative coefficient ranges (Figure 4). Near-zero coefficients could in theory have arisen in several ways. The fish may have adopted a social behavior that is "intermediate" in some way between those represented by Figures 5 and 6. Alternatively, the fish may have changed behaviors during the experiment, such that at any one time their behavior did correspond to positive or negative coefficient ranges. Animations of the trajectories from this experiment show that the fish formed two groups that were spatially distinct, and had persistent differences: One group was in a low vertical position, had relatively close and uniform, and was larger (typically 5-6 members). The other group was at a high vertical position, was more diffuse, and smaller (typically 2-3 members). Interestingly, these group characteristics remains relatively constant, but the identity of group members did not – individuals cycled in and out of the smaller group over the course of the observations. This suggests that either individuals switched their behaviors to conform more closely with that of the group being joined, or they switched groups when their behaviors more closely resembled the "norm" for the other group.

4 Extracting control algorithms from neighbor positions

To shed some light on the behavioral algorithms that may underlie the patterns in our observations, we hypothesized that the position of the nearest neighbor could be described as a biased random walk, for which the steady state PDF can be approximated (in the usual diffusion limit) by an advection-diffusion equation (ADE),

$$\nabla \left(D \nabla p - \chi(x, y) p \right) = 0 \ . \tag{5}$$

In (5), it is assumed that the diffusion coefficient (D) is constant, but that the advection term, $\chi(x, y)$, varies with relative position. With manipulation, (5) gives an expression for the distribution of the ratio of D and χ,

$$\frac{\chi(x, y)}{D} = \nabla(\log(p)). \tag{6}$$

Equation 6 is potentially useful because the ratio χ/D can be estimated directly from observations of nearest neighbor distributions, $p(x, y)$, such as those presented above. In Figures 6 and 5, we show the distributions of

$\log(p)$ in our prototypical nearest neighbor *PDF*s, together with the x- and y-direction gradients of $\log(p)$ representing the coefficients in (6).

The advective fluxes suggested by this interpretation of our data differ in important ways from the assumptions of most schooling simulations in the literature, including our own. In the lateral postion preference behavior, characterized by positive coefficient values (Figure 5), the x-direction fluxes are strongly positive when the nearest neighbor is behind the focal individual, and negative when that neighbor is ahead of the focal individual. This suggests that at least one of the fish accelerates or decelerates to match its neighbor in along-track position. The y-direction fluxes are positive directly adjacent to the focal fish to a distance of roughly 4 centimeters, but negative at lateral positions greater than 7 centimeters distant. This again suggests a regulatory behavior, in which at least one of the fish veers away from a neighbor that is too close but towards a neighbor that is too distant.

In the fore-aft position preference, characterized by negative coefficient values (Figure 6), behavioral variations occur on a finer scale. Despite the presence of some statistical noise, a pattern can be discerned in which a “basin of attraction” exists directly behind the focal fish (at roughly -11 centimeters), and another directly in front (at roughly 7 centimeters). In both these basins, advective fluxes are distributed such that a neighbor that is subjected to a small displacement forward or backwards is likely to be returned to its preferred position.

5 Discussion

Social behaviors underlying the dynamics of natural groups are complex and highly variable on a number of levels. Our laboratory observations of schooling fish are unusual in their precision, and the lengthy period over which individuals were tracked. Our data determine both individuals’ movement decisions, and the relative positions of all the other group members that may have stimulated those decisions. The extremely large sample size in our study enabled us first to generate spatial statistics of nearest neighbor position, and then to assess the qualitative and quantitative characteristics of variation of these statistics between individuals within and across experiments. The results of these analyses contain important messages for future attempts to model social behavior.

We observed what appears to be a behavioral switch, where groups of fish under similar experimental conditions exhibited one of two markedly different behaviors. One individual-level behavior is characterized in physical terms by by a preference for nearest neighbors in a lateral position, and in mathematical terms by positive values of the coefficient of the first empirical orthogonal function (*EOF*) of nearest neighbor position. This behavior is reflected at the group level by milling, slow swimming and small accelerations. The other behavior is characterized at the individual level by a preference for fore-aft nearest neighbors, and by negative values of the first *EOF* coefficient. This behavior is reflected at the group level by loose and disorganized aggregation, rapid swimming and large accelerations. For both behaviors, we described an advection-diffusion equation (Alt (1980); Othmer et al. (1988); Grünbaum (1998a, 2000)) that could generate the observed *PDF*s, and that in some respects is a measurement of the "social forces" commonly incorporated into simulations of socially grouping animals. Our observations suggest that, beyond a simple distance-modulated response, our schooling fish displayed definite and specific preferences for the relative position of their nearest neighbor. We believe that it would be fruitful to develop simulation models based on social forces estimated from nearest neighbor *PDF*s, such as those in Figures 5 and 6.

The strong association observed experimentally between the distinct nearest neighbor *PDF*s and their respective group level characteristics suggests a hypothesis that the change in preferred nearest neighbor position is the key behavioral element in the two forms of social aggregation. Furthermore, these results suggest that fish may have multiple rule sets dictating spatial aspects of social interaction, and that they facultatively switch between them as a group. To date, all simulations, including our own, have searched for unique rather than multiple rule sets to explain transitions in group-level characteristics.

We found that behaviors are quite consistent among fish within a group, but that groups observed at different times have different consensus behaviors at the individual level. We believe that each of our groups was essentially similar, and that if we had observed each group for long enough each would have displayed both prototypical behaviors (and perhaps others). However, we did not obtain detailed observations of transitions between behaviors. Pending future experiments, we can only speculate on how those transitions might occur. We note that group level transitions can occur without changes in underlying individual behaviors, associated with changes in group size (Partridge et al., 1980), or hysteresis-type historical effects (Couzin et al., 2002). Additional theoretical work that identifies and characterizes the multiple levels at which individual- and group- level changes occur in social organisms would be an important contribution to our biological understanding of these behaviors.

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