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ARTICLE

# Quantitative movement analysis of social behavior in mummichog, *Fundulus heteroclitus*

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**Abstract** Group living among fishes has notable biological significance for individual well being and survival. However, group swimming dynamics have been historically difficult to quantify due to the complexity of the different movement patterns. This study describes and evaluates software developed for the analysis of schooling, shoaling, and solitary behaviors in the mummichog, *Fundulus heteroclitus*. Analysis of simulated data sets indicated accuracy of the software to within 0.06% of known values (i.e., no functional difference in observed versus expected; $P = 0.58$–$0.93$ for all parameters tested). Results from an acclimation experiment with groups of mummichog included decreased schooling, shoaling, individual velocity, and number of interactions after 24 h ($P \leq 0.05$). In addition, there was an increase in shoaling nearest-neighbor angle (NNA) and distance (NND) over time ($P \leq 0.05$). No changes in group behaviors were observed during different periods within 1 day (09:00, 12:00, 15:00, and 18:00 h) after 72 h in the arenas ($P > 0.05$). These results describe decreased social interactions and polarization (degree of unity in movement) over time. This software is applicable to the study of behavioral ecology of fish to discern changes in group dynamic behaviors.

**Keywords** Schooling and shoaling behavior · Video-based movement analysis · *Fundulus heteroclitus* · Mummichog · Killifish

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## Introduction

Group living has beneficial effects at individual and population levels of organization by increasing survival and fitness (Hamilton 1971). Living in groups can increase foraging success and efficiency, reproduction, parental care, and vigilance against predators, while decreasing predation pressure through dilution effects (Alexander 1974). Additionally, group living reduces detrimental effects of environmental fluctuation, providing stability to individuals and populations (Grunbaum 1998). However, schools may attract some predators, thereby increasing the probability of predation, with aggregative fish having higher mortality than solitary fish (Connell and Gillanders 1997). Additionally, increases in group size of schools and shoals increase competition for resources, decreasing foraging efficiency (Grand and Dill 1999; Johnsson 2003).

Animal groups, such as fish schools and bird flocks, display a structural order, with the behavior of individuals integrated such that even though the group changes shape and direction, they appear to move as a single coherent entity (Couzin et al. 2002). Social aggregations in fish have been classified into two types, schooling and shoaling. Generally, individuals in a school are oriented in the same direction, situated at a certain distance from each other, and are unitary in all movements (i.e., polarized). Shoaling, in contrast, is more of a spatial aggregation typically attracted by a stimulus, without uniformity of movement between individuals (i.e., non-polarized) (Hoare et al. 2000; Pavlov and Kasumyan 2000). Therefore, different species of fish may display schooling and shoaling behaviors due to an inherent attraction between individuals as well as environmental stimuli.

Fish are the largest and most taxonomically diverse group of vertebrates, with 25% of species forming schools or shoals as adults, and 50% during larval and juvenile stages (Radakov 1973; Aoki 1980; Pavlov and Kasumyan 2000). Due to their high biological significance in nature, schooling and shoaling have been a research focus for nearly a century. However, schooling and shoaling behaviors have been historically difficult to quantify due to the complexity of the different movement patterns including swimming, search, and sensory behaviors (Koltrschal and Essler 1995). Tracking multiple fish over extended periods of time is computationally expensive, and many studies have resorted to investigating a small number of video frames and manually plotting fish coordinates for calculation of parameters (Partridge 1980; Koltes 1985; Fuiman and Webb 1988; Rehnberg and Smith 1988; Bumann and Krause 1993; Gallego and Heath 1994; Masuda and Tsukamoto 1998). However, recent advances in computer processing and software technology have been used to analyze schooling behaviors (Inada and Kawachi 2002; Suzuki et al. 2003) which follow strict criteria of polarization (Breder 1954; Hunter 1966; Partridge 1982; Niwa 1994, 1996; Inada and Kawachi 2002; Suzuki et al. 2003). Shoaling, in contrast, is more difficult to analyze due to the loose definition used to define aggregations of individuals, with or without movement.

This study developed and analyzed a software program to quantify group behaviors of fish aggregations using the mummichog, *Fundulus heteroclitus*, as a model. Schooling behaviors in this species have been previously studied (Nichols and Breder 1927; Symons 1971). Mummichog are eurythermal and euryhaline killifish that form aggregates, thrive in a variety of salt and estuarine marshes, and have a cosmopolitan distribution along the East coast of the United States (Teo and Able 2003), yet maintain a fairly narrow home range (Fritz et al. 1975; Smith and Able 1994). The name ‘‘mummichog’’ is a Native American word that translates to ‘‘going in crowds.’’

The novel software described in this study, in conjunction with a videography hardware system, was used to quantify schooling, shoaling, and individual swimming behaviors of groups of up to 10 fish concurrently. The objectives of this study were to examine the accuracy of the software through the analysis of simulated data sets, and to investigate fluctuations in social behaviors of mummichog over a 72-h temporal acclimation period and during a single day. The three hypotheses examined were (1) the software system will be able to describe group swimming behaviors accurately, (2) group behaviors will decrease over time as mummichog become familiar with the observational arenas, and (3) once fish have acclimated to the arenas, no differences between group behaviors will be observed during a single day. Analysis and results of the generated data sets and alterations in group behaviors over time (several days and during a single day) in experimental laboratory arenas are presented and discussed.

## Materials and methods

Fish used in the present study were collected from a reference site in Solomons, MD, treated for ectoparasites, and laboratory-acclimated for 4 weeks prior to experimentation. Fish were acclimated to laboratory conditions (14:10 light/dark cycle, 23°C, 8.1 pH, and 5.0 PSU), and optimal water quality was maintained by static renewal. Temperature, pH, and salinity of the flow-through experimental arenas were maintained at the same values as holding tanks. All fish were used only once and fasted 24 h prior to testing.

### System design

Seven round, 20-L flow-through arenas were constructed with water flow electronically controlled by digital, multichannel peristaltic pumps (Masterflex L/S, Cole-Parmer, Vernon Hills, IL) (Kane et al. 2004). The arenas, 35.6 cm diameter, were maintained with 5 L of exposure water at a depth of 5.7 cm, controlled by the height of an external standpipe, and were placed on a 14:10 L/D photoperiod combined with a computer-controlled dusk and dawn cycle. Seven color CCD cameras with manual iris and focus control were mounted above respective arenas and connected to dedicated VCR decks for recording. The VCR decks were connected to a multiplexer to support real-time display for observation of all arenas. VCR recording and stop functions were remotely synchronized and controlled (X-10, Pico Electronics, Glenrothes, Scotland) through a computer interface (Xtension, Sand Hill Engineering, Geneva, FL, USA). There was no human activity in the room during or proximate to the time of behavioral recordings and observations.

Analog video data were digitized at 3 frames per second (fps) on a Macintosh platform (G5, dual 2 GHz, 4 GB SDRAM). Data were digitized in real time, segmented in Adobe Premiere, and imported into a commercial tracking program, Videoscript Professional. The tracking program then converted the digital output into *x*, *y* coordinate data with the use of a custom algorithm designed for tracking the movement of multiple fish targets. The classified *x*, *y* coordinate data were then analyzed using a novel software program designed at the University of Maryland Aquatic Pathobiology Center to obtain the desired group behaviors. A least-squares method of path determination was used to generate individual fish paths. This method provided individual path data through the minimization of the least-squared distances between spatial coordinates in consecutive frames. The schooling, shoaling, and individual behaviors that were observed and analyzed are defined in Table 1.

## Group-behavior determination and definitions

Group behaviors were calculated according to several criteria integrated into the software program. The first criterion was the delineation among schooling, shoaling, and solitary behaviors. A moving group of at least three fish per arena was required for the software to calculate schooling or shoaling behavior. It has been demonstrated that the minimum group size in minnows, *Phoxinus phoxinus*, and bitterlings, *Rhodeus ocellatus*, to maintain stable schooling relationships is three fish (Partridge 1980; Kanehiro et al. 1985). Movement of fish was defined as 0.5 body lengths per second (35.5 mm/s) and was calculated on a frame-by-frame basis at 3 fps. An average fish body length of 50 pixels, equal to 71 mm, was used for the calculations. A shoaling event was calculated when the movement criterion of at least three fish was satisfied, and the distance of a fish from its nearest and second nearest neighbor was within 0.5 and 1.0 fish lengths, respectively, with no angular criteria. For reference, the schooling nearest-neighbor distance for two cyprinid minnows, *P. phoxinus* and *Gnathopogon elongatus*, was determined to be 0.5–0.9 and 1.1 body lengths, respectively (Aoki 1980; Partridge 1980). A schooling event met the criteria of a shoal and also had a nearest neighbor angle ≤45° for a minimum of 2 s (six frames). If schooling occurred for five frames or fewer, it was considered shoaling and calculated as such. Solitary data (vs. group data) were calculated when a frame did not meet the criteria for schooling or shoaling, and always included all five fish.

Following the behavior classification as group or solitary, the number of interactions, velocity, nearest-neighbor distance (NND) and angle (NNA), and the percent time spent in the different configurations (school, shoal, or solitary) were calculated. An interaction was defined as one fish being within 0.1 body length or less (equal to or less than five pixels, 7.1 mm) from its nearest neighbor, independent of movement. Therfore, the ‘‘interaction’’ behavior quantified the frequency of when fish were physically close enough to interact behaviorally as a group of two or more. Velocity was calculated as displacement (cm) per unit time (s), and NND was calculated as the average distance between each individual and its nearest neighbor

**Table 1** Group behaviors

| Behavior | Definition |
|---|---|
| 1. Aggregative swimming | Three or more fish; group organized |
| Percent shoaling | Number of frames satisfying shoaling criteria divided by the total number of frames multiplied by 100 |
| Shoal NNA | Angle of trajectory between two fish in a shoal; must be greater than 45° |
| Shoal NND | Average distance to nearest neighbor for each fish in a shoal (minimum of three fish) |
| Percent schooling | Number of frames satisfying schooling criteria divided by the total number of frames multiplied by 100 |
| School NNA | Angle of trajectory between two neighboring fish in a school; must be less than or equal to 45° |
| School NND | Average distance to nearest neighbor for each fish in a school (minimum of three fish) |
| Velocity | Speed of school calculated in centimeters per second |
| 2. Solitary swimming | Individual swimming; no organized group |
| Percent solitary | Number of frames not satisfying shoaling or schooling criteria divided by the total number of frames multiplied by 100 |
| Solitary NND | Average distance to nearest neighbor for individual fish |
| 3. Interactions | The number of times two fish swim within 0.1 body lengths of each other (irrespective of satisfying movement criteria) |

*NND* Nearest neighbor distance, *NNA* nearest neighbor angle for each fish in the group. NNA was calculated as the average absolute angle between the trajectory of each fish and its nearest neighbor (Higgs and Fuiman 1996; Masuda and Tsukamoto 1998). NNA had a range of 0–180°, with 0° corresponding to two fish swimming parallel and in the same direction, and 180° for two fish swimming parallel and in opposite directions. Direction of movement was used as an indicator since the orientation between the snouts of the two fish was not calculated. Percentage of time spent schooling, shoaling, and solitary was the number of frames meeting the requirements for schooling, shoaling, and solitary, respectively, divided by the total number of frames.

## Simulated group behavior for software evaluation

In order to assess the output of the behavioral quantification software (i.e., evaluate its ability to quantify group behavior accurately), simulated datasets with varying known values for the various movement behaviors were analyzed. These behaviors included percent schooling, percent shoaling, and percent solitary; schooling and shoaling NNA and NND; solitary NND; schooling and shoaling velocity. Simulated data sets to represent five fish for schooling ($n$ = 6), shoaling ($n$ = 6), and solitary ($n$ = 6) data sets, consisting of 1,000 frames each, were generated using R software (www.r-project.org). Schooling and no-group paths for each group of fish were generated as five points circumscribing a circle of fixed radius with a fixed arc length separating the individual points. The fixed radius (72.5 pixels for NND) and separating angles for schooling and individual NNAs (15° and 72°, respectively) were chosen based on meeting the grouping behavior criteria (i.e., schooling paths require a smaller separating arc length to meet schooling criteria). The frame-wise radial velocities of the points were sampled from a uniform distribution between 10 and 20°/frame (mean = 15°/frame).

Shoaling paths were generated as five points moving through separate, parallel columns (width = 1 pixel; length = 27 pixels), stacked at a distance of 17 pixels. Each point was generated to move lengthwise iteratively through the column in three frames (9 pixels/frame lengthwise), and to repeat the process in opposite directions continuously. The specific location of the point with respect to the width of the column was drawn, frame by frame, from a uniform distribution of –0.5 to +0.5 pixels from the center of the column. Therefore, shoaling NND, NNA, and schooling and shoaling velocities were stochastic variables with expected values. Further, schooling, shoaling, solitary percentages, and schooling and solitary NND and NNA, were fixed variables with known values.

The simulated data sets were analyzed by the software program, and the observed values were compared with the known (hypothesized) values. Only stochastic variables were statistically analyzed since the fixed values displayed no variation between data sets.

## Experimental procedure with mummichog

An acclimation experiment was conducted over 4 days to examine behavioral changes in the experimental arenas through time. In addition, on the final day, a second experiment was conducted to investigate if mummichog social and individual behaviors fluctuate during daylight hours.

Seven groups of five fish (35 fish total, 60–83 mm total length) were randomly selected from the acclimated laboratory population that had been fasted for 24 h, and randomly distributed into the arenas (five fish per arena, at least two of each sex). Water flow in the arenas was maintained at 7 mL/min, with two exchanges each day, in order to ensure adequate water quality over the 72-h observation period. The cameras and VCRs automatically recorded 30-min data segments beginning at noon on day 1 (30 min after introduction to the vessel at 1130 hours), day 2, day 3, and day 4. On day 4, three additional 30-min clips at 09:00, 15:00, and 18:00 h were recorded to investigate differences in behaviors during the 9.5-h recording period. Seven 30-min clips were acquired from each arena over the course of the two experiments, totaling forty-nine 30-min recordings. Video clips were digitized at 3 fps; 5,400 frames were analyzed per time period (264,600 frames total). Differences in behaviors over the 4 days, and the four 30-min periods within the last day, were then analyzed for statistical differences.

Water quality data (Table 2) were collected each day from two identical surrogate vessels (with five fish) dedicated for water quality determination and not used for behavioral observation.

**Table 2** Water quality data recorded each day during both experiments

| Water quality parameter | Day 1 | Day 2 | Day 3 | Day 4 |
|---|---|---|---|---|
| pH | 8.1 | 8.1 | 8.1 | 8.1 |
| Salinity (PSU) | 5.0 | 5.0 | 5.0 | 5.0 |
| Temperature (°C) | 23.0 | 23.5 | 23.5 | 23.5 |
| Unionized ammonia (mg/L) | <0.001 | <0.001 | <0.001 | <0.001 |
| Dissolved oxygen (mg/L) | 5.9 | 5.3 | 5.2 | 4.9 |

Data are means ($n$ = 2)

### Statistical analyses

*Analysis of simulated data*

Schooling and solitary data sets were analyzed using a one-sample, two-tailed, *t*-test. The shoaling data could not be transformed to meet the assumptions of parametric analysis, and thus a runs test was used to compare the observed values with the hypothesized values (Sokal and Rohlf 1998).

*Analysis of biological data*

An experimental unit consisted of the group of five fish in each arena ($n = 7$ groups of five fish). A completely randomized statistical design was used with behavior as the response, and day (1, 2, 3, and 4) and daily observations (09:00, 12:00, 15:00, and 18:00 h) as the categorical variables. Non-normal data were either log or square-root transformed to meet the assumptions of the ANOVA procedure. Data that could not be transformed to meet the assumptions were ranked prior to analysis. A repeated measures one-way ANOVA (PROC MIXED, repeated, SAS v. 8.1, Cary, NC, USA) was used to compare behaviors over time for both experiments. In addition, several covariance structures were investigated in an effort to discern a best-fit structure for both sets of data. The *F* and *P* values reported for each behavior resulted from the structure that provided the best fit. Covariance structures included compound symmetry (CS), heterogeneous compound symmetry (CSH), auto regressive (AR-1), heterogeneous auto regressive (ARH-1), and ante-dependence (ANTE-1). A Tukey–Kramer *post hoc* mean comparison test was used to evaluate differences (*t* value, $\alpha \leq 0.05$) between time periods in the event of a significant *F* statistic.

## Results

### Simulated behavioral data

Analyses of the simulated datasets confirmed that the tracking software was accurate, with static and stochastic simulation parameters calculated exactly and within expected variation, respectively. The software calculated all fixed variables to 100% accuracy (Table 3). For stochastic variables, the software output agreed with the expected values to within 0.06% (±0.065 SE), and displayed a high degree of accuracy, i.e., no functional difference in observed versus expected (df = 5, $P = 0.67$–$0.93$; Table 3).

**Table 3** Analysis of simulated data sets calculated by the group software program

| Behavior | Expected value | Calculated values (means ± SE; $n = 6$) | *P*-value |
|---|---|---|---|
| Schooling (%) | 100.00 | 100.00 ± 0.00 | Fixed |
| Schooling NNA (°) | 15.00 | 15.00 ± 0.00 | Fixed |
| Schooling NND (cm) | 18.93 | 18.93 ± 0.00 | Fixed |
| Schooling velocity (cm/s) | 18.98 | 18.95 ± 0.07 | 0.93[a] |
| Shoaling (%) | 100.00 | 100.00 ± 0.00 | Fixed |
| Shoaling NNA (°) | 108.00 | 107.51 ± 0.10 | 0.67[b] |
| Shoaling NND (cm) | 19.38 | 19.38 ± 0.002 | 0.67[b] |
| Shoaling velocity (cm/s) | 9.00 | 9.01 ± 0.001 | 0.67[b] |
| Solitary (%) | 100.00 | 100.00 ± 0.00 | Fixed |
| Solitary NND (cm) | 85.23 | 85.23 ± 0.00 | Fixed |

[a] One-sample *t*-test

[b] Runs test

Variables with "fixed" *P*-values were not analyzed, but are included to illustrate software accuracy

### Behavior analysis from groups of mummichog

No significant changes in schooling behaviors were observed after the first day in any of the arenas ($t \leq 0.584$, $P > 0.05$). A low frequency of schooling was observed overall, with a significant decrease in percent schooling after the first day, which then remained constant over the next 3 days ($F = 4.6$, $P = 0.015$; Fig. 1a). The decrease in percent time spent schooling was marginally nonsignificant after day 1 ($t = 2.69$; $P = 0.066$) with further significant decreases 3 days later ($t \leq 3.25$; $P \leq 0.031$). No changes in schooling NND, NNA, or velocity occurred due to the decrease in schooling behaviors observed over time ($P > 0.05$, data not shown).

Shoaling behaviors displayed several significant changes after the first day. There were significant changes in percentage of time shoaling after the first day, from 85 to 45% ($t \leq 7.07$; $P \leq 0.002$; Fig. 1b), but the percentage remained constant for the remaining 3 days ($t \leq 2.08$; $P \geq 0.222$). Analysis of variance indicated that the number of interactions between individuals and the shoaling velocities decreased over time (F = 7.77 and 10.5, respectively; P = 0.001 and 0.0004, respectively; Fig. 1c and d).These decreases were seen after the first day, with no further change over the remaining 3 days ($t \leq 5.08$; $P \leq 0.007$; Fig. 1c and 1d). In contrast, shoaling NNA and NND significantly increased after the first day and then remained constant over the following 3 days ($F \leq 12.3$, $P \leq 0.001$, and $F \leq 7.51$, $P \leq 0.023$, respectively, Fig. 2a and b). NNA significantly increased on days 2–4 when compared to day 1 ($t \leq 5.35$; $P \geq 0.001$), and NND increased on days

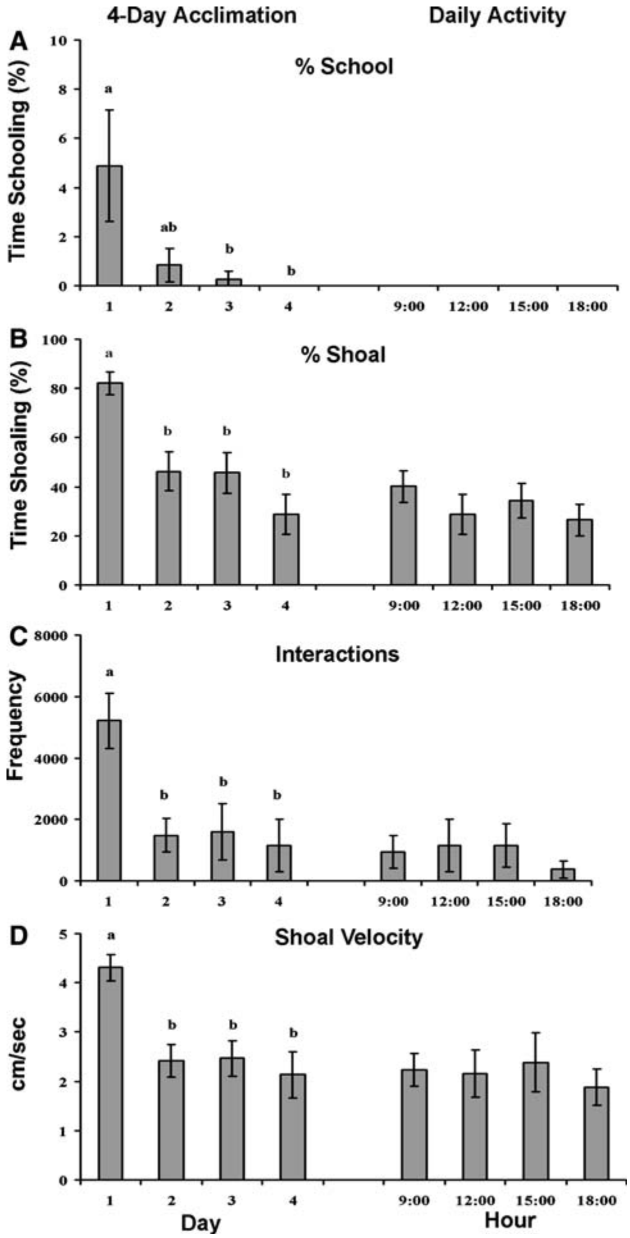


**Fig. 1** Percentage of time schooling (**a**), percentage of time shoaling (**b**), frequency of interactions (**c**), and shoaling velocity (**d**), for groups of mummichog on days 1, 2, 3, and 4 and at 09:00, 12:00, 15:00, and 18:00 h on day 4. Data are means ± SE. Days and hours with *different letters* are significantly different at the $P \leq 0.05$ level

2 and 4 ($t \leq 4.51$; $P \leq 0.057$) and marginally nonsignificantly increased on day 3 ($t = 3.06$; $P = 0.088$) when compared to day 1.

Percentage of time spent solitary and solitary NND displayed notable changes after the first day, and remained constant for the remainder of the experiment ($F = 20.12$ and 10.59, respectively; $P = 0.0001$ and 0.0003, respectively; Fig. 2c and d). Time spent solitary and NND significantly increased after day 1 ($t = 5.21$ and 3.26, respectively; $P = 0.002$ and 0.021, respectively; Fig. 2c and d) with no further significant change. Overall, this describes a decrease in shoaling cohesion through reductions in percentage and composition (NNA and NND), with an increase

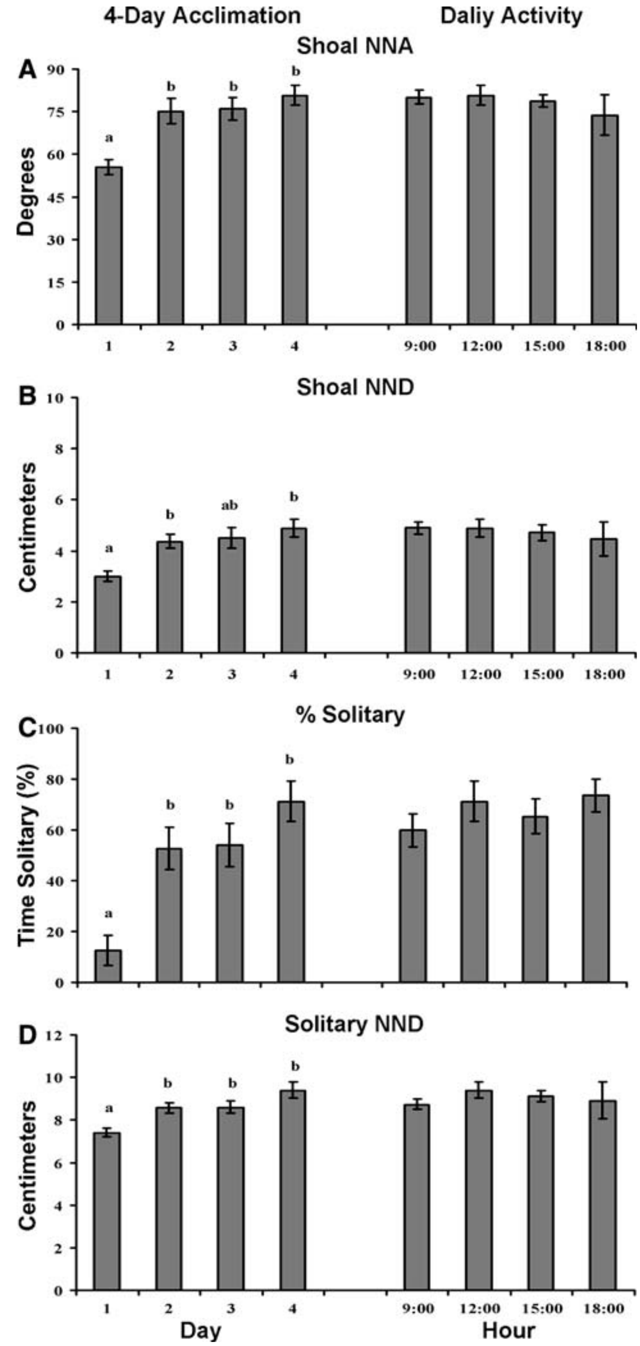


**Fig. 2** Shoaling nearest-neighbor angle (*NNA*, **a**), shoaling nearest-neighbor distance (*NND*, **b**), percentages of time fish were solitary (**c**), and individual nearest-neighbor distances (**d**) for groups of mummichog on days 1, 2, 3, and 4 and at 09:00, 12:00, 15:00, and 18:00 h on day 4. Data are means ± SE. Days and hours with *different letters* are significantly different at the $P \leq 0.06$ level

in the number of individual behaviors over time. In addition, no significant differences were observed in any of the group or individual behaviors between the four observation periods (09:00, 12:00, 15:00, and 18:00 h) during the final day (Figs. 1, 2; $F \leq 1.68$; $P > 0.05$).

## Discussion

Schooling and shoaling behaviors of fish have attracted considerable attention as model systems in an attempt to unravel the functions of group living (Hoare et al. 2000). This study developed a software system to investigate dynamic group swimming behaviors in mummichog, using mathematical criteria based on existing literature and preliminary observations. The result was a software system with the capability to quantify schooling, shoaling, and group fish behaviors. Analysis of simulated data sets demonstrated that the software program has the ability to quantify schooling and shoaling behaviors accurately in mummichog. Since schooling behaviors were infrequent and prominent primarily only within the first day, conclusions were drawn and comparisons were made for shoaling behavior only. However, schooling behavior during the initial 24 h was not unexpected since traveling in schools might provide a degree of group protection in a new environment.

The resultant data from this study describe and confirm the acclimation of groups of mummichog to observational arenas after 24 h. This acclimation period of mummichog groups is similar to the acclimation period of individual mummichog (Kane et al. 2004). Compact group swimming within the arenas in an exploratory fashion was observed initially, followed by decreased speed and inter-individual association as acclimation time progressed. Results indicate that the software system maintained the ability to consistently discriminate between and to quantify different types of group movement in fish.

The least-squares method of path determination accurately attributed a path to an individual fish under most conditions. However, care must be taken when the magnitude of frame-wise positional displacement approaches the nearest-neighbor distance. Fish swimming quickly in a restricted space can be difficult to track with the least-squares method; this situation can lead to inaccurate path determination if the paths of individual fish cross with only two video frames to describe the behavior. This limitation can be overcome either through increasing the frame rate of video capture or independent validation of the method via comparison with manual tracking. Visual inspection of the mummichog utilized in this study indicated that crossover behaviors are limited and the vast majority of paths, even with crossover, were accurately described.

The decreased schooling, shoaling, and number of interactions between individuals corresponded to increases in NNA and NND, describing a general disassociation between individuals over time. Evaluation of the various behaviors described in this study confirmed a shift in behavior over time (24 h) consistent with a group of fish familiarizing themselves with new surroundings. NNA between fish during the initial 24 h was, on average, 54.5°, which is similar to theoretical schooling values described previously (Radakov 1973). However, after 1 day, NNA increased to 80.0°, illustrating a decrease in polarization. This agrees with the expected value for random orientation of 90° (Masuda and Tsukamoto 1998). There is, however, no defined NNA value for shoaling, and given the nature of shoaling, only NND was analyzed. In addition, there are no generally accepted values for NNA and NND for schooling fish (Higgs and Fuiman 1996).

The software system described herein has the ability to quantify alterations in group behavior of any species of fish in response to environmental fluctuations. The system has the flexibility to analyze up to 12 arenas simultaneously. The computer software can be adapted to analyze any number of individuals in a school or shoal, in any arena shape or size, with the only limitation being computation time and two-dimensional output. An advantage of this custom system is that it can record and analyze up to 1 h of video at 30 fps. This represents notable increases in recording periods and frame rates over previous systems (Partridge 1980; Fuiman and Webb 1988; Rehnberg and Smith 1988; Hartwell et al. 1991; Hassan et al. 1992; Bumann and Krause 1993; Gallego and Heath 1994; Higgs and Fuiman 1996; Masuda and Tsukamoto 1998; Suzuki et al. 2003). The ability to study longer periods of time becomes more relevant when comparing interactions between fish and changes in social structure over time. The behavioral analysis system described in this study can lend significant insights into the movement patterns of groups of fish in a laboratory setting.

Further, this system has the ability to investigate changes in structure and function of group dynamics as well as movement patterns in fish over time. The quantified behaviors, as described in this study, are environmentally relevant social and movement behaviors that occur on a continuous basis in nature, and can directly affect individual fitness. Ultimately, data generated from this system can foster development of models that can relate environmentally induced changes in individuals and within populations of fish to community- and trophic-level interactions in environmental systems.

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