Supporting information for

Inferring collective behaviors from a fossilized fish shoal

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Control data of random distribution

We created datasets with a completely random distribution for comparison by placing 257 individuals within a bounding box around the fossilized fish group. Heading directions were also obtained randomly. We generated 1,000 datasets and tried to infer the interaction rules in the same way as the fossilized fish group. These datasets showed a flatter distribution of the distance to the nearest individual and no trace of interaction rules (Fig. S5).

Fossil fish groups with scattered distributions

Most slabs with fossils of fish mass mortality show a scattered distribution, which is considered to be formed by many fish carcasses sinking simultaneously due to anoxia [1]. In this type of fossilized fish group, we do not expect that interaction rules can be inferred. To test this, we analyzed two slabs with this type of fossilized fish group (Fig. S6A, B). One is from the Green River Formation of the Fossil Butte National Monument, Kemmerer, Wyoming (MSN-PV 20566; National Museum of Nature and Science, Tsukuba) and has three species of fish (*Knightia* sp.: 276 individuals, *Diplomistus* sp.: 2 individuals, *Mioplosus* sp.: 4 individuals), where we analyzed only *Knightia* sp. (Fig. S6A). The second is from the Green River Formation, Wyoming (MSN unregistered specimen) and has 35 individuals of *Gosiutichthys* sp. (Fig. S6B). The distributions of the distance to the nearest individual did not show a clear single peak and the density plots were much flatter compared to the shoaling fish fossil (Fig. 1C; Fig. S6C, D). We could not find significant traces of interaction rules in either fossil. That is, we found no evidence that individuals farther from their nearest neighbor showed attraction, while those closer to their neighbor showed repulsion (Logistic regression; A: likelihood-ratio test, df =1, χ^2 = 0.021, P = 0.884; B: df =1, χ^2 = 2.372, P = 0.124; Fig. S6E, F).

Another model for fish shoals

Other than zone models, some models have reported that parallel group motion can emerge when individuals only use an alignment or attraction type interaction rule [2,3], or when individuals use a combination of repulsion and attraction interactions [4,5]. To test if the interaction rules observed in the fossilized fish group can explain its collective structure, we also used a differential equation model which only has explicit repulsion and attraction effects [4,5]. We placed 257 individuals with random locations and directions as an initial condition. Then we calculated the time development of individual positions and heading directions for 5000 time steps, using the Runge-Kutta method with time steps, Δt = 0.1. At least in the set of parameter values (α = 1, β = 1, C_A = 100, C_R = 50, l_A = 50, l_R = 5), we found that the model produced a pattern with much higher polarization (ρ > 0.99), but without an oblong shape (length-width ratio of the bounding box ≈ 0.9) or as clear a trace of interaction rules as in our individual-based model simulations or fossilized fish group. Thus, models with only repulsion and attraction rules may not be enough to describe the shoaling behavior of *E. levatus*, suggesting that these fish also had some alignment mechanisms.
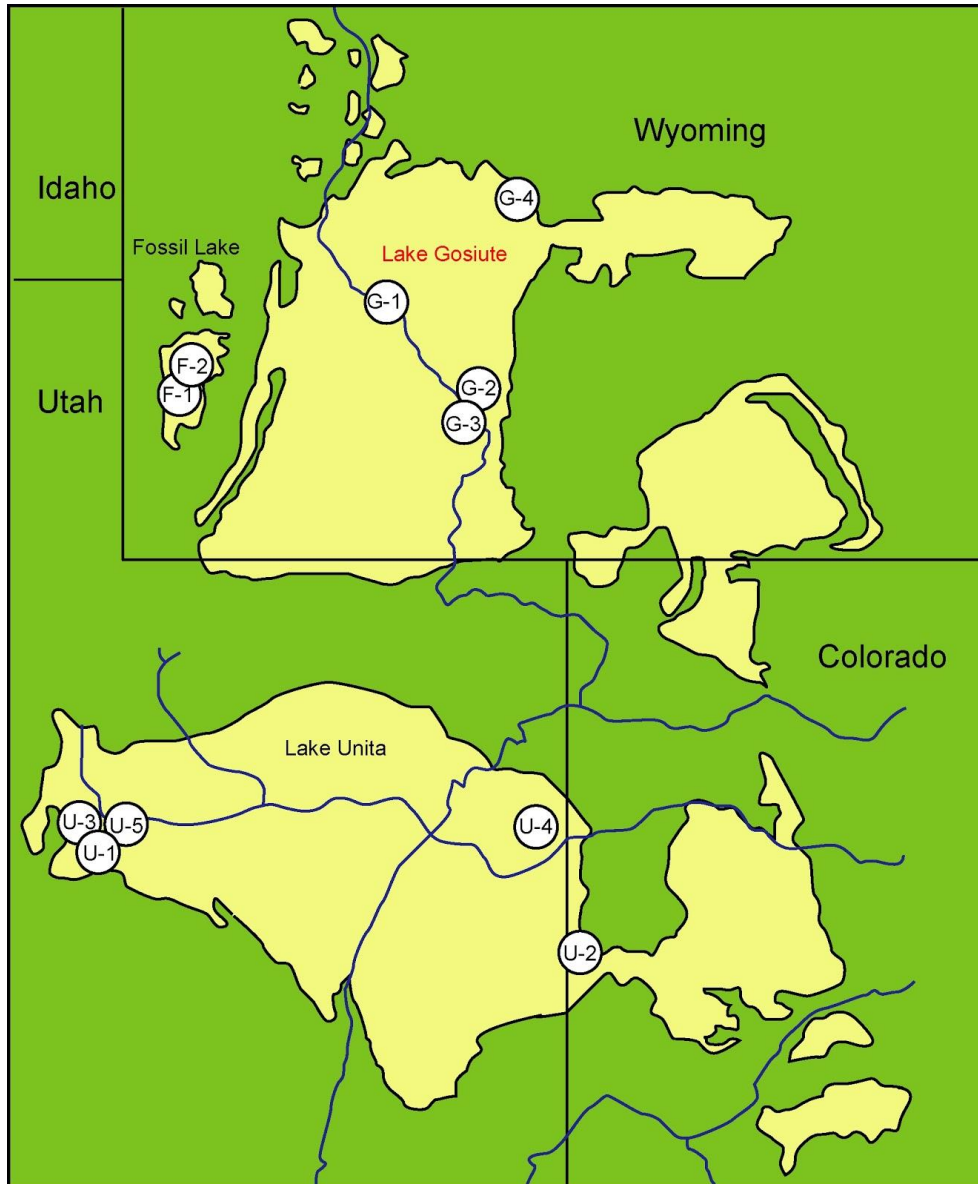
Fig. S1. The surface distribution of the Green River Formation (yellow) (modified from [6]). Circled numbers show some vertebrate fossil occurrences. *E. levatus*[†] is known from Lake Gosiute and Lake Uinta deposits [7]. Mass mortalities of this species up to 100 individual/m^2 were found in Lake Gosiute deposits at Locality G2 in Wyoming [6,7].
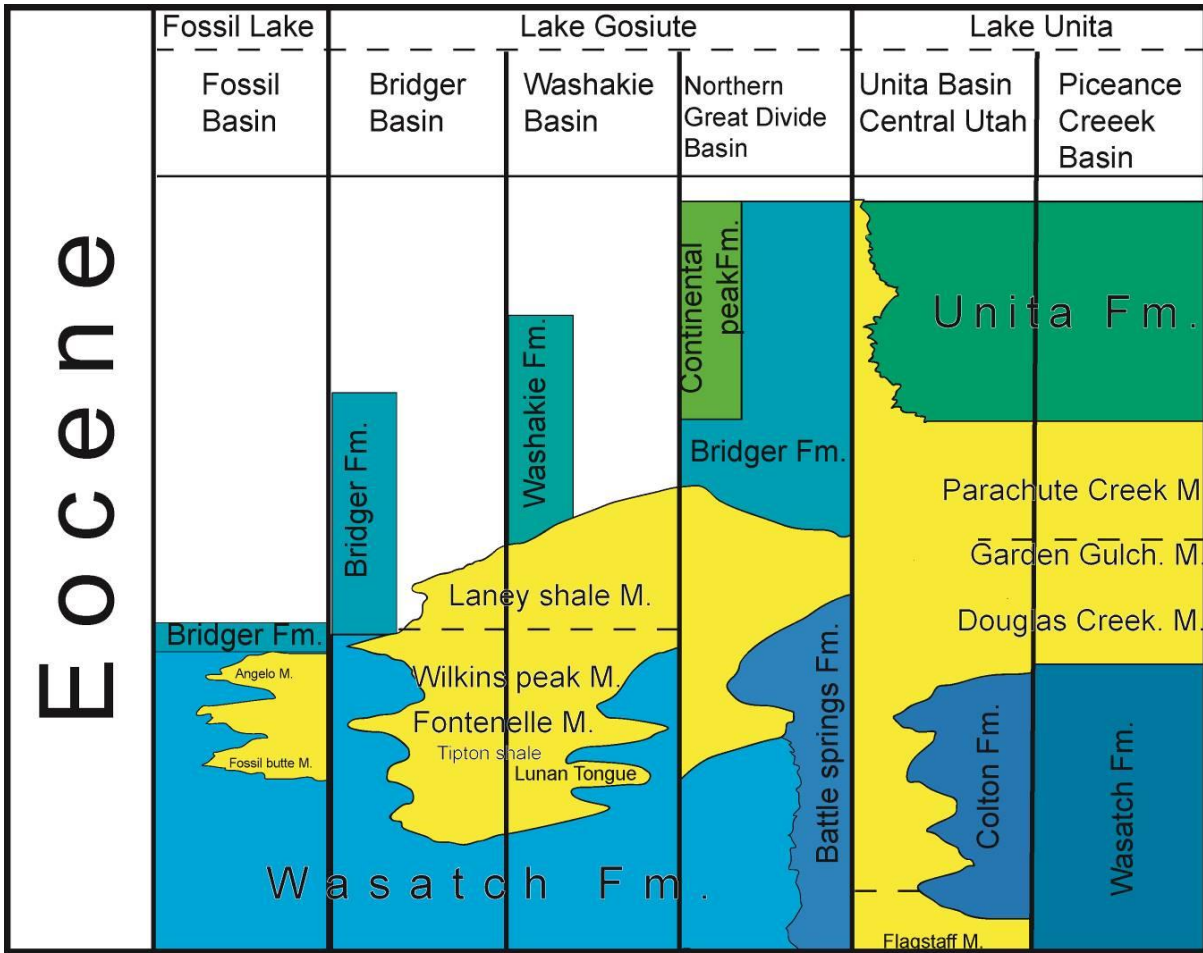
Fig. S2. The stratigraphic distribution of the members of the Green River Formation (yellow) in Wyoming, Colorado, and Utah [8]. The small and abundant *E. levatus* (length from 20 to 25 mm) is known from the lower Laney Member of Green River Formation, Wyoming [8,9].
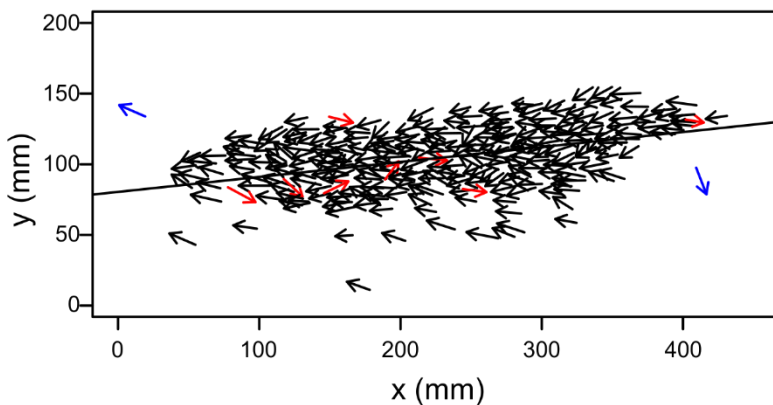

Fig. S3. The presence of individuals with abnormally divergent headings. In the group, there were eight fish with headings that were more than $\pi/2$ radians different from the average heading (shown in red arrows). Two individuals (shown in blue arrows) were dropped from the analysis because they were apart from the central aggregation (twice the average body length from their nearest neighbors) and there were no fish present in the direction that they were heading or at their side.
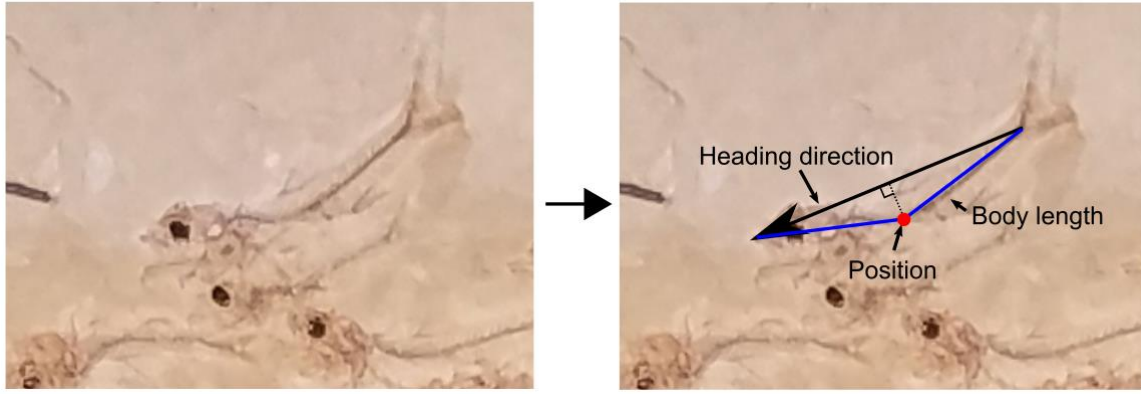
Fig. S4. Measurements of fish position, body length, and heading direction. Each heading direction was measured as a vector from the base of the tail to the tip of upper jaw. As this vector usually did not overlap with the backbone, which is curved, we approximated the body length (standard length, blue line) with two lines of equal length. The position of the fish was determined as the point of intersection of these two lines (red point).
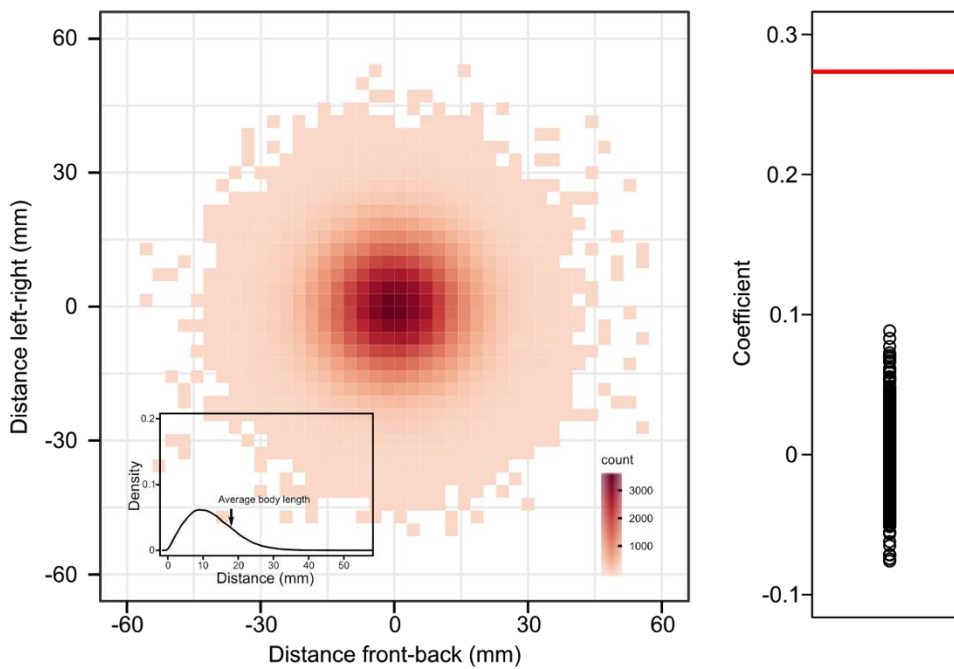

Fig. S5. Analysis of a randomly placed fish group. There was no evidence of repulsion in the frequency distribution of distance to the nearest neighbor, and the density plot of the distance between individuals was flatter than the fossilized fish group (1,000 replicates are pooled). Coefficients obtained from logistic regression were distributed around 0.
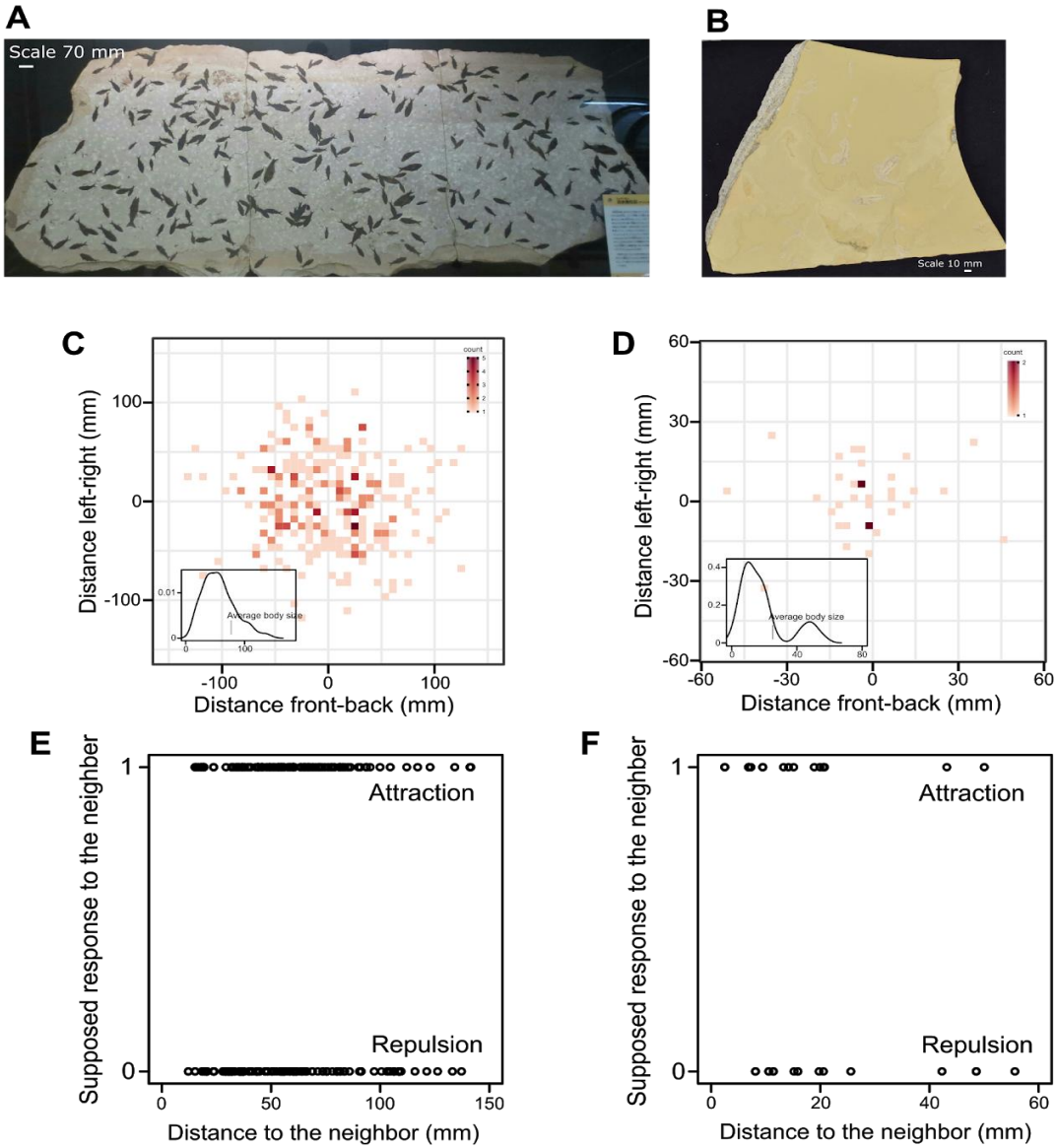
Fig. S6. Analysis of slabs with mass mortality of fish in scattered distributions. (A) A fossil fish assemblage from the Green River Formation of the Fossil Butte National Monument, Kemmerer, Wyoming, U.S.A.. (B) Thirty-five specimens of *Gosiutichthys* sp. from the Green River Formation, Wyoming, U.S.A.. (C, D) Frequency distributions of relative positions of the nearest neighbor, with an insert showing the density plot of the distance. (E, F) Inferred movement of fish toward or away from the nearest neighbor. There was no trend for attraction to distant neighbors or repulsion from close ones.
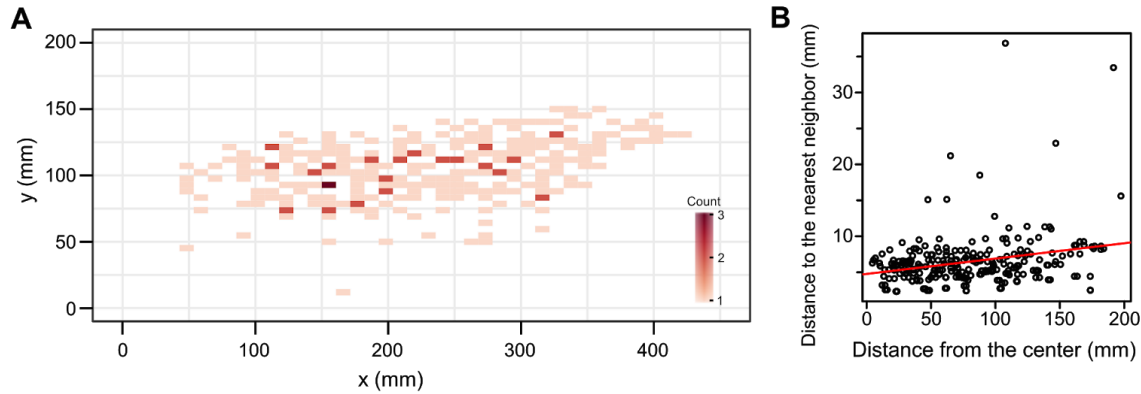
Fig. S7. Density of fish in the fossilized fish group. (A) Frequency distribution of individual fish, corresponding to Fig. 1A. (B) The relationship between the distance from the center of the group and the distance to the nearest neighbor. Red line indicates the result of linear regression (linear model; slope $\pm$ S.E. = 0.021 $\pm$ 0.005; F = 18.347, P < 0.001).

Table S1. Parameter values or ranges used in our simulations. We chose these parameter values arbitrarily from ranges used in a previous study [10]. The speed range was set by plus or minus 2 unit from the value.

Parameter	Symbol	Value (or range)
Number of fish	N	257
Space size	L	200
Repulsion zone	r_z	1
Attraction zone	r_a	16
Turning rate	θ	30°
Speed	v	3–7
Time increment	Δt	0.1
Error	σ	0.2

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