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Field

The social life of a fish shoal in ancient times

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ABSTRACT

Groups of living animals show beautiful patterns of collective behaviors. This must also be true for extinct organisms. We analyzed the fossilized fish group to infer behavioral rules for coordinated collective motions of extinct animals.

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The coordinated movements of bird flocks, fish schools, and insect swarms are among the most impressive collective behaviors in the animal world. Such coordination can be achieved by simple behavioral rules for social interactions, like avoiding a collision from close neighbors and attraction towards distant neighbors. But how long have these behaviors existed, and how did they evolve from earlier forms? With a time machine, we could find out whether extinct species also moved in coordinated groups like animals today. Fossils can provide such a time machine, but fossilized evidence of behavior is rare, and, until now, no one has found evidence for collective behavior by past organisms.

Fossils of mass mortality of fish may preserve individual positions and attitudes as a snapshot of the groups' movement. These fossils have been interpreted as shoaling groups because the size of preserved fish was similar to that seen in the current fish shoal. However, this is not enough to know if the extinct fish species performed a coordinated collective motion. Thus, we decided to analyze the fossils of mass mortality from the perspective of collective behaviors. We hypothesized that if the group was preserved while swimming together, the fossil could provide a snapshot reflecting collective behaviors and a trace of how individuals were interacting with each other.

In this study, we focused on a shale-stone slab containing 259 fossilized juvenile fish of the extinct trout-perch *Erismatopterus levatus.* The slab originated in the Green River Formation, in or near present-day Wyoming, and was formed 50 million years ago during the Eocene epoch. We photographed the slab and identified the positions of each fish to measure the distance between neighboring individuals. Then, based on their heading directions, we inferred where each fish would have moved in the next moment, to relate their anticipated move to the positions of their nearest neighbors. If the distance between neighboring individuals becomes smaller, the two would have been about to get closer; while if it grows, they would have been about to move away.

Using this method, we found the traces of two rules for social interaction: repulsion from close individuals, and attraction towards neighbors at a distance. These rules are similar to those used by extant fish species. Moreover, we further discovered that the fossilized fish group showed the same oblong shape found in present-day fish schools. Also, the fossilized fish showed high polarization, meaning that their body axes were aligned with one another. This organization would be unlike the random, disorganized orientation expected if the fish were not interacting with one another. These characteristics of fish shoals are possibly the result of natural selection for predator avoidance, indicating that *E. levatus* experienced high predation pressure in its ancient intermountain lake habitat.

These findings are striking because many forms of animal communication have been assumed to leave no fossil record, which makes it challenging to study the evolution of collective behavior. In previous studies, fossils with well-aligned assemblies of fish have been thought to result from the sorting of carcasses by wind and water currents. But, we believe that this process may not be adequate in this case because directional alignment alone cannot explain the observed pattern. Using computational methods, we simulated the arrangement of fish expected if the fossils had resulted from such a passive process. Although these simulated fossils are highly aligned, we could detect no trace of the behavioral rules found in the real fossil. Therefore, the combination of the positions and heading directions is exceptional, and thus the observed pattern reflects fish behavior, rather than the action of wind or water.

We call frozen behaviors that fossils with animals preserved while doing something. Preservation of individual positions during interactions, as we assume occurred in our fossil, requires rapid burial. A limitation of the current study is that it remains unclear how the fish shoal's structure was preserved in the fossil. Rapid fixation might be possible by sand dune collapse on shallow water, which can produce a bed in only seconds or minutes. But we could not obtain any evidence to support the occurrence of this event. Further analysis of similar specimens of mass mortality may reveal more about how such fossils can form, and what they can tell us about the origins of collective behavior.