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Editorial comments and announcements

Fish schools and their hydrodynamic function: a reanalysis

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In his recent review on the functions of schooling behaviour in teleosts, Pitcher (1986) concludes that, 'no valid evidence of hydrodynamic advantage has been produced, and existing evidence contradicts most aspects of the only quantitatively testable theory published.' We suggest that this conclusion is premature because it ignores the potential trade-offs involved in school function.

In Weih's (1973, 1975) theory on the structure of a hydrodynamically efficient school, he described three different mechanisms whereby fish could gain hydrodynamic benefits. Fish could use vortices generated within the school to reduce their relative velocity for a given absolute fish velocity (the vortex hypothesis), use other members of the school to improve thrust efficiency (the channeling hypothesis), and use the wakes from neighbouring fish to provide lift (wingtip uplift, useful only for negatively bouyant fish). To achieve optimal hydrodynamic benefits, similar (but not identical) school structures are required (see Weihs 1975 for a more complete description).

Pitcher (1986) rejects the vortex hypothesis based on the results of Partridge & Pitcher (1979) in which only four of 659 cases had fish in the positions predicted by Weihs (1975). Further, Pitcher argues that this mechanism would be evolutionarily unstable as only members in alternate rows of the school realize any energy saving. Thus, he concludes that this mechanism depends upon the unlikely assumption of stable altruistic behaviour. However, if fish shift their positions in a school, there could be a net benefit to each individual.

Pitcher also rejects the wingtip uplift mechanism for teleosts. To achieve this benefit fish must swim with their pectoral fins rigidly extended; a phenomenon not observed in teleosts.

Although Pitcher notes that Partridge et al. (1983) have observed school structure which is consistent with the channeling hypothesis and Pitcher et al. (1985) have observed fish preferring to select nearest neighbours which are of similar size (a prediction of the channeling hypothesis), he concludes that there is no unequivocal evidence in support of this hypothesis.

Abrahams & Colgan (1985) (misreferenced by Pitcher as Abrams and Colgan) examined the hydrodynamic mechanism of schooling through the perspective of a trade-off mechanism. To achieve a hydrodynamic benefit from schooling by the channeling mechanism, a school of six individuals should swim on the same vertical plane. However, this structure has the associated cost that it impairs the ability to detect an object on the same vertical plane as the school. This function would be especially important in the early detection and avoidance of a predator. Thus, if fish schools are capable of providing hydrodynamic benefits, by manipulating the environment through which schools travel, the structure of the school should change in a predictable manner. Travelling through an environment containing only shallow moving water, the school should be flat in the vertical dimension. However, when an aquatic predator is released at random times through a door in a mid-water location, the fish should stagger their positions in the vertical dimension to maximize their ability to detect the predator. If the schools were not capable of providing a hydrodynamic function, no change in school structure should occur between the two environments (see Abrahams & Colgan 1985 for a complete description of the logic and methods).

This experiment resulted in six of ten treated schools changing their school structure as predicted with no control schools showing any change. These data are consistent with the hypothesis that fish schools are capable of providing a hydrodynamic function. Pitcher claimed that Abrahams & Colgan misread Weih's theory in interpreting the results of these experiments. He further claimed that additional horizontal layers are necessary to enhance the channeling hypothesis. He is correct if very large school sizes were used. However, at the small school size used in our experiments, the benefits of entering another plane will be weak or non-existent for individuals leaving the single horizontal layer. Thus, a single horizontal layer is the optimal structure for a school of six individuals (Weihs, personal communication).

Pitcher (1986) further interprets our results as being consistent with observations he has made on other cyprinid schools, that exposure to a predator causes the school to become deeper and more compact. In fact, this was *not* the result of the experiments. Although the schools did become deeper, no changes were observed in any other dimension. Thus the schools became more diffuse rather than more compressed.

Concluding that no valid evidence exists for a hydrodynamic advantage in fish schools is partly due to a misrepresentation and partly to a different interpretation of our results. However, the most important idea from our paper was ignored; that the function of a fish school may be a dynamic process which involves trade-offs. If a hydrodynamic function is achieved at the expense of an anti-predator function, then schools providing a hydrodynamic advantage should only be observed in circumstances where an antipredator function would be of little value. Therefore, it would not be expected that Partridge & Pitcher (1979) would observe a hydrodynamic function in schools of prey species in an unfamiliar laboratory environment. In this situation, the benefits of an antipredator function would exceed that of a hydrodynamic function. Conversely, it would be expected that Partridge et al. (1983) would observe a hydrodynamic function of schools of a predator species in their natural environment. Consideration of the interaction between environment and school function is necessary before we ignore the potential hydrodynamic benefits of schooling.

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