Fish migration: a simple mathematical description

Diadromous fishes migrate between rivers and seas, and are key drivers of surface water ecosystems and food webs. Analyzing migration of diadromous fishes is therefore a core for assessment of surface water systems from both biological and ecological viewpoints.

A fish school is a set of individuals adopting shoaling behaviors, living in group, and adopting a significant degree of synchronization of displacements (in speed and polarity terms) that results from social interaction among these individuals. In general, the migratory fishes form fish schools during their migration processes. Comprehension of migration behavior of fish schools is thus a crucial research topic, which has been addressed from both experimental and theoretical point of views by many researchers. The experimental results imply that a fish school adaptively chooses its shape and swimming speed depending on the hydrodynamic conditions of the flow that the school faces. However, its theoretical explanation has not been well developed. This is a strong motivation of the present research.

Fig. 1. A photograph of P. altivelis. (Through the courtesy of Hii River Fisheries Cooperatives, Japan)

An optimal control theory, which is a mathematical tool that is able to naturally and efficiently describe decision-making processes involved in biological phenomena, turns out to successfully explain how the shape and swimming speed of a fish school is chosen. The theory considers an upstream migration process of a fish school along a river identified as a 1-D domain. The key assumption in the present mathematical modelling is that the fish school has its shape and swimming speed as the control variables, which are chosen to maximize an objective function: roughly speaking, a sum of the benefit that the fish school gains at the upstream-end (the goal of migration) and the hydrodynamic and non-hydrodynamic costs. This optimal control problem ultimately reduces to a boundary value problem of a nonlinear differential equation, which is referred to as a Hamilton-Jacobi-Bellman (HJB) equation. In fact, the derivative of the solution to the HJB equation determines the optimal shape and swimming speed of the fish school.

Although the HJB equation is a nonlinear differential equation, it could be effectively converted to an exactly-solvable algebraic equation. This means a possibility that we can predict the shape and swimming speed of a fish school without any approximation and numerical computation. Furthermore, the analytical results explicitly predict dependence of the optimal shape and swimming speed on the flow speed, which can be practically of importance. The derived analytical results have been validated with the past experimental observations results of upstream fish migration of schooling *Plecoglossus altivelis* (Ayu) (Fig. 1), which is a diadromous fish living in Japan serving as an important inland fishery resource in the country. The model parameters have been identified from the observation results, demonstrating satisfactory applicability of the present model to analysis of fish migration. Theoretical dependence of the migration behavior on the flow speed reasonably agrees with that observed in the experiments in particular; the school shape becomes longer in the flow direction as the flow speed increases.

As it is often expressed, complicated mathematical models are not necessarily required for describing complex phenomena. Resolution of key processes involved in the fish migration would be an effective way to its comprehension. The present research results clearly show high utility of a simple mathematical model in analyzing fish migration, which can actually be a complex biological phenomenon resulting from many stages of possibly not completely resolvable decision-making processes.

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