Mathematical Biosciences 281 (2016) 139–148

Contents lists available at ScienceDirect

Mathematical Biosciences

journal homepage: www.elsevier.com/locate/mbs

Mathematical analysis and validation of an exactly solvable model for upstream migration of fish schools in one-dimensional rivers

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ARTICLE INFO

Article history:
Received 8 February 2016
Revised 16 September 2016
Accepted 20 September 2016
Available online 28 September 2016

Keywords:
Fish school
Upstream migration
Optimal control problem
Dynamic programming principle
Hamilton–Jacobi–Bellman equation

ABSTRACT

Upstream migration of fish schools in 1-D rivers as an optimal control problem is formulated where their swimming velocity and the horizontal oblateness are taken as control variables. The objective function to be maximized through a migration process consists of the biological and ecological profit to be gained at the upstream-end of a river, energetic cost of swimming against the flow, and conceptual cost of forming a school. Under simplified conditions where the flow is uniform in both space and time and the profit to be gained at the goal of migration is sufficiently large, the optimal control variables are determined from a system of algebraic equations that can be solved in a cascading manner. Mathematical analysis of the system reveals that the optimal controls are uniquely found and the model is exactly solvable under certain conditions on the functions and parameters, which turn out to be realistic and actually satisfied in experimental fish migration. Identification results of the functional shapes of the functions and the parameters with experimentally observed data of swimming schools of *Plecoglossus altivelis* (Ayu) validate the present mathematical model from both qualitative and quantitative viewpoints. The present model thus turns out to be consistent with the reality, showing its potential applicability to assessing fish migration in applications.

1. Introduction

Analyzing fish migration in river environment is a core of biological and ecological assessment of surface water systems [26,61]. Ecologically and environmentally conscious management of migratory fishes as fishery resources is also a key topic [28,72], which has sometimes been performed with mathematical and numerical models [13,34]. A fish school is defined as “a set of individuals adopting shoaling behaviors, living in group and adopting a significant degree of synchronization of displacements (in speed and polarity terms) resulting from social interaction between these individuals” [11,59]. Costs and benefits of schooling have been reviewed with detailed theoretical and experimental investigations [40,41].

Many investigators have studied microscopic behavior of fish schools in the context of multibody dynamics. Hemelrijk and Hildenbrandt [22] and Hemelrijk et al. [23] numerically investigated shape of fish schools under different swimming speeds with multibody dynamics models whose behavior are consistent with recent experimental results [52]. Stability analysis of the multibody dynamics models have been performed for comprehending interactions among individuals of a school [35,43]. Topographical effects on swarm dynamics have been studied with network models where interactions among individuals are defined on conceptual complex networks [3,12,68]. Numerical simulation successfully clarified spatio-temporal evolution of fish schools under heterogeneous environment [33,62,79,86]. Mathematical and numerical analyses on inherently unsteady and possibly intermittent locomotion strategies of animals have been studied from the viewpoint of deterministic optimal control theory [53,66,70]. Experimentalists addressed unsteady locomotion [70], topological nature of fish schools [1,44,76], and local behavior of fish schools from the viewpoint of stochastic processes [42]. Onitsuka et al. [52] extensively studied migration dynamics of fish schools of *Plecoglossus altivelis* (*P. altivelis*; Ayu) in laboratorial channels with steady and uniform current. They found that the school becomes longitudinally oblong and performs less transverse movements with faster upstream migration as the flow speed increases. They also showed that the upstream swimming speed is higher for fish schools than those for isolated individuals are, which is due to enhancement of rheotaxis by schooling.

Some other investigators have studied coarse-scaled macroscopic behavior of fish schools. Peterson and DeAngelis [58] mathematically modeled movements of prey fishes in a predator field using a conceptual model and analyzed relationships between the mortality of prey and hydrodynamic and biological conditions. Gao et al. [19] developed a horizontally 2-D numerical model of

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http://dx.doi.org/10.1016/j.mbs.2016.09.014
0025-5564/

upstream fish migration in a vertical-slot fishway based on tracked trajectories of laboratorial experiments of individual fishes and a shallow water hydrodynamic model. Mean field models that consider a fish school as a cloud of individuals have effectively been used for simulating highly nonlinear natures of macroscopic behavior of fish schools [7,29,64,65]. Hongler et al. [24] have found tractable mean field models whose solutions behave like solitons. Probabilistic models of the size of fish schools have been proposed based on static optimization principles [14,30,31]. Anderson [2] presented a nonlinear dynamic model of the size of fish schools based on a stochastic differential equation driven by additive noises. The model has been reduced to obtain an explicit probability density function of the size at an equilibrium state, which compared well with experimental data of fish species in ocean. Niwa [[46,47], and [48]] statistically characterized the size distribution of fish schools and provided explicit linkages with microscopic multibody dynamics model and the macroscopic probabilistic models. Humphries et al. [25] have investigated competitions among individuals of a fish school depending on different food intake rates with extensive sensitivity analysis. Dynamic statistical models of animal groups explained the reason why many of the school size distributions found in nature are logarithmic [20,38]. Replicator dynamics has effectively been used for comprehending collective actions in a group with stochastically variable group size [56]. Partial differential equation models have been presented for better comprehending communication mechanisms in migrating animal groups ([15] and [16,37]). Stochastic differential equations also are useful tools for analyzing decision-making processes in migration of animal groups [60,77].

As reviewed above, many existing models describe dynamics of fish schools based on multibody dynamics that are driven by mutual nonlinear interactions among individuals. Such models can simulate dynamics of realistic fish schools where a variety of behaviors originating from nonlinearity, such as spatio-temporal pattern formation, phase transition, and bifurcation, are reasonably reproduced. However, they are often too complex for applications in ecological and fishery engineering, which is due to high degree of freedom, difficulty in estimating parameters and coefficients, and computational complexity. On the other hand, although most of the conceptualized models for macroscopic behavior are more efficient, they do not consider the effects of river flow such as flow speed on fish migration. The experimental results suggest that the flow conditions should be considered in modeling fish migration [6,45,67,69]. A mathematical model, which is efficient and appropriately considering the effects of flow can possibly serve as a useful tool for analyzing migration of fish schools in river environment; however, such an approach seems to be still rare at present. This is the main motivation of this paper.

The purpose of this paper is to present a simple and exactly solvable mathematical model for migration of fish schools in rivers. The present models assume that the fish migration is a consequence of optimizing evolutionary fitness, and the resulting dynamics is represented by an ordinary differential equation (ODE) that governs the longitudinal movement of fishes. This paper focuses on the upstream migration in particular, which is a key element in life histories of migratory fishes [32,49,75]. The mathematical model, which is an extended version of the previously proposed model for isolated individuals [83], is based on an optimal control theory. The model considers that a fish dynamically optimizes its swimming velocity during its migration process so that a biophysical objective function is maximized. Yoshioka and Shirai [82] derived analytical solutions to a Hamilton–Jacobi–Bellman equation (HJBE) [18] associated with the model: a nonlinear differential equation governing the optimal migration velocity of individual fishes. Yoshioka et al. [85] identified shape of the objective function to be maximized in the model for a number of migratory fish species. In this paper, a fish school with a given size is identified as a macroscopic agent migrating along a 1-D river toward upstream where its swimming velocity and shape (horizontal oblateness) are control variables. This paper shows that, under simplified conditions with a uniform flow field, the HJBE that governs the optimal control variables reduces to a tractable system of algebraic equations. Sensitivity analysis of the system shows qualitative consistency between the model and the existing theoretical and experimental results. Key functions in the model are identified with observation results of experimental fish migration. This paper thus contributes to proposing a new mathematical model for upstream migration of fish schools and its theoretical and experimental validation.

The rest of this paper is organized as follows. Section 2 presents the mathematical models focused on in this paper. Section 3 performs theoretical and experimental validation of the proposed model. Section 4 concludes this paper and presents future perspective of this research.

2. Mathematical models

The present mathematical models solely focus on the upstream migration (swimming behavior). The other activities, such as sleeping and feeding, are not considered in the models as in some of the investigations for fish migration [17,39]. Explicitly incorporating these activities would require larger numbers of functions and parameters to be specified. They are potentially important and possibly lead to more realistic biophysical theory of fish migration, but they complicate the mathematical modeling. Since the objective of this paper is to present a simple model for migration of fish schools from a biophysical viewpoint that potentially serves as a starting point of sophisticated models, such advanced models will be dealt with in the subsequent papers. The fishes are assumed to sense the flow speed V that would be affected by turbulence and know the length L where their species have evolved and the profit P_0 where they will habit or spawn.

2.1. Mathematical model for upstream migration of isolated individuals

2.1.1. Ordinary differential equation

An ODE for movements of an individual fish along a 1-D river is presented, which forms the basis of the fish migration models in this paper. The explanation of the model for the isolated individuals follows that of Yoshioka et al. [85], but it is presented for self-contentedness of this paper. A 1-D river $\Omega=(0, L)$ with the length $L(>0)$ is considered where the boundaries $x=0$ and $x=L$ represent downstream- and upstream - ends of the river, respectively. The upstream-end $x=L$ is the goal of migration where a spawning site or a feeding site exists. The flow speed along the river is assumed to be uniform in both space and time, which is denoted by the constant $V>0$. The model starts from the ODE governing 1-D Lagrangian movement of an individual fish along the river given as

$$\frac{\mathrm{d}X_t}{\mathrm{d}t}=u_t-V \tag{1}$$

where t is the time, X_t is the 1-D position of the fish along the river, and $u=u_t$ is the swimming velocity of the fish, which is a control variable to be optimized through the migration process.

2.1.2. Value function

The admissible set of the control u is $\mathcal{U}=L^\infty([0,+\infty);U)$, which is a set of bounded functions with the range U [18]. The range U is identified as the 1-D real space $\mathbb{R}$ for the sake of simplicity of the mathematical analysis unless otherwise specified.