



# A simple game-theoretic model for upstream fish migration

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Received: 28 December 2016 / Accepted: 25 April 2017 / Published online: 3 May 2017  
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**Abstract** A simple game-theoretic model for upstream fish migration, which is a key element in life history of diadromous fishes, is proposed. Foundation of the model is a minimization problem on the cost of migration with the swimming speed and school size as the variables to be simultaneously optimized. Finding the optimizer ultimately reduces to solving a self-consistency equation without explicit solutions. Mathematical analytical results lead to the sufficient condition that the self-consistency equation has a unique solution, which turns out to be identified with the condition where the unique optimizer exists. Behavior of the optimizer is analyzed both mathematically and numerically to show its biophysical and ecological consequences. The analytical results demonstrate reasonable agreement between the present mathematical model and the theoretical and experimental results of upstream migration of fish schools reported in the past research.

**Keywords** Fish migration · Fish school · Game theory · Swimming speed · School size

## Introduction

Migratory fishes, such as salmonids and sturgeons, are central aquatic species of environment and ecosystem of surface water systems, since they shape and create linkages among food webs as consumers, ecosystem engineers,

modulators of biochemical processes, and transport vectors (Winemiller and Jepsen 1998; Flecker et al. 2010). In addition, many of them are economically and culturally valuable fishery resources. Both their abundance and diversity have been highly affected by loss and degradation of habitats and migration routes (Guse et al. 2015; Logez et al. 2013; Radinger and Wolter 2015). Physical barriers, such as dams and weirs, are the major factors that fragment habitats and migration routes of fish (Jager et al. 2015; Yu and Xu 2016). Analyzing fish migration has, therefore, been a key topic in current biological and ecological research areas (Becker et al. 2015; Wang et al. 2012; White et al. 2011).

Since many of the fishes migrate by forming schools (Partridge and Pitcher 1980; Partridge 1982), analyzing migration dynamics of fish schools is a crucial topic. Migration of individuals and groups of organisms has been studied from both theoretical and practical viewpoints. For migration of isolated individual fishes, swimming path and velocity have been analyzed with the help of optimization theory where some hydrodynamic cost is minimized. The physiological energy minimization principle has been a core to determine the preferred swimming speed of individual fishes given a flow speed and water quality (Clairaeaux et al. 2006; Tucker 1975). Such models have recently been a basis of a generalized biological theory for the physiological energy minimization principle (Papadopoulos 2009, 2013). Some authors assumed that a migrating animal selects a path that minimizes the total resistance force (Bejan and Marden 2006; Lindberg et al. 2015; McElroy et al. 2012). Stöcker and Weihs (2001) analyzed a conceptual optimization model based on Weihs (1974) for energy-saving conceptual burst swimming of fishes. For migration of fish schools, increasing hydrodynamic efficiency for each individual has been considered as

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one of the most significant advantages to form schools (Mayer 2010). Increasing foraging efficiency and vigilance against predators have also been considered to be advantageous (Mayer 2010). On the other hand, increasing the foraging efficiency would not necessarily increase the net available food for each individual in a school (Beecham and Farnsworth 1999). Day et al. (2011) experimentally observed that smaller fish schools of *Poecilia reticulata* (guppy) demonstrated higher foraging efficiency than the larger ones.

Macroscopic models based on conceptualization for effectively analyzing animal group's dynamics have been proposed to comprehend group dynamics from phenomenological viewpoints. In these models, one of the most important parameters for describing migration of animal groups is the size: total number of individuals in the group. A common assumption shared by most of the models is that there is a size to compromise between advantages and disadvantages of forming groups. Gueron and Levin (1995) mathematically analyzed stability of the equilibrium of group size with the different fusion and fission rates. Anderson (1981) proposed a stochastic differential equation model for temporal evolution of the size of fish schools. Niwa (1996, 1998, 2005) established modelling frameworks for analyzing group-size distributions based on probabilistic descriptions of the merging and splitting phenomena.

On the other hand, microscopic, individual-based models with repulsion and attraction forces acting among the individuals have also been utilized to study group dynamics of animals. Behavior of individual-based deterministic and stochastic models for migrating fish schools has been studied both from mathematical and numerical viewpoints (Ebeling and Schweitzer 2001; Uchitane et al. 2015; Ngyuen et al. 2016; Ta et al. 2014). Sumpter et al. (2008) numerically investigated information transfer within moving animal groups using a 1-D time-discrete model of migration. They implied that each group has an optimal size where the group density is close to a phase transition point from disordered state to ordered state. Lee (2010) studied a noisy self-propelled particles system to analyze stability of collective motion of particles against period and intensity of the noise. Katz et al. (2011) evaluated repulsive and attractive forces acting among individuals of a fish school based on a trajectory tracking technique.

As reviewed above, both individual-based microscopic and conceptual macroscopic models have been proposed and extensively studied so far; however, the conventional theoretical research lacks analyzing migration of fish schools subject to water current, which are of great ecological and environmental interest. Important such examples include assessing passage efficiency of river reaches and hydraulic structures (Baek et al. 2015; Kerr et al. 2015; Vowles et al. 2015). There exist a series of extensive

research results on behavior of fish schools subject to water current under experimental settings by Onitsuka and his co-workers, which can be effectively utilized for development and validation of mathematical models (Onitsuka et al. 2009, 2012a, b). Development of a conceptual model for the dynamics of fish schools based on these results can significantly advance comprehending and analyzing fish migration. This is the main motivation of this paper.

Based on the above research background, this paper presents a minimal mathematical model for upstream migration of fish schools in water current based on a simple game theory: an optimization theory. The model focuses on prolonged swimming behavior of fishes rather than burst ones, the latter being relevant for much shorter timescale. Game-theoretic models have extensively been utilized for ecological and biophysical modelling of animals (Kabalak et al. 2015; Mariani et al. 2016; Metz et al. 1992; Pereira and Martinez 2010; Riechert and Hammerstein 1983; Tanaka et al. 2011); however, application of such models to biophysics of fish migration is still rare. The variables to be optimized in the present model contain the swimming speed and school size that should be chosen by the fish school, so that the net cost of migration is minimized. The present model is an extended counterpart of the model for upstream migration of isolated individuals (Yoshioka and Shirai 2015; Yoshioka et al. 2015, 2016a). Assuming that certain simplifications reduce finding the optimizer to solving a self-consistency equation. Unfortunately, general exact expressions of its solution have not been found. To overcome this issue, this paper proposes an algorithm to numerically solve the self-consistency equation. An analytical estimate of the error between the true solutions and approximate solutions is also presented. Behavior of the optimizer is then mathematically and numerically studied to show its ecological and biophysical consequences. Consistency between the present model and the experimental results of swimming behavior of migratory fishes validates its performance.

The rest of this paper is organized as follows. Section 2 presents the mathematical model for upstream migration of isolated individuals. An extended mathematical model to deal with the migration of fish schools, which is the main focus of this paper, is also presented in this section. Section 3 performs mathematical and numerical analyses of the models. Section 4 concludes this paper and provides future perspectives of this research.

## Mathematical models

This section presents two mathematical models for migration of isolated individual fishes and fish schools, the latter being an extension of the former. In this paper, an

isolated fish is regarded as a fish school whose total number of individuals is exactly one. The models assume that the fishes are migrating toward upstream in a water current defined along the 1-D space  $\mathbb{R}$  with the flow velocity of  $V > 0$ . A fish school is thus conceptualized as a particle moving along  $\mathbb{R}$ . The swimming velocity of the fish school is denoted as  $u$ , which gives its ground velocity as  $V_g = u - V$ . The school is, therefore, migrating toward upstream when  $V_g > 0$ . The total number of individuals in the fish school is denoted as  $N$ , which is regarded as a continuous variable. The variable  $N$  is hereafter referred to as the size, which is considered as another control variable to be optimized. Although the continuous approximation of the school size  $N$ , which is a discrete variable in reality, maybe problematic, it is well known that discrete optimization problems are far more technically and mathematically difficult than the continuous ones. Therefore, to avoid the above-mentioned difficulty, this paper focuses on the analysis with the school size  $N$  as a continuous variable. This approximation becomes more accurate as  $N$  increases (Niwa 2003). Although the conventional definition of the fish school (Partridge and Pitcher 1980; Partridge 1982) applies to  $N \geq 3$ , this paper assumes  $N > 0$  for the sake of simplicity of analysis. It should be noted that biologically relevant solutions should satisfy  $N \geq 1$ . The variable  $u$  (the couple of variables  $(u, N)$ ) is optimized in the model for isolated individual (fish school). We assume  $u > V$ , since the focus is upstream migration.

It should be noted that water current along a real open channel such as a river is not spatially homogenous. Such a situation is more realistic than that considered in this paper. We mention that the present model can serve as the basis of analyzing fish migration in the real open channels if it is effectively incorporated in that for the recently developed mathematical models based on the dynamic programming principle (Yoshioka 2016; Yoshioka et al. 2016b). This research topic is beyond the scope of this paper and will, therefore, be addressed elsewhere.

As shown in what follows, the present model has a number of key non-dimensional parameters, as summarized in Table 1.

## Model for upstream migration of an isolated individual

### Ordinary differential equation

The model for upstream migration of isolated individuals starts from the ODE

$$\frac{dX_t}{dt} = V - u, \quad (1)$$

where  $t$  is the time and  $X_t$  is the 1-D position of the individual fish along the flow at the time  $t$ . The ODE (1) is equipped with the initial condition  $X_0 = 0$ , which is assumed without the loss of generality. The ODE (1) is then solved as

$$X_t = (V - u)t. \quad (2)$$

### Objective function

The range  $U$  of the variable  $u$  is denoted as  $U = [0, +\infty)$ . Under this setting, it is possible to identify a swimming velocity as a swimming speed because of the non-negativity of the former. Assuming positive rheotaxis of the fish (Hinch et al. 2005; Keefer and Caudill 2014), the objective function  $\phi(u)$  to be minimized through its migration process is formulated as

$$\phi(u) = \int_0^\tau f(u) dt, \quad (3)$$

where  $\tau$  is the time at which  $X_\tau = L$ , and thus,  $\tau = L(u - V)^{-1}$ . The objective function  $\phi$  measures the total physiological energy consumed during the migration process. The cost function  $f$  is assumed to be given by the power law-type function:

$$f(u) = \frac{1}{n+1} u^{n+1}, \quad (4)$$

with a parameter  $n \geq 1$ . The cost function  $f$  in (4) shows that the fish is more high speed-averse for larger  $n$ , because it more rapidly grows for larger  $n$ . The cost function  $f$  in (4) is convex and increasing with respect to  $u$ , which is in

**Table 1** Summary of the key non-dimensional parameters

Parameter	Range or relationship	Meaning
$n$	$O(10^0)$ (Yoshioka et al. 2016a)	Growth rate of the hydrodynamic cost
$m$	$O(10^{-1})$ (Mayer 2010)	Discount rate of the hydrodynamic cost
$k$	Larger than or equal to $O(10^{-1})$	Growth rate of the non-hydrodynamic cost
$y$	$y = \frac{k(n+1)}{m+k} > 1$	Non-linearity of the self-consistency equation
$z$	$z = \frac{m}{kn-m} \tilde{z}$ , where $\tilde{z} = \left[ \frac{m}{bk(n+1)} \left( \frac{y}{y-1} V \right) \right]^{\frac{k}{m+k}}$	Inverse of the power function of the flow speed $V$

good accordance with the conventional experimental results on swimming behavior of fishes (Brodersen et al. 2008; Cucco et al. 2012; Mori et al. 2015; Roche et al. 2013; Svendsen et al. 2010; Yoshioka et al. 2016a). The objective function is rewritten with (2) as

$$\phi(u) = \frac{L}{n+1} \frac{u^{n+1}}{u-V}. \quad (5)$$

Assuming that the migration process is temporally homogeneous, we can simply set  $L = 1$  without the loss of generality.

### Optimization problem

According to the classical optimization theory (Bonnans et al. 2006), the optimal swimming speed  $u^*$  that minimizes the objective function has to solve the equation derived from the first-order condition of optimality:

$$f'(u^*)(u^* - V) = f(u^*). \quad (6)$$

This Eq. (6) admits two solutions; one of them is  $u^* = 0$  and the other is

$$u^* = \frac{n+1}{n}V > V, \quad (7)$$

the latter being inferred as a biophysically relevant optimal swimming speed to represent upstream migration. Actually, it is straightforward to check that the candidate (7) minimizes  $\phi$ .

## Model for upstream migration of a fish school

### Ordinary differential equation

This section presents a mathematical model for upstream migration of a fish school. This paper assumes that longitudinal movement of the fish school is also described by the ODE (1) where the variable  $u$  serves as the representative swimming velocity of the school.

### Objective function

The value function for upstream migration of a fish school is different from that of an isolated individual due to the appearance of an additional control variable and coefficients. Assume that all the individuals in the school share an ideal objective function  $\phi$ , which is derived with a game-theoretic argument as explained below. The cost of swimming, namely, the hydrodynamic cost during the time interval  $[0, \tau]$  is

$$\phi_1(u, N) = \int_0^\tau \frac{f(u)}{\alpha(N)} dt = \frac{L}{n+1} \frac{u^{n+1}}{(u-V)\alpha(N)}, \quad (8)$$

where the coefficient  $\alpha \geq 1$  represents the discount of the hydrodynamic cost, which is motivated by the theoretically and experimentally validated fact that increasing the size  $N$  can effectively reduce the hydrodynamic cost per individual (Marras et al. 2015; Mayer 2010). Using a conceptual model with probabilistic consideration, Mayer (2010) derived that the discount of the energy for each individual is proportional to  $N^{-\frac{1}{3}}$ , which leads to

$$\alpha(N) = N^m, \quad (9)$$

with  $m = \frac{1}{3}$  in the present model.

The conventional research suggests that schooling has many aspects of benefits, such as improvements of navigational performance (Berdahl et al. 2014; Torney et al. 2015), hearing perception (Larsson 2009, 2012), and foraging efficiency (Di-Poi et al. 2014; Wang et al. 2016). These benefits are modelled in a lumped manner as

$$\phi_2(u, N) = - \int_0^\tau adt = \phi(u) = - \frac{La}{u-V}, \quad (10)$$

using a positive constant  $a$ . It seems to be reasonable to formulate an objective function  $\phi$  by summing up  $\phi_1$  and  $\phi_2$  as  $\phi = \phi_1 + \phi_2$ . However, this formulation leads to the trivial optimizer  $N = +\infty$ , which is not reasonable from a biological viewpoint. We, therefore, conjecture that this  $\phi$  lacks the fact that schooling is not always definitely beneficial. Schooling would negatively affect collective performances of fishes, such as passage efficiency (Lemasson et al. 2014) and information transmission among individuals (Castellano et al. 2009; Shang and Bouffanais 2014). Other disadvantages of forming a school such as competitions among the individuals in the school would also exist. In addition, various environmental disturbances would also affect the fish migration. We thus assume that the net non-hydrodynamic cost of forming a school  $\phi_3$  is formulated as

$$\begin{aligned} \phi_3(u, N, \eta) &= \int_0^\tau \left( \eta N^q - \frac{1}{c(p+1)} \eta^{p+1} \right) dt \\ &= \frac{L}{u-V} \left( \eta N^q - \frac{1}{c(p+1)} \eta^{p+1} \right), \end{aligned} \quad (11)$$

where  $p > 0$ ,  $q > 0$ , and  $c > 0$  are parameters, and  $\eta \geq 0$  is the intensity of the negative effect of forming the school. The first term of (11) represents the cost of forming a school due to the above-mentioned negative influencing factors that increase as  $N$  increases, while the second term represents the mitigation effect by forming a school.

The objective function  $\phi$  for the fish school is consequently set as

$$\begin{aligned} \phi &= \phi_1 + \phi_2 + \phi_3 \\ &= \frac{L}{u-V} \left( \frac{u^{n+1}}{(n+1)N^m} - a + \eta N^q - \frac{1}{c(p+1)} \eta^{p+1} \right). \end{aligned} \quad (12)$$

The objective function is minimized by the fish school itself by choosing appropriate  $(u, N)$ , while nature maximizes it by choosing  $\eta$ . Since  $L$  can be set as 1 without the loss of generality, the optimization problem reduces to the optimizer  $(u, N, \eta) = (u^*, N^*, \eta^*)$  that gives

$$\Phi = \inf_{u,N} \sup_{\eta} \phi(u, N, \eta) = \phi(u^*, N^*, \eta^*). \quad (13)$$

The optimization problem can be seen as a game with two non-cooperative players: the fish school and nature. Straightforward calculation shows

$$\eta^*(N) = \eta^* = (cN^q)^{\frac{1}{p}}, \quad (14)$$

and

$$\begin{aligned} \Phi &= \sup_{u,N} \phi(u, N, \eta^*) \\ &= \sup_{u,N} \frac{1}{u - V} \left( \frac{u^{n+1}}{(n+1)N^m} - a + \frac{p}{p+1} c^{\frac{q}{p}} N^{\frac{q+1}{p}} \right). \end{aligned} \quad (15)$$

Assuming mathematical consistency between the model of isolated individuals and that of fish schools, setting  $N = 1$  with the objective function  $\phi$  in (12) should reduce to that in (5). This leads to the constraint of parameters

$$a = \frac{p}{p+1} c^{\frac{q}{p}} = b, \quad (16)$$

with a positive parameter  $b$ . Equation (15) is then rewritten with the positive parameter  $k = 1 + \frac{q}{p}$  as

$$\begin{aligned} \Phi &= \sup_{u,N} \phi(u, N, \eta^*) \\ &= \sup_{u,N} \frac{1}{u - V} \left( \frac{u^{n+1}}{(n+1)N^m} + b(N^k - 1) \right). \end{aligned} \quad (17)$$

Relevant values of the parameters  $n, m$ , and  $k$  can be to a certain extent inferred from theoretical and numerical analysis. On the parameter  $n$ , Yoshioka et al. (2016a) showed  $O(10^0)$  for a variety of migratory fish species. Identification of the order of the parameter  $k$  is more difficult than that for the parameters  $n$  and  $m$  because of its lumped nature. In this paper, it is assumed that the parameters  $n, m$ , and  $k$  satisfy

$$kn - m > 0, \quad (18)$$

which turns out to be a necessary condition for existence of an optimal  $u^*$  with  $u^* > V$ . A biophysical interpretation of the condition (18) is that fishes create fish schools if they have to save the hydrodynamic cost of migration, which occurs if  $k$  is large or  $m$  is small. This is qualitatively consistent with the model of Stöcker and Weihs (2001). No biophysically relevant optimizer that represents upstream migration is obtained under this condition. The assumption shows that, provided that  $m$  is around  $O(10^{-1})$  even if it is

not  $\frac{1}{3}$  (Mayer 2010), the order of the parameter  $k$  can be inferred to be larger than or equal to  $O(10^{-1})$ .

### Optimization problem

By the static optimization problem, as in the case for the model of isolated individuals, the optimizers  $u^*$  and  $N^*$  have to solve the equations derived from the first-order necessary condition of optimality:

$$(u^*)^n (u^* - V) = \frac{(u^*)^{n+1}}{(n+1)(N^*)^m} + b((N^*)^{m+k} - 1), \quad (19)$$

and

$$\frac{m(u^*)^{n+1}}{(n+1)(N^*)^{m+1}} = bk(N^*)^{k-1}. \quad (20)$$

With a technical calculation, the equations can be reduced to a self-consistency equation as follows. First, substituting (20) into (19) yields

$$(u^*)^n (u^* - V) = \frac{1}{n+1} (u^*)^{n+1} \left[ 1 + \frac{m}{k} \{1 - (N^*)^{-k}\} \right]. \quad (21)$$

Assuming that  $u^* > 0$ , (21) reduces to

$$u^* = \frac{k(n+1)}{kn - m + m(N^*)^{-k}} V. \quad (22)$$

Introduce the changes of variables

$$\begin{aligned} y &= \frac{k(n+1)}{m+k} > 1, \quad z = \frac{m}{kn - m} \frac{1}{\tilde{z}}, \quad \text{and} \\ \tilde{z} &= \left[ \frac{m}{bk(n+1)} \left( \frac{y}{y-1} V \right) \right]^{\frac{1}{m+k}}. \end{aligned} \quad (23)$$

The optimizers  $u^*$  and  $N^*$  are then expressed as

$$u^* = \frac{y}{y-1} V w^* \quad \text{and} \quad N^* = (\tilde{z})^{\frac{1}{k}} (w^*)^{\frac{y}{k}}, \quad (24)$$

respectively, with an auxiliary parameter  $w^*$ . The positivity of  $u^*$  is guaranteed by (18), since  $y > 1$ . The right side of (22) is further reduced to

$$u^* = \frac{k(n+1)}{kn - m} V \frac{1}{1 + \frac{m}{kn-m} (N^*)^{-k}} = \frac{y}{y-1} V \frac{(w^*)^y}{(w^*)^y + z}. \quad (25)$$

By (25), the equation to be solved for  $w^*$  is consequently found as

$$w^* = F(w^*) = 1 - \frac{z}{(w^*)^y + z}. \quad (26)$$

Finding the optimizer  $(u^*, N^*)$  is thus ultimately reduced to solving the self-consistency equation (26). A relevant  $w^*$  for upstream fish migration should give

$$u^* > V \quad \text{and} \quad N^* \geq 1. \quad (27)$$

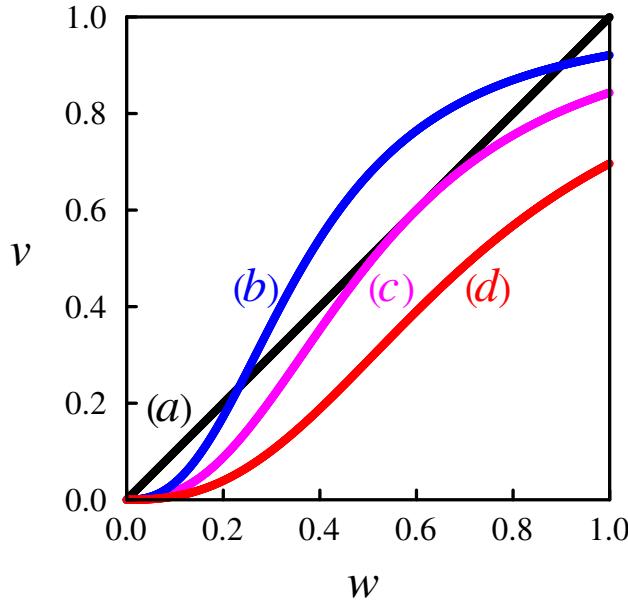
Introduce the parameter

$$\bar{z} = y^{-y}(y-1)^{y-1}, \quad (28)$$

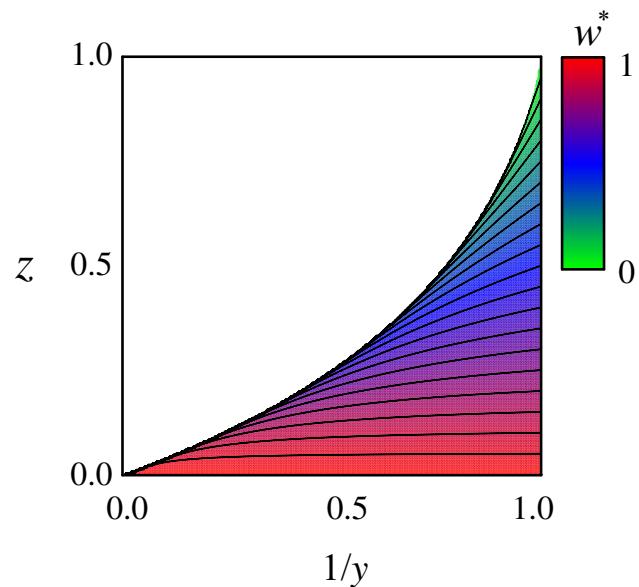
for the sake of brevity of descriptions. Straightforward calculation shows that the number of the intersections of the line  $v = w$  and the curve  $v = F(w)$  in the first quadrant of  $v - w$  space is zero ( $z > \bar{z}$ ), one ( $\bar{z} = z$ ), and two ( $0 < z < \bar{z}$ ). Figure 1 plots the graphs of  $v = w$  and  $v = F(w)$  for  $z > \bar{z}$ ,  $\bar{z} = z$ , and  $0 < z < \bar{z}$  in the square  $[0, 1] \times [0, 1]$ , which graphically validates the above-mentioned statement. For  $\bar{z} = z$ , in particular,  $v = w$  is the tangent line of the curve  $v = F(w)$  at the point  $(\bar{w}, \bar{w})$ , where  $\bar{w} = \frac{y-1}{y}$ . The above-mentioned geometrical information shows that there is no positive solution  $w^*$  for large  $z$ , such that  $z > \bar{z}$ . In addition, for  $\bar{z} = z$ ,  $u^*$  is determined from (24) as  $u^* = V$ , which does not comply with (27). The analysis in what follows, therefore, assumes  $0 < z < \bar{z}$  where the two positive solutions  $\bar{w}_1$  and  $\bar{w}_2$ , such that

$$0 < \bar{w}_1 < \bar{w} < \bar{w}_2 < 1, \quad (29)$$

solve (26) (Appendix). It turns out that the larger solution  $w = \bar{w}_2$  is the biologically relevant solution to give  $u^* > V$ , which is denoted by  $w^*$ . The condition  $0 < z < \bar{z}$  can be expressed as  $0 < b < CV^{n+1}$  with a positive constant  $C$



**Fig. 1** Plots of the graphs of **a** the line  $v = w$  and the curves  $v = F(w)$  for **b**  $z > \bar{z}$ , **c**  $\bar{z} = z$ , and **d**  $0 < z < \bar{z}$  in the unit square  $[0, 1] \times [0, 1]$ . This figure graphically shows the geometrical relationships between the line  $v = w$  and the curve  $v = F(w)$ . They have zero, one (multiplicity one), and two positive solutions for  $z > \bar{z}$ ,  $\bar{z} = z$ , and  $0 < z < \bar{z}$ , respectively. For  $\bar{z} = z$  in particular,  $v = w$  is a tangent line of  $v = F(w)$  at the point  $(\bar{z}, \bar{z})$



**Fig. 2** 2-D contour diagram of  $w = w^*$  as a bi-variate function of  $z$  and  $y^{-1}$  for  $0 < z < \bar{z}$  and  $0 < y^{-1} < 1$ . The white region represents the area where  $w^*$  does not exist. The curve that separates the white and colored regions in the figure corresponds to the curve  $z$  in (32) (color figure online)

depending on neither  $b$  nor  $V$ , meaning that the weight  $b$  for the cost of schooling should not be too large to form a school.

Figure 2 shows a 2-D contour diagram of  $w^*$  as a bi-variate function of  $z$  and  $y^{-1}$  for  $0 < z < \bar{z}$  and  $0 < y^{-1} < 1$ . It should be noted that not every  $w^*$  plotted in Fig. 2 complies with (27). This is because  $k$  is expressed with (23) as

$$k = \frac{n+1-y}{m} > 0, \quad (30)$$

meaning that a relevant  $y$  should satisfy

$$\frac{1}{n+1} < y^{-1} < 1. \quad (31)$$

In Fig. 2, the boundary curve that separates the colored and white regions represents

$$z(q) = q(1-q)^{\frac{1}{q}-1} (= y^{-y}(y-1)^{y-1}), \quad (32)$$

with  $q = y^{-1}$ , which is increasing and convex with respect to  $q$ .

## Analysis of the optimizers

Qualitative and quantitative analyses of the optimizers  $u^*$  and  $N^*$  are performed to comprehend their dependence on the model parameters. The analysis is also intended to find appropriate ranges of the parameters to give realistic  $u^*$  and  $N^*$ .

## Qualitative analysis

Qualitative analysis of the optimal controls  $u^*$  and  $N^*$  is first performed before the quantitative analysis in the next sub-section. The analysis here focuses on the signs of partial differentials of the optimal controls with respect to the model parameters, so that their biophysical and ecological consequences are clearly indicated.

**Proposition 1** *The solution  $w = w^*$  to the self-consistency Eq. (26) is decreasing with respect to  $z$  and  $y$ , namely,  $\frac{\partial w^*}{\partial z} < 0$  and  $\frac{\partial w^*}{\partial y} < 0$ .*

*Proof of Proposition 1* Partially differentiating both sides of (26) with respect to  $z$  leads to

$$\begin{aligned}\frac{\partial w^*}{\partial z} &= \frac{y(w^*)^{y-1} \frac{\partial w^*}{\partial z}}{(w^*)^y + z} - (w^*)^y \frac{y(w^*)^{y-1} \frac{\partial w^*}{\partial z} + 1}{[(w^*)^y + z]^2} \\ &= F'(w^*) \frac{\partial w^*}{\partial z} - \frac{1}{[(w^*)^y + z]^2},\end{aligned}\quad (33)$$

which is rewritten as

$$\frac{\partial w^*}{\partial z} = -\frac{1}{[(w^*)^y + z]^2 [1 - F'(w^*)]} < 0,\quad (34)$$

since  $F'(w) < 0$  at  $w = w^*$  by a geometrical consideration. Similarly, using the formula

$$\frac{\partial}{\partial y} \ln[(w^*)^y] = \ln(w^*) + y(w^*)^{-1} \frac{\partial w^*}{\partial y},\quad (35)$$

(26) leads to

$$\begin{aligned}\frac{\partial w^*}{\partial y} &= \frac{z}{[(w^*)^y + z]^2} \frac{\partial (w^*)^y}{\partial y} \\ &= \frac{z(w^*)^y}{[(w^*)^y + z]^2} \left[ \ln(w^*) + y(w^*)^{-1} \frac{\partial w^*}{\partial y} \right].\end{aligned}\quad (36)$$

Therefore, (36) shows

$$\begin{aligned}\frac{\partial w^*}{\partial y} &= \frac{z(w^*)^y \ln(w^*)}{[(w^*)^y + z]^2 [1 - F'(w^*)]} \\ &< 0,\end{aligned}\quad (37)$$

since  $\ln(w^*) < 0$ .  $\square$

**Proposition 1** has biophysical meanings. By (24), the partial derivatives of  $u^*$  and  $N^*$  with respect to  $V$  satisfy

$$\frac{\partial u^*}{\partial V} > 0 \quad \text{and} \quad \frac{\partial N^*}{\partial V} > 0,\quad (38)$$

since  $\frac{\partial z}{\partial V} < 0$ . In addition, the partial derivatives of  $u^*$  and  $N^*$  with respect to  $b$  satisfy

$$\frac{\partial u^*}{\partial b} < 0 \quad \text{and} \quad \frac{\partial N^*}{\partial b} < 0,\quad (39)$$

since  $\frac{\partial z}{\partial b} < 0$ . The first inequality in (38) shows positive rheotaxis of the fish school, which has been reported to be satisfied in experimental fish migration for a series of  $N$  against *Plecoglossus altivelis* (Ayu) (Onitsuka et al. 2012a). The second inequality in (38) shows that increasing the flow speed potentially increases the optimal number of individuals in a fish school, so that the physiological energy consumed by each individual is effectively reduced. This statement has also been experimentally validated against *P. altivelis* (Onitsuka et al. 2012a). The two inequalities in (39) show that the present mathematical model predicts that increasing the weight of the non-hydrodynamic forces a fish school to decide smaller size and slower swimming speed to be optimal.

Partial differentials of  $y$  with respect to model parameters further highlight qualitative properties of the optimizers  $u^*$  and  $N^*$  associated with the present mathematical model. Rather than dealing with the parameters  $m$  and  $k$  separately, it is efficient to consider the hybrid parameter  $mk^{-1}$  that quantifies the ratio of the discount rate of the energetic cost and the increasing rate of the schooling cost. The partial derivatives of  $y$  with respect to  $n$  and  $mk^{-1}$  satisfy

$$\frac{\partial y}{\partial n} > 0 \quad \text{and} \quad \frac{\partial y}{\partial (mk^{-1})} < 0,\quad (40)$$

respectively. The two inequalities in (40) lead to the inequalities

$$\frac{\partial u^*}{\partial n} < 0 \quad \text{and} \quad \frac{\partial N^*}{\partial n} < 0.\quad (41)$$

Equation (40) then leads to

$$\frac{\partial u^*}{\partial (mk^{-1})} > 0 \quad \text{and} \quad \frac{\partial N^*}{\partial (mk^{-1})} > 0.\quad (42)$$

The first inequality in (41) shows that a fish school with a more speed-averse energetic cost (the cost function with larger  $n$ ) chooses a smaller swimming speed to be optimal, which associates a smaller school size as indicated in the second inequality. The first inequality in (42) indicates that a higher swimming speed is decided to be optimal for relatively higher efficiency of the physiological energy discount by forming a school. The second inequality in (42) shows that a larger school size is decided to be optimal as the decreasing rate of the energetic cost becomes higher than the increasing rate of the schooling cost.

Qualitative similarity between the model for isolated individuals and that for fish schools is also discussed in this paper. Straightforward calculation shows that the optimal control  $u^*$  for the model of isolated individuals with the analytical formula (7) is decreasing with respect to  $n$ . By (41), the two models, therefore, predict  $\frac{\partial u^*}{\partial n} < 0$ . In addition,

by (7) and (38), they predict  $\frac{\partial u^*}{\partial V} > 0$ . The latter statement for isolated individuals is in accordance with the experimental results (Onitsuka et al. 2012b). Actually, it is possible to derive a sharper estimate of the partial derivative  $\frac{\partial u^*}{\partial V}$  as shown in the proposition below.

**Proposition 2** *The model for fish school leads to*

$$\frac{\partial u^*}{\partial V} > 1. \quad (43)$$

*Proof of Proposition 2* By (7) and (38), the inequality

$$\frac{\partial w^*}{\partial V} = \frac{\partial}{\partial V} \left( \frac{u^* - V}{V} \right) = \frac{1}{V} \left[ \frac{\partial u^*}{\partial V} - \frac{u^*}{V} \right] > 0, \quad (44)$$

namely,

$$\frac{\partial u^*}{\partial V} > \frac{u^*}{V}, \quad (45)$$

follows. Assuming that  $u^* > V$  derives (43)  $\square$

**Proposition 2** shows that the optimal swimming speed  $u^*$  increases as the flow speed  $V$  does and the rate of its increase is larger than one. The inequality (43) theoretically leads to the statement that the difference  $u^* - V$  is increasing with respect to  $V$ , which has been validated for upstream migration of fish schools in experimental flumes at least for not too large  $V$  (Onitsuka et al. 2012b). The inequality also applies to the model for upstream migration of isolated individuals.

## Quantitative analysis

Quantitative behavior of the optimizers  $u^*$  and  $N^*$  has been performed in the previous sub-section whose results are validated in this section through numerical analysis. Their behavior is also quantified here and realistic ranges of the model parameters are discussed.

To carry out the quantitative analysis, the value of the biologically relevant solution  $w = w^*$  to Eq. (26) has to be accurately approximated; however, it has empirically been found that this is not possible for generic  $y$ . To overcome this difficulty, this paper applies a fixed-point iteration algorithm to generate an approximate sequence of the solution  $w = w^*$ . The algorithm is formulated as

$$w_{r+1} = F(w_r) \quad \text{for } r = 0, 1, 2, \dots, \quad (46)$$

subject to the initial guess  $w_0 = 1$ . The error between the approximate solution  $w_r$  and the true solution  $w^*$  is analytically estimated as

$$0 < w_r - w^* < \theta^{(y-1)r} \quad \text{for } r = 0, 1, 2, \dots, \quad (47)$$

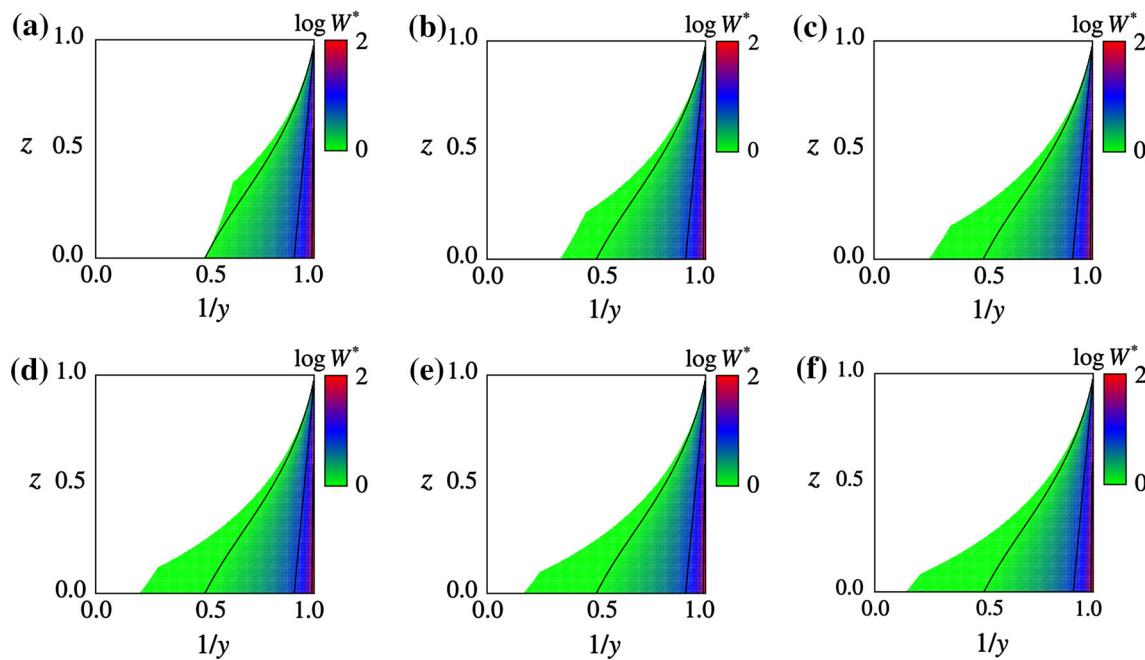
with

$$0 < \theta = \frac{yz}{w^{y-1}} < 1, \quad (48)$$

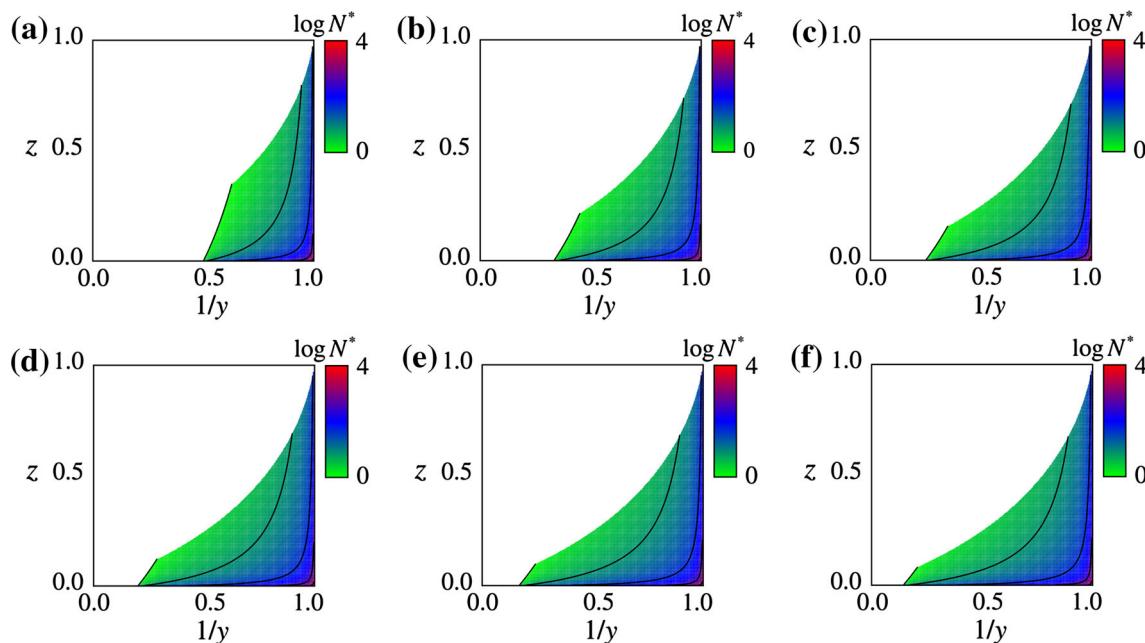
showing that this numerical algorithm can generate a decreasing sequence of approximated solutions that rigorously converges to the true solution. It is also shown that a similar algorithm with an initial guess  $w_0 = \bar{w}$  can also generate a convergent sequence with the limit  $w^*$ , which on the other hand is monotonically increasing. For each couple of the fixe parameter values of  $y$  and  $z$ , the iteration algorithm is stopped at  $r \geq 1$ , such that  $|w_{r+1} - w_r| < \varepsilon = 10^{-10}$ . Decreasing the value of the threshold  $\varepsilon$ , several orders of the magnitude do not affect the computational results presented below. Details of the iterative method for approximating solutions are described in Appendix.

The non-dimensional quantity  $W^* = \frac{u^* - V}{V}$  is introduced here with biophysically more clear meaning (non-dimensionalized ground speed) than the quantity  $w^*$  that has been employed for the sake of mathematical analysis. Figure 3a–f shows the contour diagrams of  $W^* = \frac{u^* - V}{V}$  complying with the conditions (27) for the integers  $1 \leq n \leq 6$ . Figure 4a–f shows the contour diagrams of  $N^*$  complying with the conditions (27) for the integers  $1 \leq n \leq 6$ . The white region in each panel of Figs. 3 and 4 is the area where  $W^*$  is smaller than 0 or  $N^*$  is smaller than 1. Such optimal controls are not biologically relevant, since at least  $N^*$  should be larger than or equal to 1 and an upstream migration should correspond to a positive  $W^*$ . The computational results presented in Figs. 3 and 4 are consistent with the mathematical analytical results presented in the previous sub-section:  $W^*$  and  $N^*$  are decreasing with respect to  $z$  in (23), namely, increasing with respect to  $V$ .

The flow speed  $V$  in a river under calm conditions is typically from  $O(10^{-1})$  m/s to  $O(10^0)$  m/s, and would be at most  $O(10^1)$  m/s. In addition, the maximum sustained swimming speed of fish living in rivers is at most  $O(10^0)$  m/s (Onitsuka et al. 2009). Therefore, the biologically relevant order of the non-dimensional quantity  $W^*$  can be at most  $O(10^1)$ , which roughly corresponds to green-to-blue area in each panel of Fig. 3. It would not be unrealistic to assume that the range of  $N^*$  includes the range  $1 < N^* < 100$ . Figure 5a–f shows the area with  $0 < W^* < 100$  and  $1 < N^* < 100$  for the integers  $1 \leq n \leq 6$ . These figures show that increasing  $n$  yields wider area satisfying the above-mentioned ranges of  $0 < W^* < 100$  and  $1 < N^* < 100$ . Figure 5 indicates that the lower right end of the area complying with these conditions is more insensitive to the lower left-end, which has been checked to be true for  $n$  up to 10.



**Fig. 3** Contour diagrams of  $W^* = \frac{u^* - V}{V}$  for  $0 < z < \bar{z}$  and  $0 < y^{-1} < 1$  with **a**  $n = 1$ , **b**  $n = 2$ , **c**  $n = 3$ , **d**  $n = 4$ , **e**  $n = 5$ , and **f**  $n = 6$ . The *white region* represents the area where  $w^*$  does not exist as in Fig. 2 or  $W^* < 0$ , which does not verify necessary conditions for relevant solutions

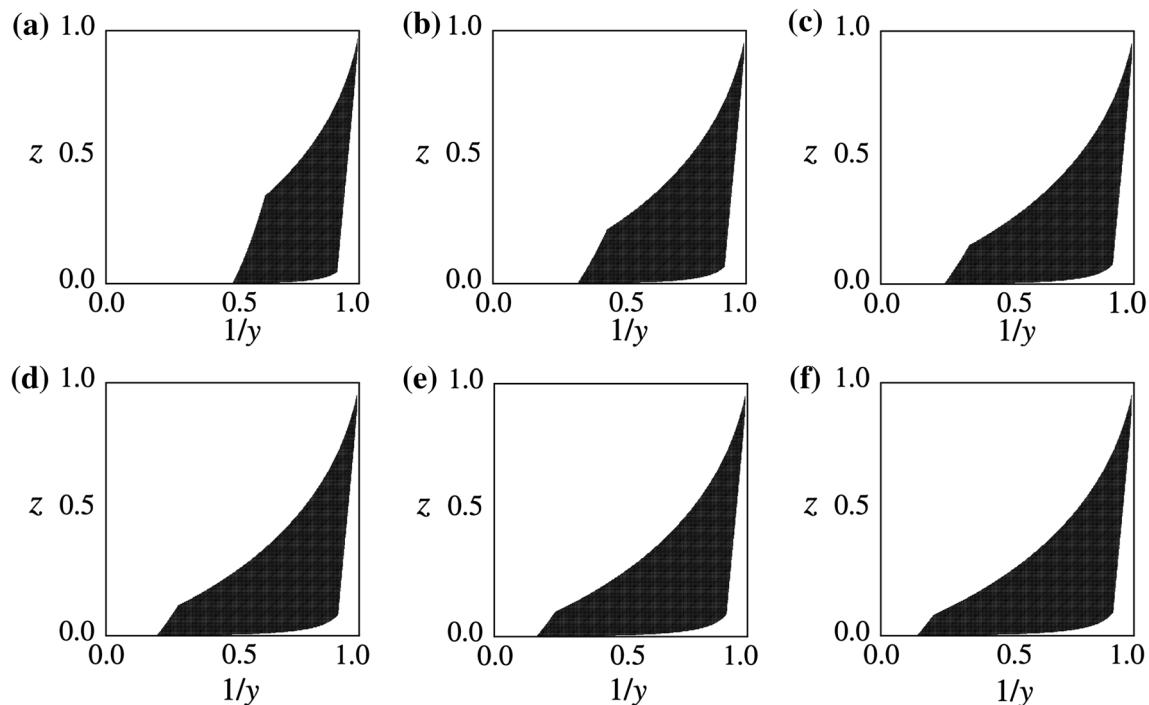


**Fig. 4** Contour diagrams of  $N^*$  for  $0 < z < \bar{z}$  and  $0 < y^{-1} < 1$  with **a**  $n = 1$ , **b**  $n = 2$ , **c**  $n = 3$ , **d**  $n = 4$ , **e**  $n = 5$ , and **f**  $n = 6$ . The *white region* represents the area where  $w^*$  does not exist as in Fig. 2 or  $N^* < 1$ , which does not verify necessary conditions for relevant solutions

## Conclusions

A minimal mathematical model for upstream migration of fish schools in 1-D environment based on a game-theoretic formulation was presented and behavior of the associated optimizers was analyzed both mathematically and numerically. The optimization problem was effectively reduced

to solving a self-consistency equation that was not explicitly solved, but its qualitative solution behavior could be analyzed with a course of elementary calculation. Dependence of the optimal swimming speed  $u^*$  and the optimal size  $N^*$  of fish schools on the model parameters was theoretically analyzed for comprehending their qualitative behavior. The analytical results obtained in



**Fig. 5** Diagrams of the area complying with the conditions  $0 < W^* < 100$  and  $1 < N^* < 100$  with **a**  $n = 1$ , **b**  $n = 2$ , **c**  $n = 3$ , **d**  $n = 4$ , **e**  $n = 5$ , and **f**  $n = 6$ , which are considered to be biologically

relevant in this paper. The *white region* represents the area where these conditions are not satisfied

“Qualitative analysis” showed that the dependence of the optimal swimming speed  $u^*$  and the school size  $N^*$  derived from the present mathematical model on the flow speed  $V$  qualitatively agrees well with the experimental results (Onitsuka et al. 2012a, b). This paper thus provided a theoretical explanation of the experimental results from a game-theoretic viewpoint, which is a first attempt to the author’s knowledge. Numerical analysis with the help of a mathematically rigorous technique of fixed-point iteration generated a monotonically increasing sequence of approximate solutions to the self-consistency equation. The computed solutions to the self-consistency equation with the appropriate ranges of the model parameters revealed quantitative behavior of the optimal controls, which validated the theoretical results obtained from the qualitative analysis. The ranges of the realistic model parameter values were estimated from the computational results. Currently, we are planning to perform artificially hatching experiments of *P. altivelis* in a river with local fishery cooperatives for the identification of the model parameters involved in the objective function.

This paper could quantify dependence of the optimal controls  $u^*$  and  $N^*$  on the model parameters under simplified conditions, so that the most part of the analysis can be performed exactly. Theoretically, it is possible to choose more complex parameterization of the coefficients to more appropriately model migration dynamics of fish schools

when necessary. However, analyzing such an extended model would require the use of a sophisticated numerical technique and considering an unnecessarily complicated model would not be beneficial from both theoretical and practical viewpoints. The present mathematical model can be a minimal model for migration of fish schools where the flow of water and both advantages and disadvantages are taken into account. Its practical extension includes considering unsteady and inhomogeneous flow field in the ODE for longitudinal movements of fish schools. The analytical results presented in this paper can be to some extent valid for analyzing behavior of the optimal controls when the rate of change of the flow speed  $V$  is not very large, so that it does not exceed the maximum swimming speed of the individual fishes. Future research will use the present mathematical models for analyzing upstream fish migration in existing river systems in Japan as their real applications with the help of numerical simulation techniques. Applicability of the present mathematical modelling framework to migration of other animals, such as migratory birds (McLaren et al. 2014; Vansteelant et al. 2017), will also be examined in future.

**Acknowledgements** The River Fund No. 285311020 in charges of The River Foundation, JSPS Research Grant No. 15H06417 and No. 17K15345, and WEC Applied Ecology Research Grant No. 2016-02 support this research. The author thanks to the reviewer for providing valuable comments and suggestions.

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## Appendix: Numerical algorithms

This supplementary material presents monotone iteration algorithms for approximating the largest positive solution to the self-consistency equation

$$w = F(w) = \frac{w^y}{w^y + z}, \quad (49)$$

with the parameters  $y$  and  $z$ , such that  $y > 1$  and  $0 < z < \frac{(y-1)^{y-1}}{y^y}$ . Under the stated conditions, the Eq. (49) admits two positive solutions  $\bar{w}_1$  and  $\bar{w}_2$ , such that

$$0 < \bar{w}_1 < \bar{w} < \bar{w}_2 \equiv w^* < 1, \quad (50)$$

with  $\bar{w} = \frac{y-1}{y}$ . Straightforward calculation shows

$$\bar{w} - F(\bar{w}) = \frac{1}{\bar{w}^y + z} \frac{y-1}{y} \left( \frac{(y-1)^{y-1}}{y^y} - z \right) > 0, \quad (51)$$

$$F'(w) = \frac{yzw^{y-1}}{(w^y + z)^2} > 0 \quad \text{for } w > 0, \quad (52)$$

and

$$F''(w) = \frac{y(y+1)zw^{y-2}}{(w^y + z)^3} \left( \frac{y-1}{y+1} - w^y \right) \quad \text{for } w > \bar{w}. \quad (53)$$

In addition, it is also shown that

$$w < F(w) \quad \text{for } \bar{w}_1 < w < \bar{w}_2. \quad (54)$$

Combining (49) and (52) yields the estimate

$$0 < F'(w^*) = \frac{yz}{(w^*)^{y+1}} \frac{(w^*)^y}{(w^*)^y + z} \frac{(w^*)^y}{(w^*)^y + z} = \frac{yz}{(w^*)^{y-1}}, \quad (55)$$

which reduces to

$$\begin{aligned} 0 &< F'(w^*) \\ &< \frac{yz}{\bar{w}^{y-1}} \\ &< \frac{y}{\bar{w}^{y-1}} \frac{(y-1)^{y-1}}{y^y} \\ &= 1. \end{aligned} \quad (56)$$

Therefore, (56) shows

$$0 < F'(w^*) < \frac{yz}{\bar{w}^{y-1}} \equiv \theta < 1. \quad (57)$$

Combining (53) and (55) then yields

$$0 < F'(w) < \theta \quad \text{for } w^* > w. \quad (58)$$

The present algorithm is thus a fixed-point type with a contraction property whose convergence is guaranteed under the conditions assumed in this paper (Atkinson and Han 2005, Chapter 5).

Two iteration algorithms for finding the solution  $w = w^*$ , which is a biophysically relevant solution, are presented in what follows. The first (second) algorithm generates a monotonically decreasing (increasing) sequence of approximated solutions.

The first algorithm is presented as

(First algorithm)

$$w_0 = 1 \quad \text{and} \quad w_{r+1} = F(w_r) \quad \text{for } r \geq 0. \quad (59)$$

On the other hand, the second algorithm is presented as

(Second algorithm)

$$w_0 = \bar{w} \quad \text{and} \quad w_{r+1} = F(w_r) \quad \text{for } r \geq 0. \quad (60)$$

The only apparent difference between the two algorithms is the initial guess  $w_0$ . The following theorems hold for these algorithms.

**Theorem 1** *The sequence  $w_r$  generated by the first algorithm satisfies*

$$w^* < \dots < w_r < \dots < w_1 < w_0 = 1, \quad (61)$$

*and converges to  $w^*$ .*

**Theorem 2** *The sequence  $w_r$  generated by the second algorithm satisfies*

$$0 < \bar{w} = w_0 < w_1 < \dots < w_r < \dots < w^*, \quad (62)$$

*and converges to  $w^*$ .*

*Proof of Theorem 1* By (51), the inequality

$$\begin{aligned} w_1 - w_0 &= F(w_0) - 1 \\ &= F(1) - 1 \\ &< 0 \end{aligned} \quad (63)$$

holds. The inequality

$$w_0 - w^* = 1 - w^* > 0 \quad (64)$$

is obvious. Assume

$$w^* < w_r < \dots < w_1 < w_0 = 1, \quad (65)$$

for a natural number  $l = r$ . Then, for  $l = r + 1$ , the inequality

$$\begin{aligned} w_{r+1} - w_r &= F(w_r) - w_r \\ &= F(w_r) - F(w_{r-1}) \\ &< 0 \end{aligned} \quad (66)$$

follows from (52) and (65). In addition, the inequality

$$\begin{aligned} w^* - w_{r+1} &= F(w^*) - w_{r+1} \\ &= F(w^*) - F(w_r) \\ &< 0 \end{aligned} \quad (67)$$

also follows from (52) and (65). Convergence of the sequence  $w_r$  follows from its monotonicity and boundedness. The limit of the sequence is unique and is clearly  $w^*$ . Proof of [Theorem 1](#) completes by the application of an inductive argument. [Theorem 2](#) can be proven in an essentially similar way.  $\square$

*Remark 3* It is possible to analytically derive a theoretical convergence estimate of the first algorithm. By (58), the sequence  $|w_r - w^*| = c_r$  satisfies

$$\begin{aligned} c_{r+1} &= |w_{r+1} - w^*| \\ &= |F(w_r) - F(w^*)| \quad \text{for } r \geq 0 \\ &\leq \theta^{y-1} |w_r - w^*| \\ &= \theta^{y-1} c_r, \end{aligned} \quad (68)$$

which leads to

$$c_r \leq \theta^{(y-1)r} c_0 < \theta^{(y-1)r} \quad \text{for } r \geq 0, \quad (69)$$

since  $c_0 = |1 - w^*| < 1$ . The convergence estimate which does not explicitly depend on is derived as follows:

$$c_r < \theta^{(y-1)r} \quad \text{for } r \geq 0. \quad (70)$$

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