Ecological Modelling 388 (2018) 80–87

Contents lists available at ScienceDirect

Ecological Modelling

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

Density-dependent population model of effective release policy for Ayu fish

Yuki Katsumata[a], Takashi Uehara[b], Hiromu Ito[c,d,e], Jin Yoshimura[f,g,h], Kei-ichi Tainaka[f], Genki Ichinose[f,*]

[a] Department of Computer Science, School of Computing, Tokyo Institute of Technology, Yokohama, Kanagawa, 226-8502, Japan
[b] Department of Preschool Education, Nagoya College, 48 Takeji, Sakae-cho, Toyoake, Aichi, 470-1193, Japan
[c] Department of General Systems Studies, University of Tokyo, Meguro, Tokyo, 153-8902, Japan
[d] Department of International Health, Institute of Tropical Medicine, Nagasaki University, Nagasaki, 852-8523, Japan
[e] Department of Environmental Sciences, Zoology, University of Basel, CH-4051, Basel, Switzerland
[f] Department of Mathematical and Systems Engineering and Graduate School of Science and Technology, Shizuoka University, Hamamatsu, Shizuoka, 432-8561, Japan
[g] Department of Environmental and Forest Biology, State University of New York College of Environmental Science and Forestry, Syracuse, NY, 13210, USA
[h] Marine Biosystems Research Center, Chiba University, Uchiura, Kamogawa, Chiba, 299-5502, Japan

ARTICLE INFO

Keywords:
Ayu *Plecoglossus altivelis*
Culture-based fisheries
Rate equation
Population dynamics
Territorial competition
Release policy

ABSTRACT

Ayu fish are actively released by many fishery cooperatives in Japan. These fish exhibit the density-dependent population dynamics within territorial competition. At low density, all fish can hold feeding territories. Once all territory sites are occupied, surplus fish become floaters. As the density further increases, all fish give up their own territories and then form a school. Territory holders are more valuable than floaters as a food source and a target of recreational fishing. Thus, the main purpose of the release of ayu is to increase the amount of territory holders. For these reasons, the release policy for ayu should take into account the influence of a change in density on the population dynamics. We develop a rate equation to describe the density-dependent population dynamics of ayu accompanied by the release of fingerlings. Our results indicate that the release of ayu demands unique policy different from other fish species. The release of ayu should be carried out so as not to break down territories due to the increase in density caused by released fingerlings. Specifically, the release policy that reduces the amount of fingerlings that are released at one time, and lengthens the time interval between each release, increases the catch of territory holders.

1. Introduction

Culture-based fisheries are important approaches to enhance fish stocks in waters that do not have enough natural supply to sustain an ecosystem, fisheries, and recreational fishing. In contrast to aquaculture, involving the cultivation of aquatic species within artificially controlled environments, culture-based fisheries control a part of the life history of certain species and release their seed or fry into open waters at the appropriate time (Honma, 1980). Thus, in culture-based fisheries, the released fingerlings propagate and flourish in a natural environment until they reach harvestable size (Liao, 1988; Thorpe, 1980). For this reason, it is important to design the release policy from ecological features in order to effectively and sustainably increase fish catches (ADCP, 1989). Here we consider the release policy for ayu fish (*Plecoglossus altivelis*, Osmeridae) which are an endemic migratory fish in Japan (Kawanabe, 1969; Miyadi, 1960; Takahashi and Azuma, 2006).

Ayu form algae-feeding territories midstream during a growing season (Iguchi, 1996; Kawanabe, 1957). In the early growing season, all fish can hold territories at low density. This feeding territory is formed in rapids where algae grow on rocks and stones of riverbeds (Biggs et al., 1998; Kawanabe, 1973). During the growing season, newcomers migrate from downstream and fish density increases day by day. Once all territory sites are occupied, surplus fish become non-territory holders (floaters) and stay in (deep) pools (Kawanabe et al., 1957). In contrast to rapids, algae cannot grow in pools because sufficient sunlight does not reach the riverbeds. Thus, floaters cannot sufficiently feed in pools. For this reason, floaters often intrude into others' territories to steal algae. Territory holders violently attack intruders in order to defend their own territories (Kawanabe, 1973; Mizuno and Kawanabe, 1957). As the density further increases, territory holders have to spend much more time defending territories, thus losing time to feed on algae. Eventually, all fish give up their own territories and then

* Corresponding author.
E-mail addresses: katsumata.y.ac@m.titech.ac.jp (Y. Katsumata), uehara@nagoyacollege.ac.jp (T. Uehara), cito@mail.ecc.u-tokyo.ac.jp (H. Ito), yoshimura.jin@shizuoka.ac.jp (J. Yoshimura), tainaka.keiichi@shizuoka.ac.jp (K. Tainaka), ichinose.genki@shizuoka.ac.jp (G. Ichinose).

https://doi.org/10.1016/j.ecolmodel.2018.09.021
Received 1 June 2018; Received in revised form 30 August 2018; Accepted 24 September 2018
Available online 08 October 2018

form a school (Iguchi et al., 2003; Katano et al., 2004). Conversely, territories are reformed from the school when the fish density decreases (Iguchi, 1996). Thus, ayu exhibit the density-dependent population dynamics within the territorial competition (Kawanabe, 1958; Tanaka et al., 2011).

In Japan, ayu are one of the most important fishery resources in inland fisheries and popular as a target of recreational fishing. In recent years, because wild ayu are decreasing remarkably due to the degradation of river environments and the division of rivers by dams, culture-based fisheries for ayu are actively carried out by many fishery cooperatives. It is important to note is that territory holders are more valuable as fish resources than floaters. Territory holders are more expensive as a food source because they are bigger on average than floaters due to rich algae (Kawanabe, 1957; Nakashima et al., 2009; Mori et al., 2008). Furthermore, the most popular style of fishing in Japan, *Tomozuri*, which utilizes territorial behaviors of ayu can be applied only to territory holders (Iguchi, 1996; Kawanabe, 1973). In *Tomozuri*, fishermen use a live decoy as an intruder for territory holders. Then, territory holders attack the decoy in order to defend their own territories. By utilizing the habit, fishermen can fish the territory holders. Based on the above relationships, the release policy for ayu should be designed to increase the amount of territory holders effectively in consideration with the ecological features of ayu.

Previous studies have proposed some release policies for ayu from various viewpoints, e.g., the lineage of ayu fingerlings (Iwata et al., 2007; Miura et al., 2012), the impact on other species (Katano et al., 2000, 2006), the river environment (i.e. river width (Tsuboi and Takagi, 2016), water quality (Awata et al., 2010; Muraoka et al., 2011) and frequency of boulders (Tsuboi et al., 2012)) and population density (Katano, 2014). However, little attention has been given to the density-dependent population dynamics which are deeply concerned with a change in density caused by release. Recently, a rate equation that describes the density-dependent population dynamics of ayu within the territorial competition has been proposed (Katsumata et al., 2017). In the present study, we incorporate the release of ayu which affects the fish density in this rate equation and examine an effective release policy for ayu by using this newly proposed model. Our results indicate that the release of ayu demands unique policy different from other fish species. The release of ayu should be carried out so as not to break down territories due to the increase in density, caused by released fingerlings. Specifically, the release policy that reduces the amount of fingerlings that are released at one time (i.e. divide the stocked fingerlings and release them frequently), and lengthens the time interval between each release, increases the catch of territory holders.

2. Model

In our previous study, we developed a rate equation that describes the density-dependent population dynamics of ayu within the territorial competition (Katsumata et al., 2017). By functionally expanding this rate equation, we build a simple model which takes into account a change in fish density caused by release. The territorial competition of ayu occurs midstream. Individual fish take one of two strategies within the territorial competition: territory holder (Th) or floater (Fl). Empty sites can be classified into rapids and pools. Let the proportions of territory holders and floaters be y_{Th} and y_{Fl}, respectively. For empty sites, let the proportions of rapids and pools be x_{rapid} and x_{pool}, respectively. The sum of these proportions denotes the whole region of the river where the territorial competition occurs ($y_{\mathrm{Th}} + y_{\mathrm{Fl}} + x_{\mathrm{rapid}} + x_{\mathrm{pool}} = 1$). From the previous studies which describe the territorial behaviors of ayu (Iguchi, 1996; Kawanabe, 1957, 1973; Miyadi, 1960; Takahashi and Azuma, 2006), we assume that each proportion y_{Th}, y_{Fl}, x_{rapid} and x_{pool} changes over time depending on the following cases:

(i) y_{Th}:

- increases when floaters find vacant rapids and become territory holders,
- decreases when territory holders give up their own territories and become floaters,
- decreases when territory holders die and the places become vacant.

(ii) y_{Fl}:

- decreases when floaters find vacant rapids and become territory holders,
- increases when territory holders give up their own territories and become floaters,
- decreases when floaters die and the places become vacant,
- increases when newcomers which migrate from downstream become floaters,
- increases when ayu fingerlings are released and become floaters.

(iii) x_{rapid} increases or decreases by the change of y_{Th}.

(iv) x_{pool} increases or decreases by the change of y_{Fl}.

Note that newcomers are wild ayu that retrograded from downstream, and fingerlings that are just released do not have their own territories. Corresponding to the cases of (i)–(iv), we obtain the following rate equations if we assume an infinite population, which can be described by the mean field theory.

$$\begin{cases} y_{\mathrm{Th}}(t+1) = y_{\mathrm{Fl}}(t)x_{\mathrm{rapid}}(t) - r(y_{\mathrm{Fl}}(t))y_{\mathrm{Th}}(t) - d_{\mathrm{Th}}y_{\mathrm{Th}}(t) + y_{\mathrm{Th}}(t) \\ y_{\mathrm{Fl}}(t+1) = -y_{\mathrm{Fl}}(t)x_{\mathrm{rapid}}(t) + r(y_{\mathrm{Fl}}(t))y_{\mathrm{Th}}(t) - d_{\mathrm{Fl}}y_{\mathrm{Fl}}(t) + M(t) + R(t) + y_{\mathrm{Fl}}(t) \\ x_{\mathrm{rapid}}(t+1) = -\Delta y_{\mathrm{Th}} + x_{\mathrm{rapid}}(t) \\ x_{\mathrm{pool}}(t+1) = -\Delta y_{\mathrm{Fl}} + x_{\mathrm{pool}}(t) \end{cases} \tag{1}$$

Fig. 1 illustrates the flow diagram of a change in fish proportion in Eq. (1). t is a time step (arbitrary unit). d_{Th} and d_{Fl} denote the death rate of territory holders and floaters. Δy_{Th} and Δy_{Fl} are the temporal variation of y_{Th} $(=y_{\mathrm{Th}}(t+1) - y_{\mathrm{Th}}(t))$ and y_{Fl} $(=y_{\mathrm{Fl}}(t+1) - y_{\mathrm{Fl}}(t))$, respectively. We explain the functions $r(y_{\mathrm{Fl}}(t))$, $M(t)$ and $R(t)$ in Eq. (1) (Fig. 2). The function $r(y_{\mathrm{Fl}}(t))$ is the rate that territory holders give up their own territories. When the proportion of floaters increases, the defense costs to protect the territories become larger, and territory holders tend to give up their own territories (Iguchi et al., 2003; Katano et al., 2004). Thus, we define the function $r(y_{\mathrm{Fl}}(t))$ as follows:

$$r(y_{\mathrm{Fl}}(t)) = \frac{1}{1 + \exp[a(\theta - y_{\mathrm{Fl}}(t))]} \tag{2}$$

where a and θ denote the increasing gradient and inflection point of $r(y_{\mathrm{Fl}}(t))$, respectively. As a increases, the shape of $r(y_{\mathrm{Fl}}(t))$ turns from a logistic curve which has the inflection point θ to a step function which has the threshold θ (Fig. 2a). This function converges towards 1 as $y_{\mathrm{Fl}}(t)$ increases. We assume that $0 \le t \le t^*$ $(t^* \ge 1)$ is the period from the beginning to the end of the season of ayu migration. Thus, as observed in the state of ayu before spring (Kawanabe, 1969; Miyadi, 1960; Takahashi and Azuma, 2006), no fish have migrated to midstream yet at $t = 0$ $(y_{\mathrm{Th}}(0) = y_{\mathrm{Fl}}(0) = 0)$. From the above, we define the function $M(t)$ that is the proportion of newcomers which are wild ayu at time t:

$$M(t) = \begin{cases} m & 0 \le t \le t^* \\ 0 & t^* < t \end{cases} \tag{3}$$

where m $(m \ge 0)$ is the proportion of newcomers during the season of ayu migration $(0 \le t \le t^*)$. Therefore, the value of m has a direct relation to the amount of wild ayu in the river. The function $R(t)$ is the proportion of fingerlings that are released at time t. In general, fishery cooperatives divide and release stocked fingerlings frequently. When fingerlings whose proportion of the total amount is V are released n separate times at regular time intervals T, the function $R(t)$ is described as the following comb function:

$$R(t) = \frac{V}{n}\sum_{i=0}^{n-1}\delta(t - iT) \tag{4}$$