Territory holders and non-territory holders in Ayu fish coexist only in the population growth process due to hysteresis

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Ayu fish form feeding territories during a non-breeding (growing) season. When the density of the fish increases, phases gradually change. In the early growing season, all fish can hold territories at low density. Once all territory sites are occupied, newcomers become floaters. As the density further increases, territory holders have to spend much more time in defending their own territory and lose the time to feed on algae. Eventually, all fish give up their own territories and then form a school. In contrast, when the density decreases, territories are directly reformed from the school. In short, ayu fish exhibit a different transition, called hysteresis, where the two transitions occur widely-apart from each other. The dynamics of this intrinsic phenomena has not been demonstrated in previous studies. We develop a rate equation to describe the population dynamics within territorial competition. Our model successfully reproduces territorial hysteresis and indicates that territory holders and floaters can coexist only in the process of population growth. Moreover, we also find that the two critical densities of territorial hysteresis are conspicuously different from each other when the increase of the density of floaters sharply influences (step-function-like) the territories.

Territoriality and group foraging are classical examples of behavioral strategies to adapt to different ecological circumstances1. These strategies are two different ways of adaptation2. Territorial behavior is an adaptation of solitary animals3-5 while group foraging is an adaptation of animals living as a group6,7. These two different evolutionary adaptations may occur in closely related species2. For example, in most migratory birds, mating pairs often form breeding territories while they forage as groups during non-breeding (growing) seasons. However, it is extremely rare to see a transition between territoriality and group foraging in a single season. Here, we provide a unique case study of fish which exhibit both territoriality and group foraging (school) as adaptive responses during a single season.

Ayu fish (Plecoglossus altivelis, Osmeridae) are an endemic migratory fish in Japan8-10. This fish has a distinctive life as follows8,9,11. The life cycle of ayu is completed in one year. In autumn (late August–early September), eggs are spawned downstream of river hatch. The hatched larvae drift to an estuary near the sea within a few days and mostly feed on zooplankton and small aquatic insects. In spring (April–May), juvenile fish migrate to midstream (and/or upstream) of a river, where algae (diatoms) grow on rocks and stones of riverbeds in rapids (swift current). They feed on these algae from spring to fall. In this stage, especially large fish can hold their own territories in rapids, and territorial competition for food violently occurs between territory holders and non-territory holders and non-territory holders.

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holders (floaters). In fall, when ayu fish mature, they swim downstream together. They spawn eggs and die soon afterwards downstream of a river. Thus, ayu is a diadromous fish\(^{11}\).

Ayu exhibit a historical effect (hysteresis): the breakdown and formation processes of territory are greatly different. When densities of fish increase, phases gradually change as follows. In early growing season (May), all fish can hold their own algae-feeding territories at low density\(^2\). This feeding territory is formed in rapids where diatoms grow on the surface of rocks\(^{13,14}\). During this growing season, many fish swim together and fish density increases day by day. Once all the rapids are occupied, surplus fish cannot form territories. These fish become floaters and stay in (deep) pools. In contrast to rapids, pools without algae are not suitable for ayu because floaters can only feed on a small amount of algae and insects which drift from the rapid. Because floaters cannot sufficiently feed in pools, they often intrude into other’s territories to steal algae. Territory holders violently attack floaters in order to defend their own territories. As the density of fish further increases and exceeds the critical limit, all fish give up their own territories and form a school. In contrast, when the density decreases and falls below the other critical limit, territories are directly reformed from the school. In the observation data, it is known that the actual critical limit in increasing phase is in between 4.1 [fish/m²] and 5.5 [fish/m²], while that limit for decreasing phase is nearly equal to 1.5 [fish/m²] (see Tables S1 and S2). From the above, the different phase transition between these increasing and decreasing processes denotes the historical effect which has two transition densities shown to greatly differ\(^{15}\). The historical effect is well known in physics, such as ice-water transition and magnetism. However, biological hysteresis is rather rare\(^{6,17}\).

In our previous study, we demonstrated the historical effect in ayu fish from the viewpoint of a cost-benefit theory\(^{9}\). However, we did not focus on the problems of the population dynamics within the territorial competition as well as the difference between two critical densities of territorial hysteresis. In the present study, to more thoroughly understand the historical effect in the territoriality of ayu, we develop a rate equation to describe the population dynamics within the territorial competition\(^{18}\). Our model successfully reproduces territorial hysteresis and indicates that territory holders and floaters can coexist only during the process of population growth. Moreover, we also find that the two critical densities are conspicuously different from each other when the increase of the density of floaters sharply influences (step-function-like) the territories.

Models and Analyses

Rate Equation for Territorial Competition. We develop a rate equation to describe the population dynamics of ayu fish within the territorial competition. The territorial competition of ayu fish occurs in the midstream of the river. We set \( y \) as the proportion of ayu fish to total ayu population and \( x \) as the proportion of vacant sites to total habitat. Individual fish takes one of two strategies: territory holder (Th) or floater (Fl), and empty sites can be classified into rapids and pools. We define the proportion of territory holder \( y_{\text{Th}} \) and floater \( y_{\text{Fl}} \).

For empty sites, we define the proportion of rapids \( x_{\text{rapid}} \) and pools \( x_{\text{pool}} \). They satisfy the conditions: \( y = y_{\text{Th}} + y_{\text{Fl}} \), \( x = x_{\text{rapid}} + x_{\text{pool}} \). Based on many previous studies which describe ecological features of ayu fish\(^{8,11,12,19-21}\), we assume that each proportion \( y_{\text{Th}}, y_{\text{Fl}}, x_{\text{rapid}} \) and \( x_{\text{pool}} \) changes over time depending on the following cases:

(i) \( y_{\text{Th}} \):
- 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 have died and the places become vacant

(ii) \( y_{\text{Fl}} \):
- 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 have died and the places become vacant
- increases when newcomers which migrate from downstream become floaters

(iii) \( x_{\text{rapid}} \):
- increases or decreases by the change of \( y_{\text{Th}} \)

(iv) \( x_{\text{pool}} \):
- increases or decreases by the change of \( y_{\text{Fl}} \)

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.

\[
\begin{align*}
\frac{dy_{\text{Th}}}{dt} + 1 &= y_{\text{Fl}}(t)x_{\text{rapid}}(t) - r[y_{\text{Fl}}(t)]y_{\text{Th}}(t) - d_{\text{Th}}y_{\text{Th}}(t) + y_{\text{Th}}(t) \\
\frac{dy_{\text{Fl}}}{dt} + 1 &= -y_{\text{Fl}}(t)x_{\text{rapid}}(t) + r[y_{\text{Th}}(t)]y_{\text{Fl}}(t) - d_{\text{Fl}}y_{\text{Fl}}(t) + v + y_{\text{Fl}}(t) \\
x_{\text{rapid}}(t) + 1 &= -\Delta y_{\text{Th}} + x_{\text{rapid}}(t) \\
x_{\text{pool}}(t) + 1 &= -\Delta y_{\text{Fl}} + x_{\text{pool}}(t)
\end{align*}
\]

where \( r \) and \( v \) denote the rate that territory holders give up their own territories and the amount of newcomers which migrate from downstream, respectively. \( d_{\text{Th}} \) and \( d_{\text{Fl}} \) denote the mortality rate of territory holders and floaters. \( \Delta y_{\text{Th}} \) and \( \Delta y_{\text{Fl}} \) are the temporal variation of \( y_{\text{Th}} = \gamma_{\text{Th}}(t + 1) - y_{\text{Th}}(t) \) and \( y_{\text{Fl}} = y_{\text{Fl}}(t + 1) - y_{\text{Fl}}(t) \), respectively. When the proportion of floaters increases, the defense costs to protect a territory become larger, and territory holders tend to give up their own territories\(^{8,11,12,22}\). Thus, we define the function \( r \) that depends on \( y_{\text{Fl}} \) as follows:
When $0 < t < t_1$, incoming fish can find empty sites among rapids and hold their own territories immediately. In this phase, some territory sites are not occupied ($y_{th} < 0.1$). When $t_1 < t < t_2$, all territory sites are occupied ($y_{th} = 0.1$), and surplus fish become floaters. Territory holders and floaters coexist in this phase. When $t_2 < t$, the proportion of floaters further increases, all fish give up their own territories and form a school (all fish become floaters). In this phase, it is likely that the same territory holders remain in the rapids because the amount does not change. But actually, they are always replaced due to the fact that the amount of territory holders and floaters balances.

In the decreasing process, the proportion of ayu fish decreases by natural death. In this process, we assume that all juvenile fish downstream have already migrated to midstream. Thus, the model parameter $v$ is 0. We set the initial proportions of territory holders and floaters equal to the final proportions in the above increasing process. Therefore, the initial proportions are $y_{th|dec}(0) = y_{th|inc}(T)$ and $y_{fl|dec}(0) = y_{fl|inc}(T)$. See $t = 0$ in Fig. 2b.
breakdown occurs even if territory sites are not fully occupied by territory holders. Therefore, since territory holders give up their own territories at low proportion of floaters, the phase transition of territory holders in rapids. Due to the above relationships, critical proportions $y_1$ and $y_2$ become the proportions of only floaters because there are no territory holders in rapids. For this reason, the critical proportions $y_1$ and $y_2$ are widely apart. These results of hysteresis are unchanged qualitatively even if the function $r$ in equation (2) approximates a step function ($1 \ll m$) (Fig. S2).

**Historical Effect.** We describe the territorial hysteresis which has two significantly different transition proportions (Fig. 4). We change the horizontal axis in Fig. 2 from time step $t$ to the total proportion of ayu fish $y = y_{th} + y_{fl}$. Thus, we see the dependence of population dynamics of territory holders and floaters on the total proportion $y$ (Fig. 4). All model parameters are the same as the conditions used in the population dynamics. In the increasing process, when $y$ exceeds the critical proportion $y_1$, all territories break down (Fig. 4a). In the decreasing process, when $y$ decreases and falls below the critical proportion $y_2$, territories are directly reformed from the school (Fig. 4b). The hysteresis that is the large difference between $y_1$ and $y_2$ occurs for the following reasons. In the increasing process, the proportion of floaters $y_{fl}$ increases after all territory sites are occupied by territory holders. When $y_{fl}$ increases to the inflection point $\theta$ of the function $r$, it becomes difficult to defend their own territories, and all territories break down. Here, $y_{fl}$ indicates the sum of proportions of territory holders and floaters. In contrast, in the decreasing process, territory holders do not have their own territories. When $y_{fl}$ decreases to the inflection point $\theta$ of the function $r$, it becomes easy to re-form their own territories, and territories are reformed from the school. Here, $y_{fl}$ becomes the proportions of only floaters because there are no territory holders in rapids. Due to the above relationships, critical proportions $y_1$ and $y_2$ are widely apart. These results of hysteresis are unchanged qualitatively even if the function $r$ in equation (2) approximates a step function ($1 \ll m$) (Fig. S2).

**Sensitivity Analysis.** We explore the sensitivity of critical proportions $y_1$ and $y_2$ by changing the parameter $m$ while keeping the others are the same as the conditions of the population dynamics in Fig. 2 and hysteresis in Fig. 4 (Fig. 5a). When $m$ is sufficiently small, the function $r(y_{fl})$ draws a quite gentle curve (Fig. 1). In this case, since territory holders give up their own territories at low proportion of floaters, the phase transition of territory breakdown occurs even if territory sites are not fully occupied by territory holders. Therefore, $y_1$ and $y_2$ are not widely apart when $m$ is sufficiently small. In contrast, when $m$ is large, the function $r(y_{fl})$ almost becomes like...
a step function. In this case, since most territory holders can hold their own territories until the proportion of floater $y_{Fl}$ reaches the inflection point $\theta$, the phase transition that territory breakdown occurs when all territory sites are occupied. Therefore, $y_1$ and $y_2$ are widely apart each other when $m$ is large.

Next, we change the parameter $\theta$ while keeping other model parameters are the same. When $\theta$ is sufficiently small, the inflection point of function $r(y_{Th})$ is small. In this case, since $y_{Th}$ reaches $\theta$ by the small amount of newcomers $v$ and the accumulation of floaters that has not found a territory yet, the phase transition of territory breakdown occurs even if territory sites are not fully occupied by territory holders. Therefore, $y_1$ and $y_2$ are not widely apart when $\theta$ is sufficiently small. In contrast, when $\theta$ is large, the inflection point of function $r(y_{Fl})$ becomes large. In this case, since $y_{Fl}$ does not reach $\theta$ until all territory sites are occupied, $y_1$ and $y_2$ are widely apart each other when $m$ is large.
m model parameter becomes larger, the difference between $y_2$ and formation $y_1$ territory breakdown, respectively. All the model parameters excluding $m$ are the same as the conditions of the population dynamics in Fig. 2 and hysteresis in Fig. 4. As the model parameter $m$ becomes larger, the difference between $y_1$ and $y_2$ becomes larger. All the model parameters excluding $θ$ are the same as the conditions of the population dynamics in Fig. 2 and hysteresis in Fig. 4. As the model parameter $θ$ becomes larger, the difference between $y_1$ and $y_2$ becomes larger.

**Figure 5.** Sensitivity analysis of $y_1$ and $y_2$. The blue cross and red diamond denote the transition proportion of territory breakdown $y_1$ and formation $y_2$, respectively. (a) $y_1$ and $y_2$ depending on $m$. All the model parameters excluding $m$ are the same as the conditions of the population dynamics in Fig. 2 and hysteresis in Fig. 4. As the model parameter $m$ becomes larger, the difference between $y_1$ and $y_2$ becomes larger. (b) $y_1$ and $y_2$ depending on $θ$. All the model parameters excluding $θ$ are the same as the conditions of the population dynamics in Fig. 2 and hysteresis in Fig. 4. As the model parameter $θ$ becomes larger, the difference between $y_1$ and $y_2$ becomes larger.

**Data availability.** The authors declare that all data supporting the findings of this study are available within the article and its Supplementary Information files or from the corresponding author upon reasonable request.

**Discussion**
In the present study, we develop a rate equation of the population dynamics of ayu fish within territorial competition. Our model indicates that territory holders and floaters can coexist only in the process of population growth (Figs 2 and 3). This coexistence does not appear in the decreasing process. This is the cause of producing territorial hysteresis which has two significantly different transition proportions (Fig. 4). These results are unchanged qualitatively even if the function $r$ in Eq. (2) approximates a step function ($1 ≪ m$) (Figs S1 and S2). Moreover, we also find that the two critical proportions conspicuously differ from each other when the increase of the proportion of floaters sharply influences (step-function-like) the territories (Fig. 5).

Few studies have reported such biological hysteresises. Caraco (1980) reported an animal hysteresis of avian flocks. These flocks forage for food in two patches. Flock alarm calls and white tail feathers alert the existence of predators so that individual birds can reduce predator scanning as group size increases. As the population size increases, the incoming birds continue to join a single crowded feeding ground. However, as the density of birds greatly increases, food resources per bird are reduced. In that case, choosing a vacant risky site becomes better than joining the crowded patch. In contrast, when the population size decreases so that birds leave the feeding ground, the number of birds in both patches becomes much less than the optimal flock size. In this way, the dynamics of the flock sizes are shifted from the optimal flock size (a single transition point) depending on the situations. Here we demonstrate territoriality of ayu as a significant case of animal hysteresis.

Ayu territory holders are important for biodiversity in a river ecosystem because they specifically feed on algae. In recent years, because many rivers are divided by dams, the ayu cannot migrate to midstream, so many fishery cooperative associations actively release ayu into rivers in Japan. We demonstrated that the population dynamics of territory holders and floaters are different between the increasing and decreasing processes due to hysteresis. Thus, those who release ayu should take into account the effect in order to keep the proper number of territory holders. We believe that our model is useful in designing more effective release policies.

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Author Contributions
Y.K., K.T. and G.I. conceived the study and built the model. T.U., H.I. and J.Y. introduced biological interpretation of the results. Y.K. and G.I. wrote the manuscript. Y.K. collected references and data. All authors approve the final manuscript.

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