

SCIENTIFIC REPORTS



OPEN

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 animals^{3–5} while group foraging is an adaptation of animals living as a group^{6,7}. 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 Japan^{8–10}. This fish has a distinctive life as follows^{8,9,11}. 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 mid-stream (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

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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 fish¹¹.

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 density¹². 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 differ¹⁵. The historical effect is well known in physics, such as ice-water transition and magnetism. However, biological hysteresis is rather rare^{16,17}.

In our previous study, we demonstrated the historical effect in ayu fish from the viewpoint of a cost-benefit theory¹⁵. 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 competition¹⁸. 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_{Th} and floater y_{Fl} . For empty sites, we define the proportion of rapids x_{rapid} and pools x_{pool} . They satisfy the conditions: $y = y_{Th} + y_{Fl}$, $x = x_{rapid} + x_{pool}$. Based on many previous studies which describe ecological features of ayu fish^{8,11,12,19–21}, 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 have died 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 have died and the places become vacant
- increases when newcomers which migrate from downstream 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} .

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.

$$\begin{cases} y_{Th}(t+1) = y_{Fl}(t)x_{rapid}(t) - r[y_{Fl}(t)]y_{Th}(t) - d_{Th}y_{Th}(t) + y_{Th}(t) & (1a) \\ y_{Fl}(t+1) = -y_{Fl}(t)x_{rapid}(t) + r[y_{Fl}(t)]y_{Th}(t) - d_{Fl}y_{Fl}(t) + v + y_{Fl}(t) & (1b) \\ x_{rapid}(t+1) = -\Delta y_{Th} + x_{rapid}(t) & (1c) \\ x_{pool}(t+1) = -\Delta y_{Fl} + x_{pool}(t) & (1d) \end{cases} \quad (1)$$

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_{Th} and d_{Fl} denote the mortality rate of territory holders and floaters. Δy_{Th} and Δy_{Fl} are the temporal variation of y_{Th} ($=y_{Th}(t+1) - y_{Th}(t)$) and y_{Fl} ($=y_{Fl}(t+1) - y_{Fl}(t)$), 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^{9,11,12,22}. Thus, we define the function r that depends on y_{Fl} as follows:

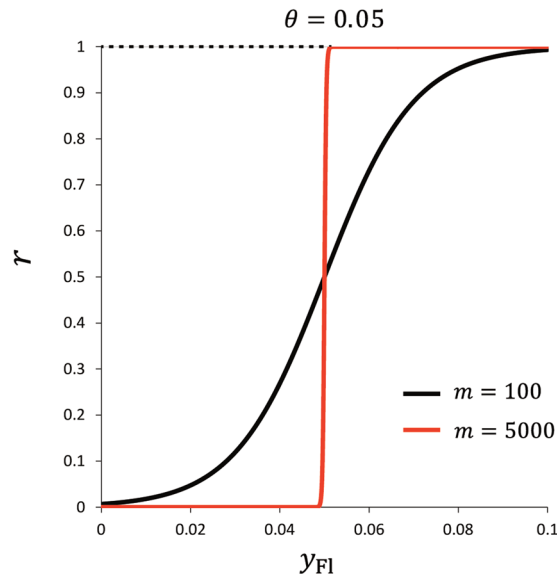


Figure 1. Examples of the function r . The function r in Eq. (2) indicates the probability that territory holders give up their own territories. This function depends on y_{FI} and two parameters m and θ , where m and θ denote the increasing gradient of r as a function of y_{FI} and the inflection point, respectively. $r(y_{FI})$ represents a logistic curve which has the inflection point θ and converges towards 1 as y_{FI} increases (black line). When m is sufficiently large, $r(y_{FI})$ approximates a step function which has the threshold θ (red line).

$$r(y_{FI}) = \frac{1}{1 + e^{m(\theta - y_{FI})}} \quad (2)$$

where m and θ denote the increasing gradient of r as a function of y_{FI} and the inflection point, respectively. This function $r(y_{FI})$ represents a logistic curve which has the inflection point θ and converges towards 1 as y_{FI} increases (Fig. 1). When m is sufficiently large, the $r(y_{FI})$ approximates a step function which has the threshold θ .

We put some limitations on y_{Th} , y_{FI} , x_{rapid} and x_{pool} based on the actual evidences as follows. In a typical Japanese river, midstream consists of about 55% rapids and about 45% pools¹². Among these rapids, territory sites that have algae for feeding are estimated to be about 20%. Thus, we assume that rapids which are suitable for territory are about 10% ($0.55 \times 0.20 = 0.11$) of the whole. y_{Th} becomes 0.1 when they occupy all rapids (where $x_{rapid} = 0$). In contrast, y_{Th} becomes 0 when no one has rapids (where $x_{rapid} = 0.1$). Thus, $y_{Th} + x_{rapid}$ is always 0.1. Similarly, y_{FI} becomes 0.9 when they occupy all pools (where $x_{pool} = 0$) while y_{FI} becomes 0 when no one has pools (where $x_{pool} = 0.9$). Thus, $y_{FI} + x_{pool}$ is always 0.9. Based on the above relationships, y_{Th} , y_{FI} , x_{rapid} and x_{pool} are:

$$\begin{cases} y_{Th} + x_{rapid} = 0.1 \\ y_{FI} + x_{pool} = 0.9 \\ y_{Th} + y_{FI} + x_{rapid} + x_{pool} = 1 \end{cases} \quad (3)$$

Population Dynamics. By the use of the above model, we demonstrate the population dynamics of territory holders and floaters within territorial competition between the increasing and decreasing stages of proportion (Fig. 2). In Fig. 2a, the proportion of ayu fish increases due to newcomers migrating from downstream. Thus, the model parameter ν means that the amount of newcomers is larger than 0. We assume that both initial proportions of territory holders and floaters are 0 ($y_{Th}(0) = y_{FI}(0) = 0$). This setting means that no fish have migrated to midstream yet, as observed in the state of ayu before spring. We simulate the population dynamics in the increase process where time proceeds from 0 to T (Fig. 2a). Here, we set $T = 5000$ as the final time step.

In the increase stage of proportion, the phases transit as $Th \rightarrow (Th + FI) \rightarrow School (Sc)$ gradually (Fig. 2a). 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 $t_2 < t$, as 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 ν 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 $y_{FI|dec}(0) = y_{FI|inc}(T)$. See $t = 0$ in Fig. 2b.

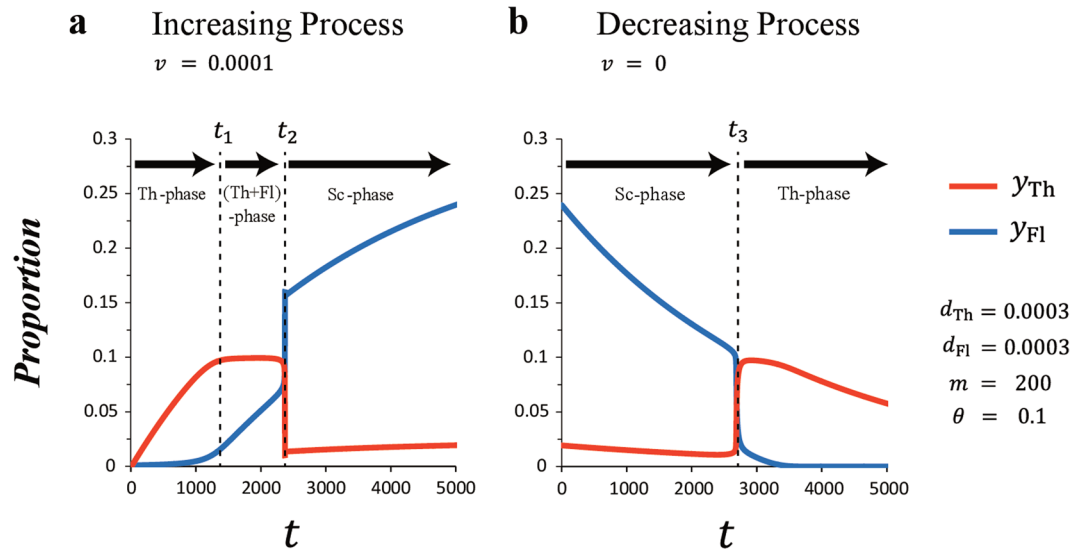


Figure 2. Population dynamics of territory holders and floaters within territorial competition. Model parameters are $d_{Th} = 0.0003$, $d_{Fl} = 0.0003$, $m = 200$ and $\theta = 0.1$. The time step t is arbitrary. The red (blue) lines denote the proportion of territory holders (floaters). **(a)** Result in increasing stage. In this process, $y_{Th}(0) = y_{Fl}(0) = 0$ and $v = 0.0001$. The final time step T is 5000. The phases transit as Th \rightarrow (Th + Fl) \rightarrow Sc as follows. When $0 < t < t_1$, all fish can hold their own territories in rapids at low proportion. When $t_1 < t < t_2$, all territory sites are occupied ($y_{Th} = 0.1$), and surplus fish become floaters. When $t_2 < t$, all fish give up their own territories and form a school. **(b)** Result in decreasing stage. In this process, $y_{Th|dec.}(0) = y_{Th|inc.}(T)$, $y_{Fl|dec.}(0) = y_{Fl|inc.}(T)$ and $v = 0$. The phases transit as Sc \rightarrow Th as follows. When $0 < t < t_3$, all fish are floaters and cannot hold their own territories. However, when $t_3 < t$, territories are directly reformed from the state of a school.

We simulate the population dynamics of the decreasing process until the proportion of ayu becomes sufficiently small. Figure 2b shows part of the simulation (until 5000 time steps) because further steps are redundant.

In the decrease stage of proportion, the phases transit as Sc \rightarrow Th (Fig. 2b). When $0 < t < t_3$, all fish are floaters and cannot hold their own territories. However, when $t_3 < t$, the proportion of fish becomes lower and territories are directly reformed from a school. Amazingly, in contrast to the increasing process (Fig. 2a), the coexisting phase: (Th + Fl)-phase does not appear in the decreasing process. These results mean that territory holders and floaters can coexist together only in the process of the population growth. Figure 3 illustrates the breakdown and formation processes of a territory. Our results indicate that the breakdown and formation processes of territory greatly differ between the increasing and decreasing stages. These results are consistent with studies which describe some ecological features of ayu fish^{8–12,19–21}. Moreover, these results of population dynamics are unchanged qualitatively even if the function r in equation (2) approximates a step function ($1 \ll m$) (Fig. S1).

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 θ of the function r , it becomes difficult to defend their own territories, and all territories break down. Here, y_1 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 θ of the function r , it becomes easy to reform their own territories, and territories are reformed from the school. Here, y_2 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

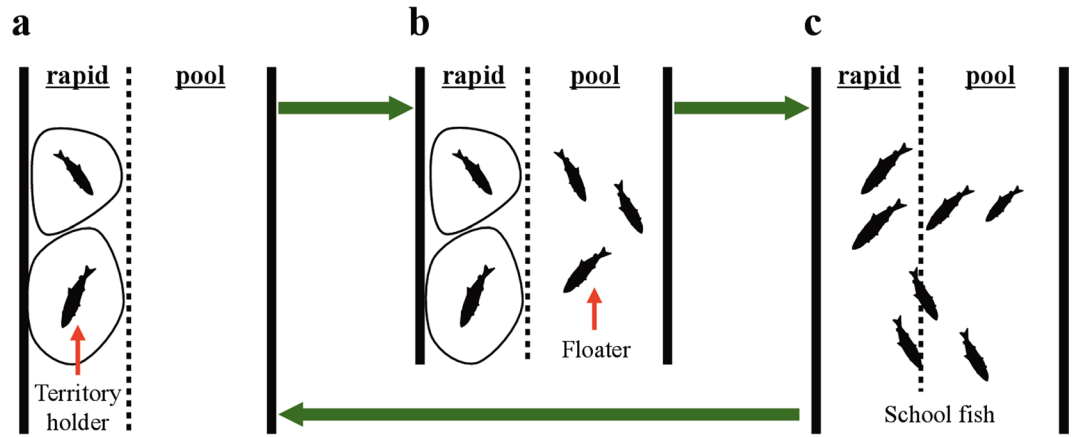


Figure 3. Breakdown and formation processes of territoriality. As the proportion of fish increases, the phases transit as $a \rightarrow b \rightarrow c$. (a) In this Th-phase, all fish can hold their own territories in rapids at low proportion, and some territory sites are not occupied. (b) In this (Th + Fl)-phase (coexisting phase), when the population size exceeds the territory capacity, newcomers cannot form territories and become floaters in pools. (c) In this Sc-phase, as the proportion of fish further increases and exceeds the critical limit, all fish give up their own territories and form a school. In contrast, when the proportion of fish decreases, the phases directly transit as $c \rightarrow a$. In other words, when the proportion falls below the critical limit, territories are directly reformed from a school. In contrast to the increasing process, the coexisting phase does not appear in the decreasing process.

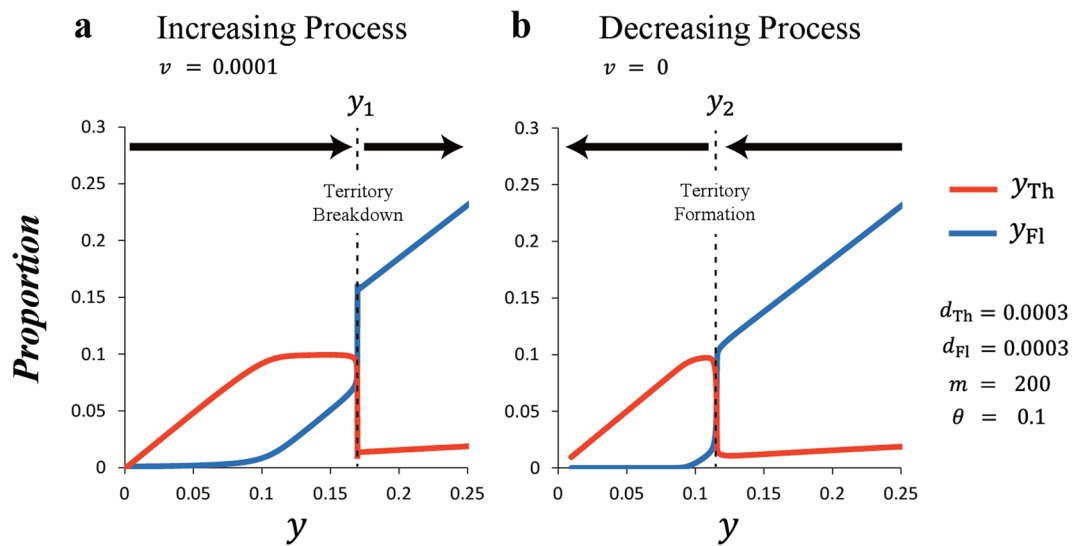


Figure 4. Territorial hysteresis has two significantly different transition proportions. We change the horizontal axis of Fig. 2 from time step t to the total proportion of ayu fish $y (=y_{Th} + y_{Fl})$. All model parameters are the same as the conditions used in Fig. 2. The red (blue) lines denote the proportion of territory holders (floaters). (a) In the increasing process, when y exceeds the critical proportion y_1 , all territories break down. (b) In the decreasing process, when N decreases and falls below the critical proportion y_2 , territories are directly reformed from the school. These two transition proportions y_1 and y_2 greatly differ.

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 θ , 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 θ while keeping other model parameters are the same. When θ is sufficiently small, the inflection point of function $r(y_{Fl})$ is small. In this case, since y_{Fl} reaches θ 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 θ is sufficiently small. In contrast, when θ is large, the inflection point of function $r(y_{Fl})$ becomes large. In this case, since y_{Fl} does not reach θ until all territory sites are occupied. y_1 and y_2 are widely apart each other when m is large.

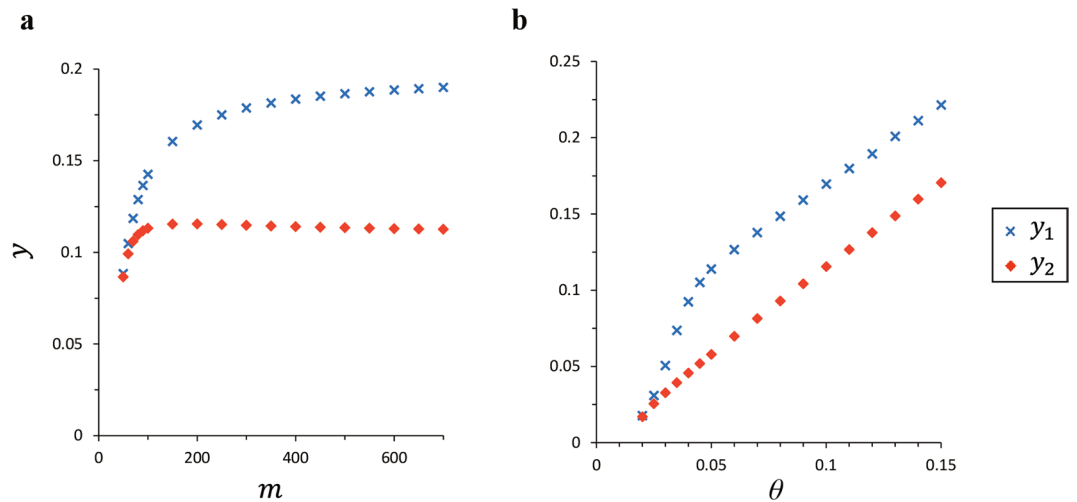


Figure 5. Sensitivity analysis of y_1 and y_2 . The blue cross and red diamond denote the transition proportion of territory breakdown y_1 and formation y_2 , respectively. **(a)** y_1 and y_2 depending on m . All the model parameters excluding m are the same as the conditions of the population dynamics 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 ($1 \ll m$) (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^{16,17}. Caraco (1980) reported an animal hysteresis of avian flocks¹⁶. 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^{23–25}. 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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Acknowledgements

This work was partly supported by a Japan Prize Foundation award to H.I., and JSPS KAKENHI Grant Number 14J02983, 16H07075, 17J06741, and 17H04731 to H.I., 22255004, 26257405, 15H04420 and 22370010 to J.Y. and 15K00334 to K.T.

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.

Additional Information

Supplementary information accompanies this paper at <https://doi.org/10.1038/s41598-017-16859-4>.

Competing Interests: The authors declare that they have no competing interests.

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