Numerical Investigation of Effects of Species Specific Characteristics on Community Dynamics Affected by Stream Drying in Rivers with Pools as Refugia

Kohei Yokota¹ and Masayuki Fujihara²

Abstract: A mathematical model was presented and parameter studies of the model were performed to investigate changes in the effect of stream drying on aquatic community dynamics in response to species specific characteristics. The community in the model was composed of producers, grazers and predators, and the river was assumed to have pool-riffle structure. Grazers and predators could move between the riffle and the pool according to their habitat preference. The temporal scale was enough short that grazers and predators did not reproduce. When the flow reduction began, grazers and predators tended to move from the riffle to the pool by the time the riffle dried up. Both of them could survive in the pool during the stream drying. After the stream drying ended and the water depth recovered, they tended to move from the pool to the riffle. The parameter studies on the sensitivity of grazers and predators to the flow velocity and the predation pressure for grazers revealed following: (i) grazers and predators which had the higher sensitivity to the flow velocity had advantage to reduce the decrease in their density due to the stream drying, (ii) predators had advantage to reduce the decrease in their density due to the stream drying if grazers had the higher sensitivity to the flow velocity, (iii) grazer density in the case of the stream drying became larger than that in the case of no flow reduction if predation pressure for grazers was high relative to the natural mortality rate of grazers, and (iv) the lower sensitivity of predators to the flow velocity had positive effects on grazer density after the stream drying if the predation pressure for grazers was high relative to the natural mortality rate of grazers.

Keywords: Stream drying; Pool-riffle structure; Refugia; Mathematical model; Community dynamics

1 Introduction

In recent years, water demand is globally increasing with population growth (Oki and Kaname, 2006). Moreover, droughts will occur more frequently and their magnitude will become larger (Burke et al., 2006). One of the ways to utilize more water resources is to construct water-use structures such as dams to collect more water. However, these structures would change flow regime in downstream reaches of them (Tanida and Takemon, 1999). Flow reduction is a typical example related to such human activities (Tanida and Takemon, 1999; Rader and Belish, 1999; Zhang et al., 1998), and it is one of disturbances in stream ecosystems (Lake, 2000).

Disturbance can be classified into three groups by its temporal pattern (Lake, 2000). Pulse disturbance is the disturbance whose impact continues during short period and declines sharply. Press disturbance is the disturbance whose impact arises sharply and attains a constant level which is maintained. Rump disturbance is the disturbance whose impact is intensified with time. Flow reduction is regarded as rump disturbance. Flow reduction has direct effects and indirect effects on aquatic organisms (Lake, 2003). Direct effects are those caused directly by flow reduction. For example, decrease of water depth and wetted perimeter, and shrink of habitat are direct effects. Indirect effects are those associated with flow reduction. For example, change in pH, water temperature and electric conductivity, and intension of interspecific interaction strength due to habitat shrink are indirect effects.

Flow reduction finally causes stream drying. Stream drying means disappearance of habitats in the surface water. Thus, it causes critical damage to aquatic organisms. For example, Ledger et al. (2013) experimentally showed that sequential drying caused extinction of species which did not have tolerance to such environment and that the foodweb structure was changed by the stream drying. There are habitats which have a function as refugia during stream drying. For example, Chester and Robson (2011) showed that pools in rivers were refugia which a lot of species used during drying period. It is important for aquatic organisms to survive stream drying whether they can use refugia or not. Magoulick and Kobza (2003) suggested that a source-sink model is suitable for explaining dynamics of fish community during stream drying. At the beginning of flow reduction, habitat connectivity starts decreasing, and the migration of fish from habitats which are not refugia to refugia begins. Thus, refugia are sink habitats, and the others are source habitats during this period. Habitat patches finally become isolated due to stream drying, resulting in the high mortality in habitats which are not refugia and the limited dispersal. After stream drying, the migration from refugia begins. Thus, refugia are source habitats, and the others are sink habitats during this period.

¹Ph.D student, Graduate School of Agriculture, Kyoto University, Kita-shirakawa-oiwake-cho, Sakyoku, Kyoto 606-8502, Japan (Corresponding Author) E-mail: yokota.kohei.65w@st.kyoto-u.ac.jp
²Professor, Graduate School of Agriculture, Kyoto University, Kita-shirakawa-oiwake-cho, Sakyoku, Kyoto 606-8502, Japan
Most of the previous studies regarding the effects of flow reduction on aquatic community were conducted by field observations (e.g. Rader and Belish, 1998; Dohi et al., 2008; Chester and Robson, 2011) or experiments (e.g. Ledger et al., 2013; Walters and Post, 2011; Dewson et al., 2007a). It is true that such field studies are important because data on what happen in natural rivers during flow reduction can be obtained, but it is difficult to infer what is an intrinsic factor to affect community dynamics from these studies because of different characteristics of different rivers and species specific characteristics. On the other hand, studies using mathematical models have advantages to study which factor is important to community dynamics. Moreover, mathematical models are necessary for quantitative prediction of community dynamics. However, there are few mathematical studies on effects of flow reduction. Bell et al. (2000) investigated the trout population dynamics under the both conditions of the normal rainfall and the drought using a mathematical model. The model constructed in Bell et al. (2000) was a single species model, so that the phenomenon through the interspecific interaction affected by droughts could not be directly derived from their model. Multitrophic models are needed to investigate a variety of ecological process affected by disturbances (Wootton, et al., 1996; Wootton, 1998). There are not enough knowledge and tools at present to predict both of qualitative and quantitative consequences of community dynamics affected by stream drying.

In this study, a mathematical multitrophic model was proposed and a numerical investigation was performed to investigate aquatic organisms community dynamics in an intermittent river with pool-riffle structure. We focused on how species specific characteristics had effects on the consequence of a stream drying through interspecific interactions. The sensitivity to the change in the flow velocity caused by the flow reduction which was related to the rapid migration to refugia and the predation pressure for the intermittent species were particularly focused on as the species specific characteristics.

2 Mathematical model

The proposed mathematical model includes two types of habitats: riffle and pool. Riffles are shallow areas with high current velocity, whilst pools are deep areas with low current velocity (Kani, 1944). Community compositions are different between riffles and pools because aquatic organisms generally have their preference for the specific environment in habitats (Kani, 1944). Flow velocity, water temperature and substrate are typical examples of factors which have the relation to their preference.

The community to be discussed is composed of three species: producers, grazers and predators. The examples of these species are benthic algae, aquatic insects, and small carnivorous fish, respectively. For simplicity, grazers feed only on producers, and predators feed only on grazers. No species feed on predators. In this study, it was assumed that the flow reduction occurs during short-term in terms of Nisbet et al. (1997) which means enough short period during which grazers and predators do not reproduce but producers reproduce.

Based on the assumptions mentioned above, community dynamics is described by following equations:

$$ \frac{dV_i}{dt} = r_i \left(1 - \frac{V_i}{K} \right) V_i + g_V(h_1, h_2)R_V(V_j - V_i) - \frac{b_GV_i}{a_G + V_i} G_i, \quad (1) $$

$$ \frac{dG_i}{dt} = g_G(h_1, h_2)(D_G G_j - D_G G_i) - \frac{b_P G_i}{a_P + G_i} P_i - \mu_G G_i, \quad (2) $$

and

$$ \frac{dP_i}{dt} = g_P(h_1, h_2)(D_P j P_j - D_P i P_i) - \mu_P P_i \quad (3) $$

where $t$ is time (day), $i, j$ are the habitat number (($i, j) = (1, 2)$ or $(2, 1)$, and 1 and 2 represent the riffle and the pool, respectively), $h_i$ is the water depth in habitat $i$ (m), $V_i$ is the biomass of producers in habitat $i$ (mg m$^{-2}$), $G_i$ is the number of grazers per unit area (hereafter, numerical density) in habitat $i$ (m$^{-2}$), $P_i$ is the numerical density of predators in habitat $i$ (m$^{-2}$), $r_i$ is the intrinsic growth rate in habitat $i$ (day$^{-1}$), $K$ is carrying capacity (mg m$^{-2}$), $R_V$ is the rate of releasing propagules by producers (day$^{-1}$), $a_G$ is the half saturation constant of grazers (mg m$^{-2}$), $b_G$ is the maximum predation rate of grazers (mg day$^{-1}$), $D_G$ is the rate of migration of grazers from habitat $i$ (day$^{-1}$), $a_P$ is the half saturation rate of predators (m$^{-2}$), $b_P$ is the maximum predation rate of predators (day$^{-1}$), $\mu_G$ is the natural mortality rate of grazers (day$^{-1}$), $\mu_P$ is the rate of migration of predators from habitat $i$ (day$^{-1}$), and $\mu_P$ is the natural mortality rate of predators (day$^{-1}$).

The functions $g_V$, $g_G$, $g_P$ are used to restrict migration between habitats when the water depth is too shallow for each species to move from a present habitat. Using $X$ as a subscript which represents species $X$, it is expressed as follows:

$$ g_X(h_1, h_2) = \begin{cases} 0 & \min(h_1, h_2) < h_X \\ 1 & \min(h_1, h_2) \geq h_X \end{cases} \quad (4) $$

where $h_X$ is the shallowest water depth in the habitat where species $X$ ($V, G, P$) can migrate (m).

Intrinsic growth rate of producers decreases with increase in the water depth due to attenuation of light in water (Misaki and Tsuchiya, 2008). Thus, this is described as below:

$$ r_i = r_0 \exp(-kh_i) \quad (5) $$

where $r_0$ is the maximum growth rate (day$^{-1}$), and $k$ is the attenuation coefficient (m$^{-1}$).

Grazers and predators are assumed to have their preference to flow velocity (Kani, 1944) and that they move from a present habitat when there are not enough prey (Kohler et al., 1985). Based on these assumption, the rate of the migration of grazers and predators is described as below using the subscript $X$:
Table 1: Values of parameters

| Parameter | Unit   | Value | Parameter | Unit   | Value | Parameter | Unit   | Value |
|-----------|--------|-------|-----------|--------|-------|-----------|--------|-------|
| $r_0$     | day$^{-1}$ | 0.28  | $\mu_G$  | day$^{-1}$ | 0.03  | $\mu_P$  | day$^{-1}$ | 0.022 |
| $K$       | mg m$^{-2}$ | 400   | $a_G$    | mg m$^{-2}$ | 100   | $a_P$    | m$^{-2}$   | 0–1000 |
| $k$       | m$^{-1}$   | 0.33  | $b_G$    | mg day$^{-1}$ | 0.025 | $b_P$    | day$^{-1}$ | 0.1–10 |
| $R_V$     | day$^{-1}$ | 0.03  | $h_G$    | m      | 0.02  | $h_P$    | m      | 0.02  |
| $h_V$     | m       | 0     | $D_G$    | day$^{-1}$ | 1     | $D_P$    | day$^{-1}$ | 1     |
| $\mu_{vd}$ | day$^{-1}$ | 1     | $v_G$    | m s$^{-1}$   | 0.72  | $v_P$    | m s$^{-1}$ | 0.72  |
| $s_G$     | m$^2$ s$^{-2}$ | 0.001–1 | $s_P$    | m$^2$ s$^{-2}$ | 0.001–1 |
| $\alpha_G$ | mg m$^{-2}$ | 100   | $\alpha_P$ | m$^{-2}$ | 500   |
| $\mu_{Gd}$ | day$^{-1}$ | 1     | $\mu_{Pd}$ | day$^{-1}$ | 1     |

The community dynamics during the stream drying is assumed to be expressed as below using the subscript $X$:  

$$ D_X = D_X \left( 1 - \frac{y_i}{y_i + \alpha_X} \exp \left( \frac{(v_i - v_X)^2}{s_X} \right) \right) \tag{6} $$

where $D_X$ is the maximum migration rate of species $X (= G, P)$ (day$^{-1}$), $y_i$ is a prey density (mg m$^{-2}$ or m$^{-2}$), $\alpha_X$ is the dependence of species $X$ on the prey density (mg m$^{-2}$ or m$^{-2}$), $v_i$ is flow velocity in habitat $i$ (m s$^{-1}$), $v_X$ is the flow velocity which species $X$ prefer (m s$^{-1}$), and $s_X$ is the sensitivity to flow velocity (m$^2$ s$^{-2}$).

The community dynamics during the stream drying is assumed to be expressed as below using the subscript $X$:  

$$ \frac{dx_i}{dt} = -\mu_{Xd}x_i \tag{7} $$

where $x_i$ is the density of species $X (= V, G, P)$ (mg m$^{-2}$ or m$^{-2}$), and $\mu_{Xd}$ is the death rate due to stream drying (day$^{-1}$).

The model mentioned above needs the flow velocity and the water depth as hydraulic parameters. The most suitable way to obtain them is a simulation using hydraulic models, but it is difficult to simulate stream drying. The model needs only the characteristics of riffles and pools in terms of the flow velocity and the water depth. For simplicity, Manning’s equation and the continuity equation were used to calculate the flow velocities in the riffle and the pool, respectively:

$$ v_1 = \frac{1}{n} I^{1/2} h_1^{3/2}, \tag{8} $$

$$ v_2 = \frac{v_1 h_1}{h_2} \tag{9} $$

where $n$ is Manning’s coefficient (s m$^{-1/3}$), $I$ is channel slope. We used $n = 0.025$ which is the minimum value of $n$ in the small stream on the plain (Japan Society of Civil Engineers, 1999) and $I = 7.0 \times 10^{-3}$ (measured at Takano River in Kyoto City, Japan) in this study.

3 Numerical method

Forth order Runge-Kutta method was used for the time integration. Table 1 shows parameters used in the model. Preliminary calculations were performed to obtain suitable initial conditions reflecting their preference for the environment. We used $b_p = \mu_G = \mu_P = 0$ (day$^{-1}$) in these calculations, and other parameters were the same as in Table 1. Referring to Dohi et al. (2006) and Nakano et al. (2008), initial conditions in these calculations were $V_i = 100$ (mg m$^{-2}$), $G_i = 1000$ (m$^{-2}$), $P_i = 1$ (m$^{-2}$) for $i = 1, 2$. The constant water depth in each habitat was set as $h_1 = 0.1$ (m) and $h_2 = 1$ (m). Each calculation was continued until the solution was converged. This procedure means choosing the habitat under the condition of no predation and no mortality. The converged solution was used as the initial condition of the simulation investigating effects of stream drying on community dynamics.

The computation period was $0 \leq t \leq 85$ with a fixed time increment of 0.01 (day). This computation period was enough long to balance the amount of the movement between the riffle and the pool after the stream drying ($t \geq 25$). Two cases of calculation were performed. One is the case in which the flow reduction does not occur, the other is the case in which the flow reduction occurs and finally it causes the stream drying. In this study, the former case is referred to as the non-drying case, and the later case is referred to as the drying case. The initial water depth was the same as the preliminary calculations, and dynamics of the water depth in the drying case was expressed as

$$ \frac{dh_i}{dt} = -0.005. \tag{10} $$

To compare community dynamics between these two cases, population density ratio at time $t$ (PDR$_t$) was defined as below:

$$ \text{PDR}_t = \frac{\text{Population at time } t \text{ in the drying case}}{\text{Population at time } t \text{ in the non-drying case}}. \tag{11} $$

The water depth was constant throughout the computation period in the non-drying case. The flow reduction started at $t = 0$, and ended at $t = 25$ in the drying case. The stream drying occurred at $t = 20$ in the riffle, which was determined by equation (10) and the initial the water depth. Thus, the stream drying period was 5 (day). The water depth recovered to the initial condition at $t = 25$, which represented the rapid
recovery due to the rainfall. After $t = 25$, the flow reduction did not occur. To study how sensitivity of grazers and predators to the flow velocity has effects on differences between community dynamics in the non-drying case and the drying case, $\text{PDR}_{\text{end}} = \text{PDR}_{85}$ was compared between cases of different sets of $(s_G, s_P)$. The range was $0.001 \leq s_G \leq 1$ and $0.001 \leq s_P \leq 1$ and the increment of $s_G$ and $s_P$ was 0.0099 $(\text{m}^2 \text{s}^{-2})$. Small value of $s_G$ and $s_P$ means high sensitivity to flow velocity, so that they tend to move from a present habitat even if the difference between the preferred flow velocity and the flow velocity in the present habitat is very small. Different sets of $(a_P, b_P)$ were also used to study how the predation pressure for grazers had an effect on $\text{PDR}_{\text{end}}$. We used $a_P = 10, 100, 1000$ and $b_P = 0.1, 1, 10$. Small value of $a_P$ and large value of $b_P$ means high predation pressure.

Abe et al. (2002) ($r_0, K$), Misaki and Tsuchiya (2008) ($k$), Stevenson and Peterson (1991) ($R_G$), Mosisch (2001) ($\mu_{G_d}$), Ogitani and Nakamura (2008) ($\mu_G$), Naito et al. (2002) ($\mu_P$), Kohler (1985) and Minshall and Winger (1968) ($D_G$), Lancaster and Ledger (2015) ($\mu_{G_d}$) and Nakano et al. (2008) ($\mu_{P_d}$) were referred to for estimating values of parameters. The value of $b_G$ was determined not to extirpate producers in preliminary calculations. The values of $a_G$ and $a_G$ were assumed to be less than the carrying capacity of producers because carrying capacity is the maximum value of producers in the system. Hence, the initial value of producers in the preliminary calculations $(V_i = 100)$ were used as these values. In contrast, $\alpha_P$ were assumed to be less than the initial value of grazers because the grazers density decreased with time passing, so that the half of the initial value of grazers in the preliminary calculations $(G_i = 1000)$ was used. $\alpha_V$, $h_G$ and $h_P$ are parameters related to their body size. Since propagules of producers are transported by the flow, $h_V = 0$ was assumed. The body size of grazers and predators are larger than the size of propagules of producers, so that $h_G$ and $h_P$ were assumed not to be zero. $h_G = h_P = 0.02$ were used in this study. These values were less than the depth caused by an experimental low flow in Dewson et al. (2007a) in which the drift behavior was seen. The same value of $D_G$ was used as $D_P$. $v_G$ and $v_P$ were determined based on the flow velocity calculated using the initial water depth and the assumption that grazers and predators prefer a riffle.
4 Results

The computational results of PDR$_t$ variation of each species with time are shown in Figure 1 ($(s_G, s_P) = (0.01, 0.01)$ and $(a_P, b_P) = (1000, 0.1)$) and Figure 2 ($(s_G, s_P) = (0.01, 0.01)$ and $(a_P, b_P) = (10, 10)$). Hereafter, the case of $(a_P, b_P) = (1000, 0.1)$ and $(a_P, b_P) = (10, 10)$ are referred to as the low predation pressure case and the high predation pressure case, respectively. PDR$_t$ of producers in the riffle rapidly decreased when the stream drying began. After the water depth recovered, PDR$_t$ increased due to the immigration of propergules from the pool and the reproduction in the habitat. Because producers reproduce until their biomass reached their carrying capacity and the decrease in grazers with time passing, the difference of biomass of producers between the non-drying case and the drying case finally became small, resulting in PDR$_t \approx 1$ (Figure 1, 2).

From the beginning of the flow reduction, grazers and predators moved from the riffle to the pool; their PDR$_t$ decrease in the riffle and increased in the pool. A lot of them died in the riffle during the stream drying, whereas they were able to survive in the pool. Thus, PDR$_t$ of grazers and predators in the riffle tremendously decreased, whereas those in the pool did not decrease during the stream drying. After the stream drying, they rapidly moved from the pool to the riffle, resulting in an increase of their PDR$_t$ in the riffle and a decrease of those in the pool (Figure 1, 2). Changes in PDR$_t$ of grazers in both habitats after the balance of the migration were small in the low predation pressure case (Figure 1). In contrast, it began to increase finally in the high predation pressure case (Figure 2).

Figure 3 and 4 are shown as the examples of results of parameter studies. Figure 3 shows the effect of the sensitivity to the flow velocity of grazers and predators on their PDR$_{end}$ in the low predation pressure case. The producers results are omitted here since their PDR$_{end}$ are approximately 1 in any cases. Effects of $s_G$ and $s_P$ were qualitatively the same in both of the riffle and the pool. PDR$_{end}$ of grazers were higher at lower values of $s_G$. The influence of $s_P$ on PDR$_{end}$ of grazers was little in this case. In contrast, PDR$_{end}$ of predators were affected by both of $s_G$ and $s_P$, and were higher at lower values of $s_G$ and $s_P$.

Figure 4 shows effects of the sensitivity to the flow velocity in the high predation pressure case. The producers results are also omitted because of the same reason in the low predation pressure case. The qualitative tendency of the results on predators was the same as in the low predation pressure case. However, the results on grazers showed a different tendency. First, PDR$_{end}$ of grazers were clearly affected by $s_P$. Larger $s_P$ led to larger PDR$_{end}$ of grazers. Second, PDR$_{end}$ of grazers exceeded 1, which means that the population density at the end of calculation in the drying case was higher than that in the non-drying case. Results using other sets of $(a_P, b_P)$ showed that an increase in $b_P$ strengthened the effect of $s_P$ on PDR$_{end}$ of grazers. However, PDR$_{end}$ did not exceed 1 except the case of $(a_P, b_P) = (10, 10)$.

The rate of decrease per capita in grazers population dynamics due to the predation by predator is proportional to the density of predators ($b_P(P_i/(a_P + G_i))$). Thus, the predation pressure for grazers per capita after the stream drying is much lower than that before the stream drying, whereas the
natural mortality rate is constant throughout the computation period. Therefore, if the predation pressure is originally low relative to the natural mortality rate, the stream drying would have little influence on the rate of decrease of grazers. On the other hand, if the predation pressure is originally high relative to the natural mortality rate, the stream drying would have large influence on the rate of decrease of grazers because of the considerable reduction in the predation pressure. These would result in differences between the low predation pressure case and the high predation pressure case.

Based on the consideration mentioned above, additional numerical calculations were performed to investigate the relationship between $b_p/\mu_G$ and $PDR_{\text{end}}$ of grazers using $a_p = 10, 100, 1000$ and $(s_G, s_P) = (0.01, 0.01)$. The results of the additional calculations are shown in Figure 5. $PDR_{\text{end}}$ of grazers increased with $b_p/\mu_G$. In the case of $a_p = 100$ or $1000$, $PDR_{\text{end}}$ increased slightly with an increase in $b_p/\mu_G$, and $PDR_{\text{end}}$ was less than 1. However, in the case of $a_p = 10$, $PDR_{\text{end}}$ remarkably increases at around $b_p/\mu_G = 250$, and $PDR_{\text{end}}$ became larger than 1 in the range of $b_p/\mu_G > 320$. These results support the consideration mentioned above and mean that community composition after the stream drying depends on the relative strength of the predation pressure for grazers to the natural mortality rate of grazers.
5 Discussion

It should be discussed whether dynamics described by the present model expresses dynamics in previous studies performed as field observations and experiments. The model described that grazers and predators moved to the pool when the flow reduction occurred. As a result, the numerical density of grazers and predators in the riffle became smaller and those in the pool became larger during the flow reduction.

Walters and Post (2011) showed that the numerical density of scrapers which is the finer category of grazers decreased in a riffle and the numerical density of predators increased in a pool, and concluded that these changes in the density were caused mainly by their mobility. Minshall and Winger (1968) found a clear increase in invertebrates in the drift when the flow reduction occurred and indicated that it was related to the change in the water depth and the flow velocity. According to the review by Dewson et al. (2007b), the drift behavior increased when the flow reduction occurred in a lot of studies. These studies support the present results qualitatively.

In contrast, Dewson et al. (2007a) showed that an invertebrate density increased during the flow reduction in a riffle and concluded that it was caused by the reduced wetted area. This is apparently contrary to present results. However, effects of habitat contraction are not included in the present model. Thus, it can not be decided that present results are contrary to results of Dewson et al. (2007a).

The sensitivity to the flow velocity had an effect on the community composition. Both of grazers and predators which have the higher sensitivity resulted in higher PDRend. As a result, the numerical density of grazers and predators in the riffle became smaller and those in the pool became larger during the flow reduction.

Dewson et al. (2007b) showed that an increase in invertebrates in drift was observed when the flow reduction occurred and that it was related to the change in the water depth and the flow velocity. According to the review by Dewson et al. (2007b), the drift behavior increased when the flow reduction occurred in a lot of studies. These studies support the present results qualitatively.

In contrast, Dewson et al. (2007a) showed that an increase in invertebrate density occurred during the flow reduction in a riffle and concluded that it was caused by the reduced wetted area. This is apparently contrary to present results. However, effects of habitat contraction are not included in the present model. Thus, it can not be decided that present results are contrary to results of Dewson et al. (2007a).

The sensitivity to the flow velocity had an effect on the community composition. Both of grazers and predators which have the higher sensitivity resulted in higher PDRend. Although PDR is not an index of the survival, PDR of grazers and predators in this case reflects the survival rate because the variation in PDR in the low predation pressure case was little after the end of the drying (Figure 1). Therefore, these results indicate that rapid emigration from a riffle is beneficial to survival.

PDR of predators depended on the sensitivity of grazers. This would result from the fact that the rate of migration of predators depends on the numerical density of grazers. When the sensitivity of grazers is high, grazers rapidly move to the pool during the flow reduction, resulting in the rapid decrease in the numerical density of grazers in the riffle. Because the less numerical density of grazers means less amount of prey to predators, the rate of migration of predators in the riffle becomes high. Therefore, the sensitivity of grazers has similar effects to the high sensitivity of predators on the rate of migration of predators.

In the case of higher predation pressure relative to the natural mortality rate of grazers, the numerical density of grazers in the drying case became larger than that in the non-drying case because the predation pressure reduced by the stream drying made the rate of decrease of grazers lower. This result explains the reason why the sensitivity of predators to the flow velocity had effects on PDRend of grazers in the high predation pressure case although it had little effects in the low predation pressure case. In the high predation pressure case, PDRend of grazers depended on how many predators survived because it determine the degree of reduction in the predation pressure. Predators could survive more if they had high sensitivity to the flow velocity. Therefore, the high sensitivity of predators had clear effects on PDRend of grazers in the high predation pressure case.

Increase in the numerical density due to the reduced predation pressure by flow reduction in natural rivers was indicated by Zhang et al. (1998). Zhang et al. (1998) developed models to predict richness and abundance of blackfly larvae based on the data at unregulated sites, and used the models to predict the indices at regulated sites. As a result, the blackfly larvae abundance observed at regulated sites with flow reduction was higher than predicted one. In contrast, the abundance of competitors and predators observed at regulated sites with flow reduction was less than predicted one. Zhang et al. (1998), therefore, concluded that the reduced predation pressure and competition were factors of increase in the blackfly larvae abundance. This is the same mechanisms by which a numerical density of grazers in the drying case became larger than that in the non-drying case in the present model. However, Zhang et al. (1998) also concluded that other mechanisms which increased blackfly larvae abundance was reproduction. Thus, the temporal scale in Zhang et al. (1998) was not short-term in terms of Nisbet et al. (1997). Hence, Zhang et al. (1998) is not consistent with the assumption in the present study.

It is also reported in wetland ecosystems that the combination of reduced predation pressure and reproduction makes numerical density of intermittent species higher (Chase and Knight 2003, Dorn 2008). Therefore, reduced predation pressure caused by drying is important to population dynamics of intermittent species in aquatic ecosystems.

The present study indicated the possibility that intermittent species can make the population density higher than that in the non-drying case in the generation due to the reduction of the predation pressure by the stream drying. If it takes too longer time than the period not including reproduction season for intermittent species to achieve it, the effect of reduced predation pressure will not be observed in natural rivers. In such a case, the next generation would get the benefit. How long the positive effect of reduced predation pressure continues is further research.

6 Conclusions

A mathematical model was proposed and its numerical investigation was done to investigate aquatic community dynamics in an intermittent river in the period during which grazers and predators did not reproduce. The model described migration between the riffle and the pool in response to the change in the flow velocity and the water depth caused by the flow reduction. From the results of parameter studies, we concluded that more grazers and predators could survive if they were sensitive to the change in the flow velocity, and that the numerical density of grazers became larger than that in the non-drying case if the predation pressure for grazers were high relative to the natural mortality rate of grazers. The degree of reduced predation pressure is an important factor for population dynamics of intermittent species after stream drying, and further studies are needed in order to investigate how long the positive effects of reduced predation pressure continue.
Acknowledgements
We thank Dr. Koichi Unami, Associate Professor of Kyoto University, and Dr. Junichiro Takeuchi, Assistant Professor of Kyoto University, for their helpful comments.

References
[1] Abe, S., Nagumo, T., and Tanaka, J. (2002): Analysis of benthic algal biomass accrual using the logistic model, *Japanese Journal of Limnology*, 63, pp.209-213, (in Japanese with English abstract).
[2] Bell, V.A., Elliott, J.M., and Moore, R.J. (2000): Modelling the effects of drought on the population of brown trout in Black Brows Beck, *Ecological Modelling*, 127, pp.141-159.
[3] Burke, E.J., Brown, S.J., and Christidis, N. (2003): Drought-induced mechanisms: an experimental and observational approach, *Journal of the North American Benthological Society*, 22(3), pp.401-415.
[4] Chase, J.M., and Knight, T.M. (2003): Drought-induced mosquito outbreaks in wetlands, *Ecology Letters*, 6, pp.1017-1024.
[5] Chester, E.T., and Robson, B.J. (2011): Drought refuges, spatial scale and recolonisation by invertebrates in non-perennial streams, *Freshwater Biology*, 56, pp.2094-2104.
[6] Dawson, Z.S., James, A.B.W., and Death, R.G. (2007a): Invertebrate responses to short-term water abstraction in small New Zealand streams, *Freshwater Biology*, 52, pp.357-369.
[7] Dawson, Z.S., James, A.B.W., and Death, R.G. (2007b): A review of the consequences of decreased flow for instream habitat and macroinvertebrates, *Journal of the North American Benthological Society*, 26(3), pp.401-415.
[8] Dohi, S., Minematsu, Y., Inoue, M., and Miyake, Y. (2006): Comparison of stream fauna between upstream and downstream of intermittent reach, *Environmental systems research*, 34, pp.57-66, (in Japanese with English abstract).
[9] Dorn, N.J. (2008): Colonization and reproduction of large macroinvertebrates are enhanced by drought-related fish reductions, *Hydrobiologia*, 605, pp.209-208.
[10] Japan Society of Civil Engineers (1999): *Hydraulics Formu-

lae*, Maruzen, p.89, (in Japanese).
[11] Kani, T. (1944): Ecology of torrent-inhabiting insects, *Insects*, 1, pp.171-317, (in Japanese).
[12] Kohler, S.L. (1985): Identification of stream drift mechanisms: an experimental and observational approach, *Ecology*, 66(6), pp.1749-1761.
[13] Lake, P.S. (2000): Disturbance, patchiness, and diversity in streams, *Journal of the North American Benthological Society*, 19(4), pp.573-592.
[14] Lake, P.S. (2003): Ecological effects of perturbation by drought in flowing waters, *Freshwater Biology*, 48, pp.1161-1172.
[15] Lancaster, J., and Ledger, M.E. (2015): Population-level responses of stream macroinvertebrates to drying can be density-independent or density-dependent, *Freshwater Biology*, 60, pp.2559-2570.
[16] Ledger, M.E., Brown, L.E., Edwards, F.K., Milner, A.M., and Woodward, G. (2013): Drought alters the structure and functioning of complex food webs, *Nature Climate Change*, 3, pp.223-227.
[17] Magoullick, D.D., and Kobza, R.M. (2003): The role of refugia for fishes during drought: a review and synthesis, *Freshwater Biology*, 48, pp.1186-1198.
[18] Minshall, G.W., and Winger, P.V. (1968): The effect of reduction in stream flow on invertebrate drift, *Ecology*, 49(3), pp.580-582.
[19] Misaki, T., and Tsuchiya, M. (2008): Studies on growth rate of attached algae affected by sun light and turbidity in a river ecosystem, *Environmental Systems Research*, 36, pp.437-444, (in Japanese with English abstract).
[20] Mosisch, T.D. (2001): Effects of desiccation on stream epilithic algae, *New Zealand Journal of Marine and Freshwater Research*, 35, pp.173-179.
[21] Naito, W., Miyamoto, K., Nakanishi, J., Masunaga, S., and Bartell, S.M. (2002): Application of an ecosystem model for aquatic ecological risk assessment of chemicals for a Japanese lake, *Water Research*, 36, pp.1-14.
[22] Nakano, H., Dohi, S., Minematsu, Y., Inoue, M., and Miyake, Y. (2008): Dynamics of animal community in an intermittent river reach, *Environmental systems research*, 36, pp.445-455, (in Japanese with English abstract).
[23] Nisbet, R.M., Diehl, S., Wilson, W.G., Cooper, S.D., Donaldson, D., and Kratz, K. (1997): Primary-productivity gradients and short-term population dynamics in open systems, *Ecological Monographs*, 67(4), pp.535-553.
[24] Ogitani, M., and Nakamura, H. (2008): Distribution and seasonal population change of Heptageniidae nymph in the Oguro river (the branch of Tenryu River), *The Annals of Environmental Science, Shinshu University*, 30, pp.57-66, (in Japanese).
[25] Oki, T., and Kanae, S. (2006): Global hydrological cycles and world water resources, *Science*, 313(5790), pp.1068-1072.
[26] Rader, R.B., and Belish, T.A. (1999): Influence of mild to severe flow alterations on invertebrates in three mountain streams, *Regulated Rivers: Research and management*, 15, pp.353-363.
[27] Stevenson, R.J., and Peterson, C.G. (1991): Emigration and immigration can be important determinants of benthic diatom assemblages in streams, *Freshwater Biology*, 26, pp.279-294.
[28] Tanida, K., and Takemon, Y. (1999): Effects of dams on benthic animals in streams and rivers, *Ecology and Civil Engineering*, 2(2), pp.153-164, (in Japanese with English abstract).
[29] Walters, A.W., and Post, D.M. (2011): How low can you go? Impacts of a low-flow disturbance on aquatic insect communities, *Ecological Applications*, 21(1), pp.163-174.
[30] Wootton, J.T. (1998): Effects of disturbance on species diversity: A multitrophic perspective, *The American Naturalist*, 152, pp.803-825.
[31] Wootton, J.T., Parker, M.S., and Power, M.E. (1996): Effects of disturbance on river food webs, *Science*, 273(5281), pp.1558-1561.
[32] Zhang, Y., Malmqvist, B., and Englund, G. (1998): Ecological processes affecting community structure of blackfly larvae in regulated and unregulated rivers: a regional study, *Journal of Applied Ecology*, 35, pp.673-686.

Discussion open until June 30, 2018