

Norio Yamamura · Arndt Telschow
Kimiko Uchii · Zen'ichiro Kawabata

A basic equation for population dynamics with destruction of breeding habitats and its application to outbreak of cyprinid herpesvirus 3

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Abstract In reproduction, many animal species migrate to local habitats that are appropriate for reproduction and for growth of newly born offspring. The examples are ubiquitous among crabs, freshwater fishes, amphibians, migratory birds, and sea animals. We propose a basic equation for population dynamics of such animals, assuming that the number of offspring is proportional to the area of the local breeding habitats as a first approximation. This equation is very simple to be solved analytically, and useful for representing environmental issues of habitat destruction and degradation. According to the equation, the adult density in breeding habitats increases temporarily during habitat destruction and returns to the original density afterwards. The temporal peak value is higher for a larger proportion of area with destruction, a higher temporal rate of destruction, and a higher survival probability of the adults. In contrast, habitat degradation results simply in a decrease of the adult density in breeding habitats. Using this equation, we will discuss the vulnerability of populations to epidemic diseases due to temporal local high densities with decreasing breeding habitats by human activities, exemplifying an outbreak of cyprinid herpesvirus 3 for wild carps in Lake Biwa.

Keywords Breeding habitat · Mathematical model · Temporal high density · Infectious disease · Cyprinid herpesvirus 3

N. Yamamura (✉) · A. Telschow · K. Uchii · Z. Kawabata
Research Institute for Humanity and Nature, 457-4 Motoyama,
Kamigamo, Kita-ku, Kyoto 603-8047, Japan
E-mail: yamamura@chikyu.ac.jp
Tel.: +81-75-7072354; +81-75-7072310
Fax: +81-75-7072507

A. Telschow
Institute for Evolution and Biodiversity,
Westfalian Wilhelms University, Muenster, Germany

K. Uchii
Department of General Systems Studies,
University of Tokyo, Tokyo, Japan

Introduction

Population dynamics of micro-organisms, especially in aquatic systems, have been described and analyzed basically by the Malthus and logistic equations. The dynamics of macro-organisms with generation overlapping have also been represented approximately by these equations. In these cases, the population occupies a single habitat where reproduction, growth, and survival proceed in the same habitat. However, in reproduction, many macro-animals migrate to local habitats that are appropriate for reproduction and for growth of newly born offspring, called breeding migration (Dingle 1996; Nakazawa and Yamamura 2007). The examples are ubiquitous among crustaceans (Moksnes et al. 1997), fishes (Hendry and Stearns 2004), amphibians (Gittins 1983), reptiles (Luschi et al. 2003), birds (Berthold 2001), and mammals (McConnell and Fedak 1996).

Due to recent human activities, breeding habitats have been intensely destructed and deteriorated (Bretagnolle and Inchausti 2005; Golawski and Meissner 2008; Luschi et al. 2003; Newton 2004). In general, the number of offspring will depend both on the area of the habitat and adult density, but we assume in the model that it depends only on the area because the assumption seems to be satisfied when we consider limited breeding habitats expanded over large geographical regions. That is, when the area becomes half, then the total number of offspring in the population becomes half. We assume this here as the first approximation.

We propose a basic equation for population dynamics of animals with breeding migration where their recruitment depends on the area of local breeding habitats. This equation is a very simple difference equation so that both the population size in the original habitat and the adult density in breeding habitats can be given as analytical solutions. We consider that this equation is useful for analyzing extensive environmental issues of habitat destruction and degradation.

As one of the applications of this equation, we discuss the vulnerability of populations to epidemic diseases, exemplifying an outbreak of the disease caused by cyprinid herpesvirus 3 (CyHV-3), also known as koi herpesvirus in common carp (*Cyprinus carpio* L.), in Lake Biwa (Matsui et al. 2008). The CyHV-3 disease first emerged in Europe in the late 1990s and was detected in Japan in 2003 before it caused mass mortality of wild common carp in Lake Biwa in 2004 (Iida and Sano 2005). More than 100,000 carp, corresponding to ca. 70% of the Lake Biwa population, were killed in the first outbreak with a mortality rate exceeding 80% (Gilad et al. 2003). One of the reasons for such a major outbreak is possibly attributed to the high infection rate of CyHV-3 due to the high density of adult carps. Especially, the decrease of breeding habitats in the lakeshore due to lakeshore protection works and water level control (Biwako Handbook Editors Commission 2007) could accelerate the infection because the latest study suggested that CyHV-3 transmits among adult carps in the breeding habitats while group mating (Uchii et al. 2009, 2010). The phenomenon of disease transmission in the spawning phase has also been reported in salmonoid fishes (Nylund et al. 2003). We discuss the possibility that the outbreak of disease was caused by high host density in breeding habitats due to habitat destruction.

The model

The basic model under constant environment

We consider a population where adults migrate to breeding habitats once a year. The definitions of variables and parameters in the model are summarized in Table 1. The breeding habitats may be several separated habitats or only one habitat where A denotes the total area of breeding habitats. We assume that the habitats have equal reproductive potential per unit area. N_t denotes the numbers of adults just before the migration at year t . We assume that adults distribute proportionally

Table 1 Variables and parameters in the model

N_t	Total population size of adults at year t
N^*	Equilibrium value of population size
x_t	Adult density in breeding sites at year t
x^*	Equilibrium value of adult density
x_τ	Maximum adult density
x_C	Critical density for outbreak
s_N	Survival probability of adults
s_J	Survival probability of juveniles
A_t	Habitat area at year t
A_i	Habitat area before change
A_f	Habitat area after change
b_t	Reproduction at year t
b	Reproduction before change
b'	Reproduction after change
k	Rate of change in habitat area or reproduction
τ	Period of change in habitat area or reproduction

to the area among breeding habitats, the distribution called ideal free distribution (Fretwell and Lucas 1970). Thus, the adult density x_t is equal among habitats:

$$x_t = \frac{N_t}{A} \quad (1)$$

The adults mate there and reproduce b offspring per unit area, so that the total recruitment at the year is bA . We note that there is strong density dependence because the number of offspring is constant independent of the adult number. After the breeding period, adults and bA newly born offspring return to the original habitat and the offspring join in juvenile population. s_N and s_J denote survival probabilities of adults and juveniles until the next breeding period, respectively, assuming the original habitat is large enough that the population density does not affect mortality. The survival probabilities take values between 0 and 1. A part of all juveniles J_{t+1} become adults just before migration period at year $t+1$. Thus the number of adults just before breeding migration N_{t+1} is described as

$$N_{t+1} = s_N N_t + g J_{t+1} \quad (2)$$

where g is conversion rate from juveniles to adults. We can give dynamics of juveniles as

$$J_{t+1} = s_J(1-g)J_t + s_J b A \quad (3)$$

because juveniles that did not become adults and newly born offspring at the previous year survive with probability s_J . As Eq. (3) is a linear difference equation, the solution is analytically given as

$$J_t = s_J^{t-1}(1-g)^{t-1}J_1 + \frac{1-s_J^{t-1}(1-g)^{t-1}}{1-s_J(1-g)}s_J b A \quad (4)$$

where J_1 is the initial number of juveniles at year 1. Applying Eq. (4) to Eq. (2), we can obtain the solution of a non-autonomous linear difference equation for N_t :

$$N_t = s_N^{t-1}N_1 + \frac{s_N^t - s_J^t(1-g)^t}{s_N - s_J(1-g)}gJ_1 + \left(\frac{1-s_N^t}{1-s_N} - \frac{s_N^t - s_J^t(1-g)^t}{s_N - s_J(1-g)} \right) \frac{s_J g b A}{1-s_J(1-g)} \quad (5)$$

where N_1 is the initial number of adults at year 1. The calculation is shown in Appendix 1. Using Eq. (5), we can give the solution of adult density of breeding habitats x_t in Eq. (1).

We can see in Eq. (5) that N_t approaches an equilibrium N^* with any initial values of N_1 and J_1 :

$$N^* = \frac{s_J g b A}{(1-s_N)(1-s_J(1-g))} \quad (6)$$

It is reasonable that the equilibrium value is higher for higher values of b , A , s_J , s_N , or g . Especially when s_N is close to 1, the equilibrium becomes very high due to accumulation of adults. From Eq. (1), the equilibrium value of adult density in breeding habitats is

$$x^* = \frac{s_J g b}{(1 - s_N)(1 - s_J(1 - g))} \quad (7)$$

which is independent of the total area of breeding habitats.

The inverse of g represents the average length of juvenile period, and when $g = 1$, all the juveniles become adults after 1 year. In this case, Eq. (5) is simplified to

$$N_t = s_N^{t-1} N_1 + \frac{1 - s_N^{t-1}}{1 - s_N} s_J b A \quad (8)$$

where N_t monotonously approaches the equilibrium, starting from any initial value. This is the solution for

$$N_{t+1} = s_N N_t + s_J b A \quad (9)$$

which is a special case for Eq. (2).

Habitat destruction and degradation

Equations (1–3) may be useful for describing population dynamics under destruction and/or degradation of breeding habitats because they include parameters representing habitat area A and reproduction per area b in the simple way: destruction and degradation are given as decreases in A and b , respectively. Naturally, regeneration of breeding habitats can be treated as increases in these parameters. Even if the parameters change temporarily as A_t and b_t , Eqs. (1–3) are still non-autonomous linear equations, and the solutions for adult population size and adult population density in breeding habitats can be explicitly written down as functions of initial values, parameters, and time, although the representation may be very complicated in general cases. Here, we give solutions for simple cases where $g = 1$ represented by Eq. (9) but A or b changes to A' or b' , respectively. We assume that the change proceeds at constant rate over τ years. When $\tau = 1$, the change is the most rapid one within 1 year.

Suppose that the habitat area decreased from A to A' , and kept its value A' afterwards. In Eq. (9), this means that A is time-dependent as

$$A_t = A - kt \quad (10)$$

where k denotes decreasing rate of the habitat area per year. Therefore, the period of the change is given as

$$\tau = \frac{A - A'}{k} \quad (11)$$

As shown in Appendix 2, the solution for this case is given as

$$N_t = \frac{s_J b}{1 - s_N} \left(A - k \left(t - 1 - \frac{s_N(1 - s_N^{t-1})}{1 - s_N} \right) \right) \quad (12)$$

for $1 \leq t \leq \tau$

which is a monotonously decreasing function of time. Since the area is a constant A' for $t > \tau$, applying Eq. (8), we have

$$N_t = s_N^{t-\tau} N_\tau + \frac{1 - s_N^{t-\tau}}{1 - s_N} s_J b A' \quad \text{for } t > \tau \quad (13)$$

The initial value N_τ is given from Eq. (12), and the final equilibrium value is

$$N^* = \frac{s_J b A'}{1 - s_N} \quad (14)$$

Using Eq. (11), we can see that N_τ is larger than the equilibrium and thus, Eq. (13) is a monotonously decreasing function of time as well as Eq. (12). We can also show as in Appendix 3 that x_t increases for $1 \leq t \leq \tau$, but decreases for $t > \tau$, finally approaching the original equilibrium value:

$$x^* = \frac{s_J b}{1 - s_N} \quad (15)$$

In conclusion, the adult population size decreases monotonously and the adult density in breeding habitats has a maximum value x_τ at the final year of the change in breeding habitats as shown in Fig. 1a, b.

From Eqs. (11), (12), and 15,

$$\frac{x_\tau}{x^*} = \frac{A}{A'} - \left(\frac{A}{A'} - 1 \right) \frac{1}{\tau} \left(\tau - 1 - \frac{s_N(1 - s_N^{\tau-1})}{1 - s_N} \right) \quad (16)$$

As shown in Appendix 4, the value of the right-hand side is higher for larger A/A' , smaller τ and larger s_N . In other words, the temporal increase in the adult density in breeding habitats for habitat destruction is more intense when the destruction area is larger, the destruction is faster, and the adult mortality is lower. The quantitative parameter dependence of Eq. (16) is shown in Fig. 2. We can see that x_τ/x^* is equal to A/A' when $\tau = 1$, which is evident from the equation. In this case, it holds, for example, that x is doubled when A is made half. For smaller values of s_N , as in Fig. 2a, x_τ/x^* decreases much as τ becomes large, but for larger values of s_N as in Fig. 2c, x_τ/x^* does not decrease much as τ becomes large. This is because the decrease of adult population is delayed in species with long-lived adults even if the habitat destruction is slow.

For habitat degradation, suppose that the habitat quality decreased gradually from b to b' , and kept its value b' afterwards. In Eq. (9), this means

$$b_t = b - kt \quad (17)$$

where k denotes decreasing rate of the habitat quality per year. Therefore, the period of the change is given as

$$\tau = \frac{b - b'}{k} \quad (18)$$

By a similar calculation as in the previous section, the solution for this case is given as

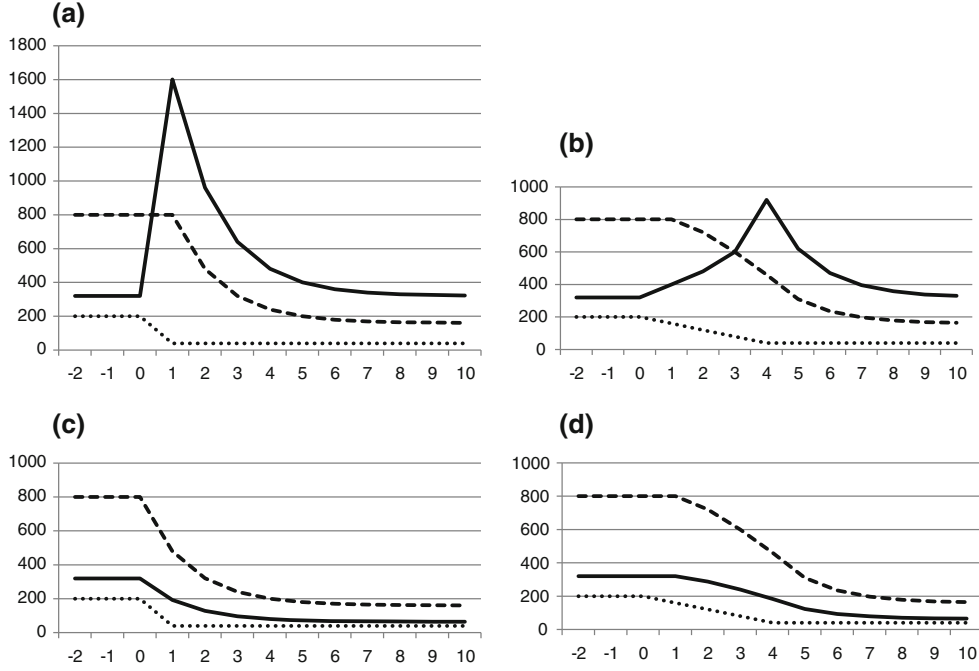


Fig. 1 Patterns of destruction (change in A) and degradation (change in b), shown by *dotted lines*, with the dynamics of adult population size (N_t), shown by *broken lines*, and density (x_t), shown by *solid lines*, in breeding habitats. $s_J = 0.2$, $s_N = 0.5$. **a** Rapid habitat destruction ($\tau = 1$, $A = 100$, $A' = 20$, $b = 20$), **b** slow

habitat destruction ($\tau = 4$, $A = 100$, $A' = 20$, $b = 20$), **c** rapid habitat degradation ($\tau = 1$, $A = 100$, $b = 20$, $b' = 4$), and **d** slow habitat degradation ($\tau = 4$, $A = 100$, $b = 20$, $b' = 4$). In the figure, the value of A is doubled, that of b is taken ten times, and that of x_t is taken 40 times

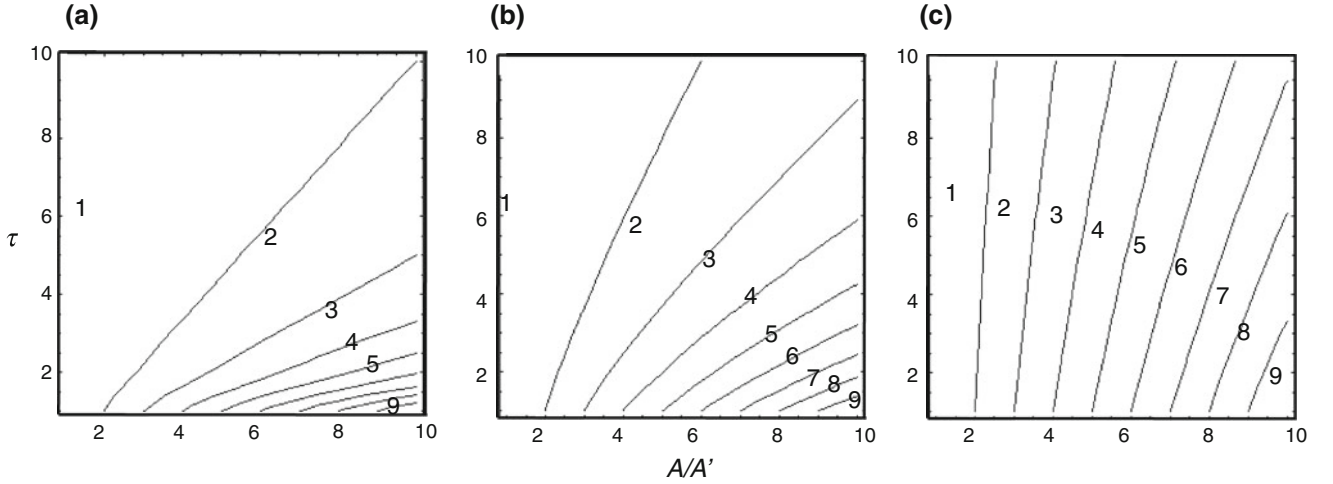


Fig. 2 Parameter dependence of x_t/x^* on τ and A/A' in Eq. (16) is shown as isoclines for **a** $s_N = 0.1$, **b** $s_N = 0.5$, and **c** $s_N = 0.9$, where all juveniles become adults after 1 year ($g = 1$). Eight lines in each panel represent isocline of x_t/x^* , which values are 2 to 9 from *left to right*. The value 1 corresponds to the vertical axis

$$N_t = \frac{s_J A}{1 - s_N} \left(b - k \left(t - 1 - \frac{s_N (1 - s_N^{t-1})}{1 - s_N} \right) \right) \quad (19)$$

for $1 \leq t \leq \tau$

which is a monotonously decreasing function of time. Applying Eq. (8) further, we have

$$N_t = s_N^{t-\tau} N_\tau + \frac{1 - s_N^{t-\tau}}{1 - s_N} s_J b' A \quad \text{for } t > \tau \quad (20)$$

Using Eq. (18), we can see that N_τ is larger than the final equilibrium value:

$$N^* = \frac{s_J A b'}{1 - s_N} \quad (21)$$

and thus, Eq. (20) is a monotonously decreasing function of time as well as Eq. (19). In this case, x_t is simply represented by Eq. (1) and the changing pattern is the same as that of N_t as shown in Fig. 1c, d.

In conclusion, the total adult population size decreases to a new equilibrium both for habitat destruction and degradation. On the other hand, the adult density in breeding habitats temporarily increases for habitat

destruction before it returns to the original equilibrium, but that for habitat degradation decreases to a new equilibrium.

Application to CyHV-3 in Lake Biwa

As stated in the “Introduction”, the outbreak of CyHV-3 disease caused mass mortality of wild common carp at Lake Biwa in Japan (Matsui et al. 2008). Infection of CyHV-3 primarily occurred in adults (Uchii et al. 2009) and the mortality peak came just after the breeding season (Biwako Handbook Editors Commission 2007), strongly suggesting that the infection occurred at the breeding habitats. One reason for this outbreak is possibly attributed to the high infection rate of CyHV-3 due to high density of adult carps in breeding habitats, the area of which has recently decreased intensely by human activities. We apply the model to this system, and discuss how habitat destruction can promote disease outbreaks.

Since the common carp in Lake Biwa starts to breed at age 3 or 4 (Barus et al. 2002; Miyadi et al. 1976), we have to use the model for the case where g is smaller than one in Eqs. (2) and (3). Assuming that habitat destruction from A to A' is represented by Eq. (10) for $1 \leq t \leq \tau$, we can write down the explicit solution (see Appendix 5):

$$J_t = \frac{s_J b}{1 - s_J(1 - g)} \times \left(A - k \left(t - 1 - \frac{s_J(1 - g)(1 - s_J^{t-1}(1 - g)^{t-1})}{1 - s_J(1 - g)} \right) \right) \quad (22)$$

and

$$N_t = s_N^t \frac{s_J b g A}{(1 - s_N)(1 - s_J(1 - g))} + g \sum_{i=1}^t s_N^{t-i} J_i \quad (23)$$

Although we could not analytically examine patterns of changes in N_t and $x_t = N_t/A_t$, our numerical calculations suggested that N_t decreases monotonously and x_t has a maximum value x_τ at the final year of the change in breeding habitats. This is the same qualitative behavior as in the previous section where $g = 1$. The parameter dependence on x_τ/x^* has also the same trend, that is, x_τ/x^* is higher for larger A/A' , smaller τ and larger s_N . Moreover, it is lower for smaller g . When $0 < g < 1$, x_τ/x^* depends on s_J also, and it is higher for larger s_J . The parameter dependence of x_τ/x^* is shown in Fig. 3 for the case $g = 0.23$. This value corresponds to the inverse of an average time until maturation of 3.5 that is the case in common carp. Comparing Figs. 3 and 1, we see that both g and s_J have a rather minor effect on x_τ/x^* while the main factors determining peak density are destruction proportion A'/A , destruction period τ and adult survival rate s_N .

A general conclusion of (theoretical) epidemiology is that a disease enters an epidemic state when the host

population density exceeds a critical value (Anderson and May 1991). This is in concordance with the many empirical examples where infectious diseases emerge in the season when the hosts aggregate (Altizer et al. 2006). In case of CyHV-3 disease in Lake Biwa, the virus is suggested to transmit among adult carps by contact through group mating in the limited breeding habitats where the adult density is much higher than that in other seasons (Uchii et al. 2009, 2010). We consider that the outbreak of disease may occur within one breeding season, starting from a few infected individuals, where there is no recruitment of adult individuals. In this condition, the simplest model of epidemiology (Kermack and McKendric 1927) can be applied, and there is a threshold for initial density of individuals above which the infectious disease spreads. The threshold value is represented by death, transmission, and recovery rates. We denote this threshold density by x_C .

Suppose that

$$x^* < x_C < x_\tau \quad (24)$$

where x^* is the adult density before habitat destruction and x_τ the peak density during habitat destruction. As the adult density at the beginning of breeding season increases monotonically towards x_τ , it inevitably exceeds x_C until year τ . The outbreak of disease occurs at the year when the density exceeds x_C first. Thus Eq. (24) is the condition for a disease outbreak to occur due to habitat destruction. In case of CyHV-3 in Lake Biwa, accurate parameter values are only known for s_N and g : s_N is estimated as 0.875 by Fujiwara (Shiga Prefectural Fisheries Experimental Station, <http://www.pref.shiga.jp/g/suisan-s/seika/files/seikah1711.pdf> [in Japanese]), and g can be given as the inverse of maturation age 3–4 (Barus et al. 2002; Miyadi et al. 1976).

From Eq. (24), it follows that a CyHV-3 outbreak is likely to occur for parameter values that result in high x_τ values. For Lake Biwa it is well known that the number and size of breeding habitats decreased severely over the last decades due to the operation of Lake Biwa Comprehensive Development Plan (Biwako Handbook Editors Commission 2007). We also showed that the peak density x_τ becomes considerably high when s_N is high such as 0.875. Although these factors are likely to increase x_τ , and thus possibly promote disease outbreak, the observed data are not sufficient for determining whether the disease outbreak actually occurred due to habitat destruction. For this, we need more detailed information of the habitat destruction pattern, the original adult density in breeding habitats x^* and the critical epidemic density x_C in CyHV-3 for wild carps in Lake Biwa.

Discussion

We formulated a basic equation for animal population dynamics with destruction and degradation of breeding habitats. We obtained explicit solutions for the equation

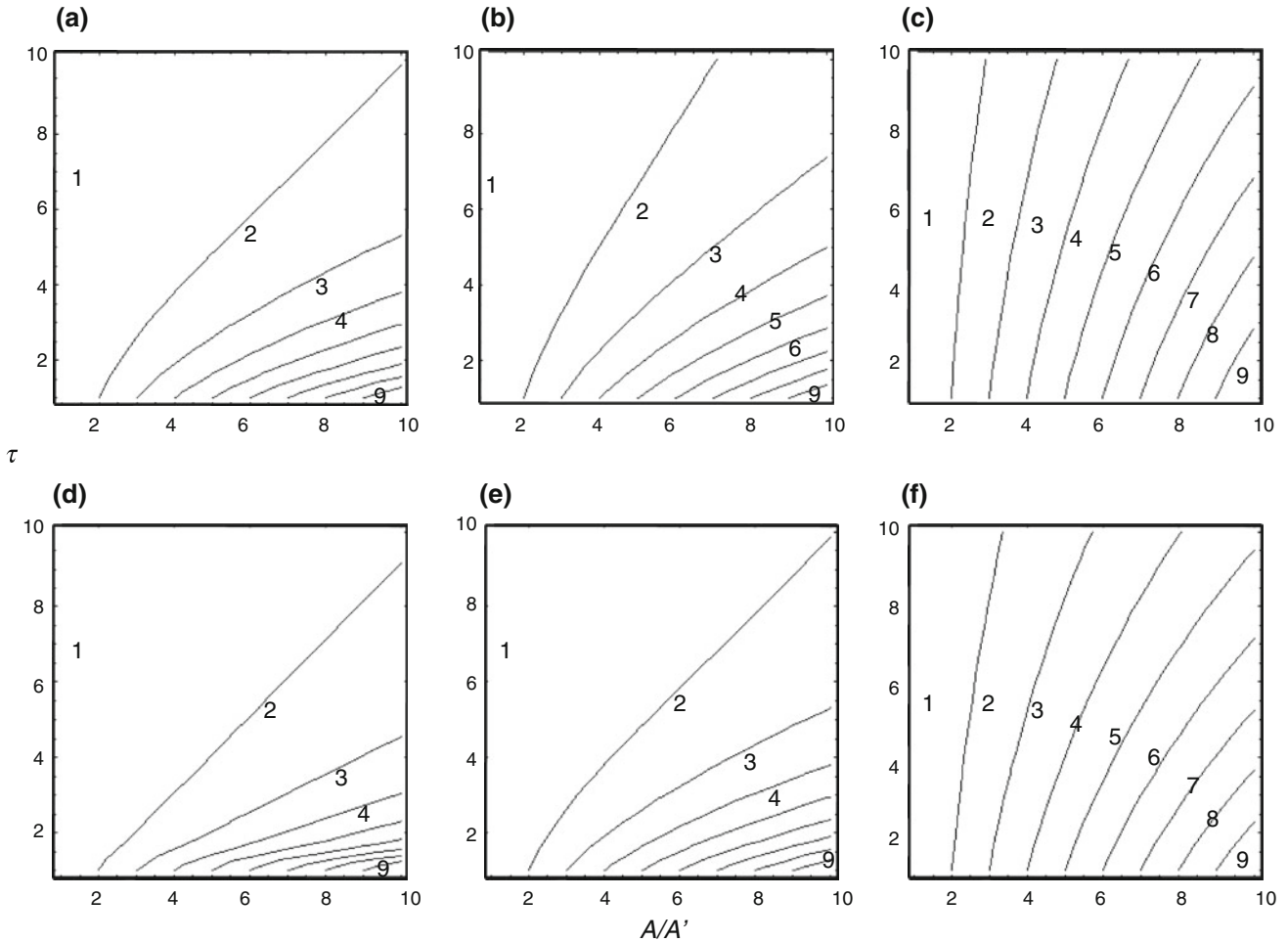


Fig. 3 Parameter dependence of x_t/x^* obtained from Eqs. (22) and (23) is shown as isoclines, where juveniles become adults with a probability ($g = 0.23$). Eight lines in each panel represent isocline of x_t/x^* , which values are 2–9 from left to right. The value 1

corresponds to the vertical axis. **a** $s_N = 0.1$ and $s_J = 0.1$, **b** $s_N = 0.5$ and $s_J = 0.5$, **c** $s_N = 0.9$ and $s_J = 0.9$, **d** $s_N = 0.1$ and $s_J = 0.02$, **e** $s_N = 0.5$ and $s_J = 0.1$, and **f** $s_N = 0.9$ and $s_J = 0.18$

and applied them to the outbreak of cyprinid herpesvirus 3 in common carps in Lake Biwa. Although we could not determine quantitatively whether the outbreak occurred due to habitat destruction because of lack of detailed data, we can gain interesting insights from a qualitative discussion through the model.

Many other fishes smaller than common carp in Lake Biwa also utilize lakeshore habitats as breeding sites. One might therefore ask why no epidemic disease was reported in these species, given that a severe disease occurred in common carps. Our model gives the following explanation. Small fish species have generally smaller values of s_N when compared to those of common carp. Therefore, the effect of temporal increase in population density is less pronounced in small fishes, diminishing the risk of disease outbreak.

A general conclusion about threshold population density of disease outbreak by Anderson and May (1991) is very important in our context because almost all CyHV-3 outbreaks in Japan are connected to the high density of carp. According to Iida and Sano (2005),

the first major outbreak in Japan occurred in an aquaculture farm in Lake Kasumigaura in October, 2003. The following year, many outbreaks occurred throughout Japan both in farms and lakes and rivers in spring. In addition to Lake Biwa, the large outbreaks occurred in several wild habitats in 2004, such as Tama River, Tsurumi River, and Chikugo River (Ministry of Agriculture, Forestry and Fisheries of Japan, http://www.maff.go.jp/j/syouan/tikusui/koi/pdf/07_summary.pdf [in Japanese]). In those areas, as well as in Lake Biwa, breeding habitats may have been decreased due to shore protection. Also, a large amount of juveniles seem to have been released, and the adult density might be increased by this artificial effect. The high adult density in breeding habitats may be the reason of outbreak of CyHV-3, whether it is caused by habitat destruction, juvenile release or both.

After 2004, no large disease outbreak has occurred in Lake Biwa. Why is that so? The model suggests that the adult density decreases in breeding habitats after stopping destruction of the habitats. The host density also

decreased largely by the disease mortality itself, which may have made the density lower than the critical density of disease outbreak. Another factor suppressing the outbreak will be acquisition of immunity in infected but survived carps. A high proportion of common carps in Lake Biwa seem to acquire and maintain immunity (Uchii et al. 2010), which works as resistance to the disease at the population level (John and Samuel 2000). The relative importance between density and immunity on suppression of disease outbreak in Lake Biwa and other wild habitats should be further studied.

The large outbreaks of CyHV-3 disease occurred in several habitats in Lake Biwa only in 2004. Considering that the symptoms of the disease occur within several days after infection and the infectivity of CyHV-3 is very high (Ilouze et al. 2006), it is reasonable to assume that the disease can spread within one breeding season. This justifies our approach to separate the timescales of the (short-term) infection dynamics and the (long-term) population dynamics. We remark that this might not be appropriate for infectious diseases of other wild animals. For the general case with timescales of infection and population dynamics of same order, more elaborated theories will be needed for analyzing the relationship between habitat destruction and disease outbreak.

Our main theoretical finding is that the adult density in breeding habitats increases temporarily during habitat destruction and returns to the original value afterwards. The temporal increase is higher for a larger area of destruction, a higher rate of destruction, and a higher survival probability of the adults. In contrast, habitat degradation results simply in a decrease of the adult density in breeding habitats. In real ecological systems, habitat destruction and degradation will often occur simultaneously. From a theoretical point of view, however, it is important to clarify the characteristics of population changes for destruction and degradation, separately.

Our results, represented by a few simple equations, are based on several assumptions in the model. First, population structure is composed of only juveniles and adults, and the transition from juveniles to adults is represented by a single parameter. We can easily extend the model and include more precise age- or size-structure. So far as we assume that recruitment is proportional to the area of breeding habitats, the equation is still a non-autonomous linear equation for which the solution can be written down explicitly although the expression becomes quite cumbersome. Second, an ideal free distribution is assumed for adults among breeding habitats. In reality, habitats may be spatially structured as a metapopulation (Opdam 1991), which can intensely affect the dynamics of the population. Therefore, our model should be modified when applied to a specific system for which information for population structure can be obtained.

The assumption that recruitment is proportional to the area of breeding habitats was adopted as a first approximation. The reasoning behind this is that recruitment depends on the total amount of resources

that is available for a population in a certain area. This is supported by several experimental studies. For example, Martin (1987) stated that food is, in general, an important limiting factor of breeding success in birds, and Golawski and Meissner (2008) showed that the area of breeding habitats within territories was correlated with the number of nestlings in the Red-backed Shrike. Newton (2004) pointed out that it is not just the area size of habitats that determines the reproductive output of a population but that habitat fragmentation can also have a strong effect. Our model can be applied to such cases if we define an “effective area” which is proportional to recruitment instead of the real area.

Our model can be formally applied to regeneration of new breeding habitats of endangered species. In this case, the total population size will increase monotonously to a new equilibrium and the adult density in breeding habitats will show a temporal decrease. A main model assumption is, however, that recruitment is proportional to the area of breeding habitats, supposing that individuals of the population utilize the resource thoroughly in the area. Although the model is less suitable to cases of regeneration of habitats because individuals may not utilize resources of new habitats exhaustively, we may surmount this shortage by using again the concept of “effective area”.

Habitat destruction and degradation by human activities are a major issue for loss of biodiversity and degradation of ecosystem service at the global scale (Millennium Ecosystem Assessment 2005). We provide here a basic model that can represent directly habitat destruction and degradation, and that has explicit and simple solutions. We expect this model will be extensively applied for various problems of habitat destruction and degradation with some necessary modification, including more realistic assumptions when applied to concrete situations.

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Appendix 1

The calculation of Eq. (5)

Using Eq. (3) repeatedly,

$$\begin{aligned} J_t &= s_J(1-g)J_{t-1} + s_JbA = s_J(1-g)(s_J(1-g)J_{t-1} + s_JbA) \\ &\quad + s_JbA = \dots = s_J^{t-1}(1-g)^{t-1}J_1 + (1+s_J(1-g) \\ &\quad + \dots + s_J^{t-2}(1-g)^{t-2})s_JbA \end{aligned}$$

Summing up the geometric progression, we have Eq. (4).

Using Eq. (2) repeatedly,

$$\begin{aligned} N_t &= s_N N_{t-1} + gJ_t = s_N(s_N N_{t-2} + gJ_{t-1}) + gJ_t \\ &= \dots = s_N^{t-1} N_1 + (J_t + s_N J_{t-1} + \dots + s_N^{t-2} J_1)g \end{aligned}$$

Inserting Eq. (4) and summing up the geometrical progression, we have Eq. (5)

Appendix 2

The calculation of Eq. (12)

From Eq. (9) with Eq. (10),

$$N_{t+1} - N_t = s_N(N_t - N_{t-1}) - s_J b k$$

Using this equation repeatedly, we have

$$\begin{aligned} N_{t+1} - N_t &= s_N(N_t - N_{t-1}) - s_J b k = s_N(s_N(N_{t-1} - N_{t-2}) \\ &\quad - s_J b k) - s_J b k = \dots = s_N^{t-1}(N_1 - N_0) \\ &\quad - (1 + s_N + \dots + s_N^{t-2})s_J b k \end{aligned}$$

As $N_1 = N_0 = N^*$, we have

$$N_{t+1} - N_t = -\frac{1 - s_N^{t-1}}{1 - s_N} s_J b k \quad (25)$$

Thus

$$\begin{aligned} N_t &= N_1 - \sum_{i=2}^t \frac{1 - s_N^{i-1}}{1 - s_N} s_J b k \\ &= \frac{s_J b A}{1 - s_N} - \frac{s_J b k}{1 - s_N} \left(t - 1 - \frac{s_N(1 - s_N^{t-1})}{1 - s_N} \right) \end{aligned}$$

This is equivalent to Eq. (12).

Appendix 3

The change in x_t for habitat destruction from A to A'

From Eqs. (1) and (10)

$$\begin{aligned} x_{t+1} - x_t &= \frac{N_{t+1}}{A - k(t+1)} - \frac{N_t}{A - kt} \\ &= \frac{A(N_{t+1} - N_t) - kt(N_{t+1} - N_t) + kN_t}{(A - k(t+1))(A - ktA)} \\ &= \frac{A(N_{t+1} - N_t) - kt(N_{t+1} - N_t) + kN_0 + k \sum_{i=0}^{t-1} (N_{i+1} - N_i)}{(A - k(t+1))(A - ktA)} \end{aligned} \quad (26)$$

From Eq. (25),

$$\begin{aligned} A(N_{t+1} - N_t) + kN_0 &= -\frac{1 - s_N^{t-1}}{1 - s_N} s_J b k A + k \frac{s_J b A}{1 - s_N} \\ &= \frac{s_N^{t-1}}{1 - s_N} s_J b k A > 0 \end{aligned}$$

and

$$-kt(N_{t+1} - N_t) + k \sum_{i=0}^{t-1} (N_{i+1} - N_i) > 0$$

because

$$N_{i+1} - N_i > N_{t+1} - N_t \text{ for } 0 \leq i \leq t-1$$

using Eq. (25). Therefore, the numerator of Eq. (26) is positive, which means x_t increases monotonously for $1 \leq t \leq \tau$. Since A_t is constant for $t > \tau$, x_t decreases to the original equilibrium.

Appendix 4

Parameter dependence in Eq. (16)

In Eq. (6),

$$\frac{1}{\tau} \left(\tau - 1 - \frac{s_N(1 - s_N^{\tau-1})}{1 - s_N} \right) = 1 - \frac{1 + s_N + s_N^2 + \dots + s_N^{\tau-1}}{\tau} \quad (27)$$

is a decreasing function of s_N , and as $A/A' > 1$, x_τ/x^* is an increasing function of s_N . Since each term of the numerator of the second term in Eq. (27) is not larger than 1 and the number of terms is τ , Eq. (27) is positive and clearly smaller than 1. Therefore, x_τ/x^* is an increasing function of A/A' . The second term of Eq. (27) is an average of geometric series s_N^i , the average is smaller for the larger number of terms. Therefore, the average is a decreasing function of τ , and so x_τ/x^* is also a decreasing function of τ .

Appendix 5

The calculation of Eqs. (22) and (23)

From Eq. (3) with Eq. (10),

$$J_{t+1} - J_t = s_J(1 - g)(J_t - J_{t-1}) - s_J b k$$

By the similar calculation as in Appendix 2, we have Eq. (22).

Using Eq. (2) repeatedly,

$$\begin{aligned} N_t &= s_N N_{t-1} + gJ_t = s_N(s_N N_{t-2} + gJ_{t-1}) + gJ_t \\ &= \dots = s_N^t N_0 + (J_t + s_N J_{t-1} + \dots + s_N^{t-2} J_1)g \end{aligned}$$

Inserting the equilibrium value before the habitat change in Eq. (6) into N_0 , we have Eq. (23).

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