

An Information-Theoretic Model for Managing Predator–Prey Ecosystems Facing Climate Changes

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Abstract—We have developed a theoretical model for managing predator–prey ecosystems undergoing climate-related changes. This model estimates the amount of information transferred between the number of predator and prey categories, and the uncertainty of the number of the prey categories in a predator–prey ecosystem as measured by Shannon entropy, which is achieved by predation events and decay in the ecosystem. We examined the model with a numerical experiment using a well-studied bass–crayfish predator–prey ecosystem in a closed lake. Furthermore, we have evaluated the model comparison using Lotka–Volterra equation, which is a conventional predator–prey ecosystem model.

Keywords—*Mathematical model; Information theory; Predator–prey ecosystem; Climate change.*

I. INTRODUCTION

This article is a revised version of conference paper presented at the Eleventh International Conference on Bioinformatics, Biocomputational Systems and Biotechnologies [1]. This extended version of the original paper offers results from our preliminary studies on a mathematical model for predator–prey ecosystems facing climate changes.

Over the past three decades, environmental changes, such as global warming, desertification, and air pollution have become much worse, raising the concerns of their effects on life systems [2]. Previous studies on the environmental responses of life systems focused on specific networks such as the genetic and ecological networks [3,4].

Life system takes orderliness from its environment and sustains itself at a fairly high level of orderliness, or at a fairly low level of thermodynamic entropy [5]. Kauffman investigated on how the dynamic behavior of a Boolean network suddenly becomes orderly. He made the analogy that the behavior approximates cell fate which is characterized by expression patterns of multiple genes in an organism [6,7]. Barabási and Albert found that generic mechanisms form an ordered network structure with a scale-free property [8]. However, the previous observations were not validated by a mathematical model that clarifies the varying orderliness of biological systems undergoing environmental changes.

Recent studies for mathematical model of predator-prey ecosystems, examined the model with double free boundaries [9], developed an agent-based model of an ecosystem to predict interactions of competition and predation [10]. Further studies showed a simple two-species predator-prey ecosystem that can display rich dynamical complexity when the prey evolves in response to predation, based on coupled differential equations [11].

Environmental factors including air pollution could influence the prey-predators relation [12,13]. Atmospheric change may influence predator-prey interactions by altering prey quality, defensive behavior of prey, predator location, prey community structure and/or predator competition [12]. Fish behavior can be altered by contaminants as a means that the mummichog from more contaminated areas are poor predators and slower to capture active prey, the grass shrimp [13]. Thus, to study the simultaneous effect of pollution stress and the effect of infection in an interacting species is

important for deriving the feasible situations of an ecosystem [14].

In this study, we quantify the environmental stimuli and orderliness achieved in state variables in life systems with Shannon entropy based on their probability distributions. The state variables represent the state of the system, such as expression levels in a genetic network. We then hypothesize a relationship between environmental changes and orderliness in the life systems. We validate the hypothetical relationship using numerical experiments based on a computational model of differential equations for the ecosystem with the climate-shift model [15]. In the model, a climate-attribute change is modeled as a shift in the probability distribution of the climate attribute. We evaluate control performance by a difference of Shannon entropy as $\Delta H \equiv H(X) - H(X')$, where X and X' represent the state variable X at t_0 and at t_1 (unit time after t_0), respectively [16]. The Shannon entropy $H(X)$ indicates the uncertainty of X [17]. We elucidate predator-prey ecosystem degradation, which is unavoidable, in the current progression of climatic changes and develop an information-theoretic framework for performing systematic countermeasures against climate change. The details are given below under Section II: formulation, Section III: numerical experiments, and Section IV: comparison with Lotka-Volterra equations. Finally, in Section V, we conclude with final remarks and discuss future works.

II. FORMULATION

A closed lake is considered in our study as a predator-prey ecosystem (Figure 1a). The probability distribution of the number of viable predators, known as “capacity”, varies according to the climate shift of a climate attribute against a range of climate attributes (survival region) in which the predator is viable. The predator capacity decreases with an

increase in climate shift (Figure 1b). We derived Equation (1), which shows that the Shannon entropy ($H(Y)$) of the number of predators decreases with an increase in the climate shift (Figure 1c) based on a numerical analysis (see “Numerical Analysis for Equation (1)” at the end of this section):

$$H(Y)_{e+\delta e} \leq H(Y)_e, \quad (1)$$

where e and δe indicate the level of the climate attribute and its increment. Generally, $I(X;Y) \leq \min\{H(X), H(Y)\}$, thus

$$I(X;Y)_{e+\delta e}^U \leq I(X;Y)_e^U, \quad (2)$$

where $I(X;Y)^U (\equiv H(Y))$ denotes an upper bound of the mutual information between X and Y . The causal relationship in the ecosystem model shown in Figure 1a is derived and shown as in Figure 2. Predators limit the growth of prey by consuming the prey [18]. Increases or decreases in the prey population lead to corresponding increase or decrease in the number of predators. This scenario configures a closed-loop circuit into which an environmental stimulus can be introduced. An information-theoretic limit (3) for closed-loop control systems [16]:

$$\Delta H_{\text{closed}} \leq \Delta H_{\text{open}}^{\text{max}} + I(X;Y), \quad (3)$$

where ΔH_{closed} and $\Delta H_{\text{open}}^{\text{max}}$ are the Shannon entropy reduction of the state variable X in a closed-loop control system and the maximum Shannon entropy reduction of the state variable X in a general open-loop control system, respectively, over the transition $X \rightarrow X'$ between t_0 and t_1 (unit time after t_0). We merged Equation (2) with the

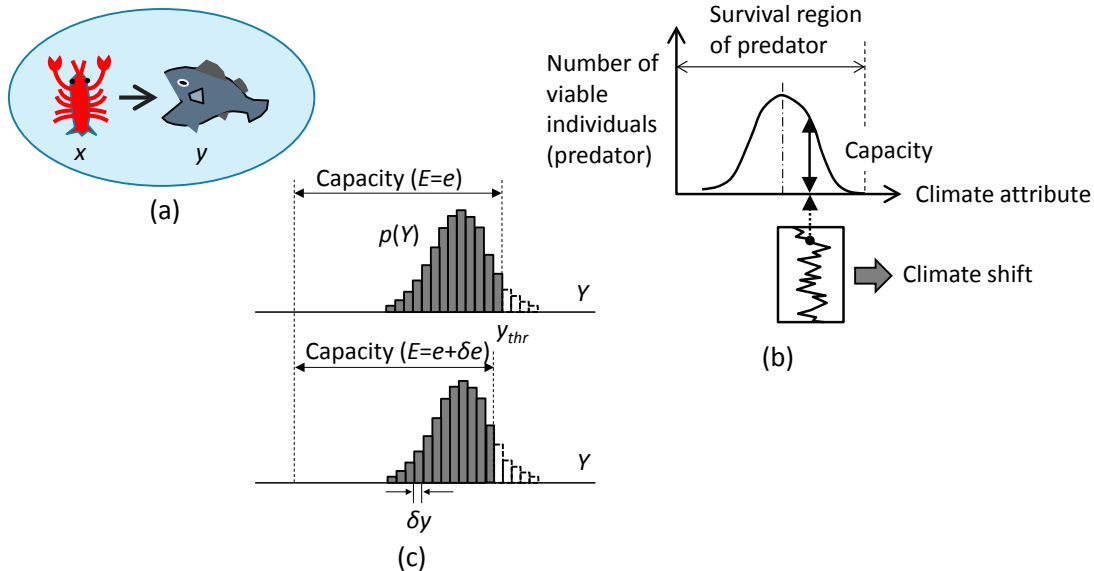


Figure 1. An ecosystem model: (a) Predator-prey ecosystem in a closed lake. The arrow denotes feeding relationship. (b) Number of viable predators and climate shift. (c) Probability distribution of the number of predators before (upper panel) and after (lower panel) an increase in climate shift by δe .

information–theoretic limit for closed-loop control systems (Equation (3)), to derive Equation (4):

$$\Delta H_{e+\delta e}^U \leq \Delta H_e^U, \quad (4)$$

where $\Delta H^U (\equiv \Delta H_{\text{open}}^{\text{max}} + I(X;Y)^U)$ denotes an upper bound of the Shannon entropy reduction of the state variable X (the number of prey individuals) over the transition $X \rightarrow X'$ between t_0 and t_1 . It represents the control performance of the predator–prey ecosystem. Equations (2) and (4) suggest that the mutual information between the number of prey individuals (X) and predators (Y), as well as the control performance of the predator–prey ecosystem, decreases with an increase in climate shift. Furthermore, the control performance of the predator–prey ecosystem appears to degrade from the level of a closed-loop control system to an open-loop control system, based on the information–theoretic limits of control (Equation (3)).

The derived inequalities of Equations (1), (2) and (4) are independent of the dynamics of the target ecosystem. Thus, our model can be applied to analyses of unknown dynamics in ecosystems.

It should be noted that the decrease in the reduction of uncertainty in the state variable (represented by ΔH^U in Equation (4)) is unavoidable under the progressive environmental change ($\delta e \geq 0$).

Numerical Analysis for Equation (1)

We calculated the Shannon entropy of the number of predators $H(Y)$ against the climate shift (Figure 3). We

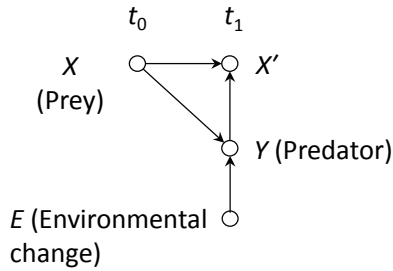


Figure 2. Causal relationship in the ecosystem model represented in a directed acyclic graph [19].

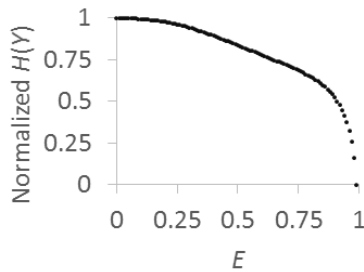


Figure 3. Normalized $H(Y)$ against the climate shift.

assumed that Y (number of predators) follows a normal distribution, and calculated a normalized $H(Y)$. The normalized $H(Y) = 1$ and 0 indicate that the Shannon entropy $H(Y)$ is equivalent to the Shannon entropy at $E=0$ (the region between $\mu-3\sigma$ and $\mu+3\sigma$ of the normal distribution lies inside of the capacity of the predator) and 1 (the region between $\mu-3\sigma$ and $\mu+3\sigma$ of the normal distribution gets out of the capacity of the predator), respectively. Where, μ and σ are the mean and the standard deviation of the normal distribution of the number of predators, respectively. As the result the normalized $H(Y)$ continuously decreases (Figure 3).

III. NUMERICAL EXPERIMENTS

Equations (2) and (4) suggest the two relationships: mutual information between the number of prey and predator individuals decreases with an increased climate shift (relationship-1). Control of the number of prey individuals becomes worse in a predator–prey ecosystem with an increased climate shift (relationship-2).

A. Numerical Experiment Methods

To validate these two relationships and evaluate management actions for protecting predator–prey ecosystems against climate-related changes, we conducted numerical experiments in which we used a well-studied nondimensionalized bass–crayfish predator–prey ecosystem in a closed lake [20]:

$$\begin{aligned} \frac{dx}{dt} &= x(1-x-\alpha y) - \frac{\delta yx^2}{\kappa^2 + x^2} \\ \frac{dy}{dt} &= \gamma y(1-\beta x-y) - \varepsilon \frac{\delta yx^2}{\kappa^2 + x^2} \end{aligned} \quad (5)$$

where $x = X/K_x$, $y = Y/K_y$ (X and Y : crayfish and bass biomass, K_x and K_y : crayfish and bass carrying capacity), and α , β , δ , γ , ε , and κ are model parameters (positive real constants), and were set to 0.7, 0.9, 0.075, 1.5, 0.01, and 0.1, respectively. Random noise with normal distribution with mean=0, and variation=0.02² was added to x and y . The right side of Equation (5) represents Lotka–Volterra-style intra- and interspecific competition and predation [4].

B. Validation of the Degradation of the Mutual Information and the Control Performance Suggested by the Model

The nondimensionalized biomass of bass y was limited to mimic the decreased capacity by the increasing climate shift. The decrease of the mutual information between the nondimensionalized biomass of crayfish x and bass y by the decreasing capacity for the nondimensionalized biomass of bass was observed (Figure 4). The result suggests the relationship-1 is valid. The increase of the control bias by the decreasing capacity for the nondimensionalized biomass of bass was observed (Figure 5). This result suggests the relationship-2 is valid.

C. Evaluation of the Management Actions for Protecting Predator–Prey Ecosystems Against Climate-Related Changes

From the definitions $I(X;Y)^U \equiv H(Y)$ and $\Delta H^U \equiv \Delta H_{\text{open}}^{\text{max}} + I(X;Y)^U$ in Formulation, ΔH^U depends on Y but independent of X .

We mimic two types of management actions, (i) reduce the number of crayfish, and (ii) increase the number of bass, and conducted numerical experiments using Equation (5) to compare the efficiency by the two management actions (Figure 6a–6c). The deviation from the average without limitation of the biomass of bass was improved with the management action for bass (Figure 6c) better than with the management action for crayfish (Figure 6b). The proposition mentioned in the previous paragraph, which is based on our model, validates the numerical experiment results.

IV. COMPARISON WITH LOTKA-VOLTERRA EQUATIONS

The Lotka–Volterra equations are a pair of first-order nonlinear differential equations, frequently used to describe the dynamics of predator-prey ecosystems [21,22,23]. Assumptions made in the creation of the Lotka–Volterra equations include:

- (i) There is no shortage of food for the prey population.
- (ii) The amount of food supplied to the prey is directly related to the size of the prey population.
- (iii) The rate of change of population is directly proportional to its size.
- (iv) The environment is constant and genetic adaptation is inconsequential.
- (v) Predators will never stop eating.

Under the assumptions, the Lotka–Volterra equations are written as:

$$\begin{aligned} \frac{dx}{dt} &= \alpha x - \beta xy \\ \frac{dy}{dt} &= \delta xy - \gamma y \end{aligned} \quad (6)$$

where x and y are the number of prey and predators, respectively, and α , β , δ , γ are model parameters (positive real constants) [24]. As the differential equations are used (Equation (6)), it is implied that births, deaths, and movements are continuous, and there are overlapping generation [25].

Compared to the Lotka–Volterra equations, our model (Figure 2) only assumes the number of prey and predator interact. The continuity about the births, deaths, and movements is similarly implied in our model. The important thing is that our model allows the effect of the environmental change by the capacity for the number of predator (Figure 2).

V. CONCLUSIONS AND FUTURE WORKS

We have developed an information–theoretic predator–prey ecosystem model that is independent of the dynamics of the ecosystem and validated the model through numerical experiments. Numerical experiment results also suggested our model is effective for evaluating management actions for

predator-prey ecosystems against environmental changes, which include the uncertainties of the environmental factors such as air pollution. We compared our model with Lotka–Volterra equations and clarified our model that needs a few assumptions but, nevertheless, still adequately predicts environment-related changes in predator-prey ecosystems. The information-theoretic framework will be useful to the environmental responses of other life systems such as genetic regulatory networks. Studies on more comparisons between the environmental responses of the life systems and elucidation of universal rules over them are needed to validate the theory.

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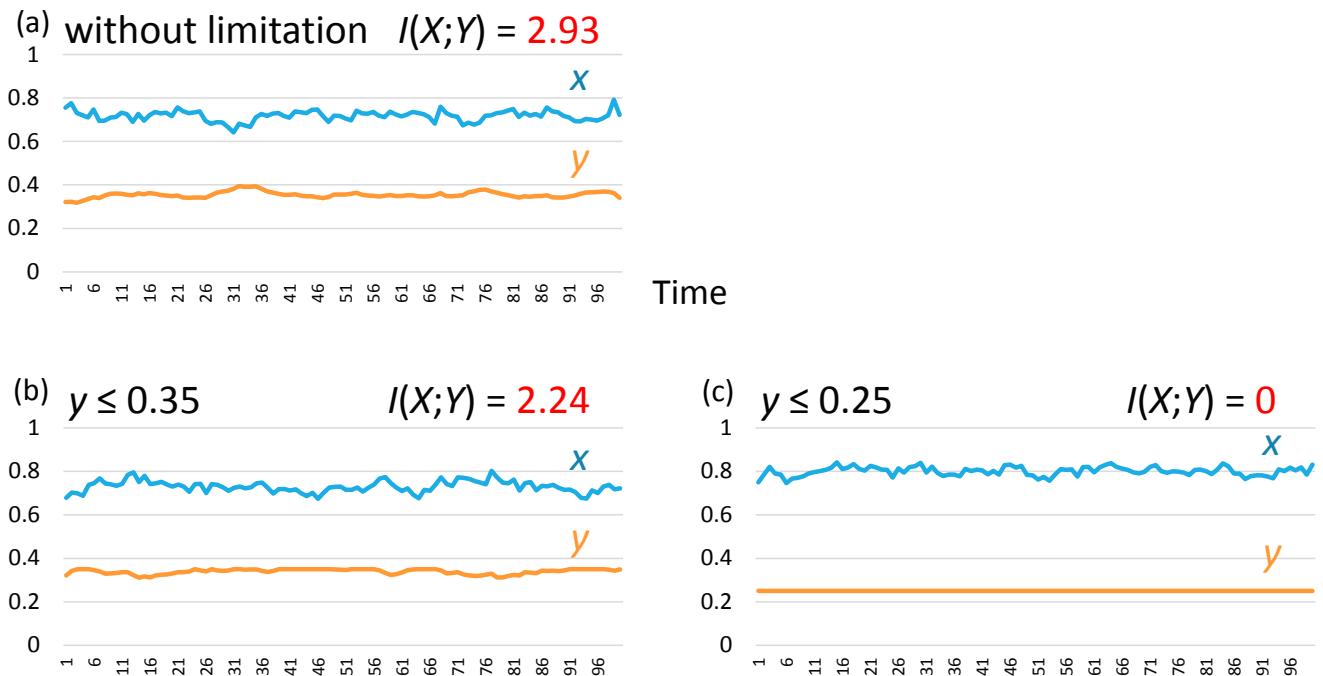


Figure 4. Numerical experiment results for the mutual information between the number of prey individuals and predators: (a) Without limitation for the nondimensionalized biomass of bass y. In (b) and (c), the nondimensionalized biomass of bass y was limited equal or lower than 0.35 and 0.25, respectively, to mimic the decreased capacity by the climate shift. Horizontal axes mean the number of iteration in the calculation for the differential equations (Equation (5)). $I(X;Y)$ means the mutual information between the nondimensionalized biomass of crayfish x and bass y.

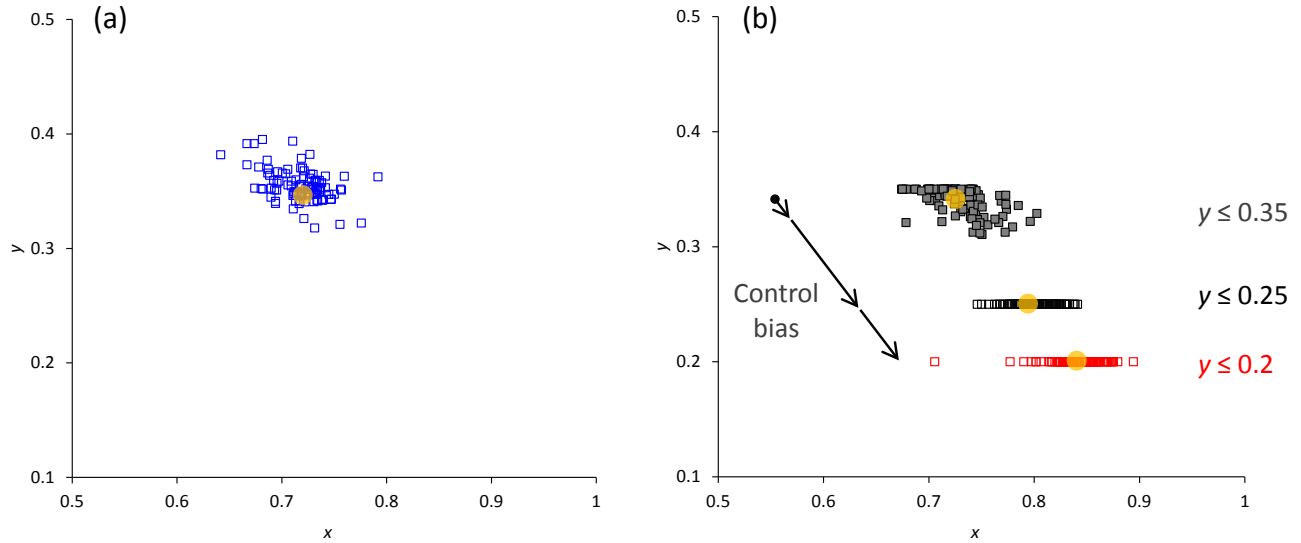


Figure 5. Numerical experiment results for the control performance of the bass-crayfish ecosystem: (a) Without limitation for the nondimensionalized biomass of bass y . (b) The nondimensionalized biomass of bass y was limited equal or lower than 0.35 (gray), 0.25 (black), and 0.2 (red) to mimic the decreased capacity by the climate shift. In each panel, horizontal and vertical axes mean the nondimensionalized biomass of crayfish and bass, respectively. Each rectangle means the result after n -th ($n \leq 100$) iterations in the calculation for the differential equations (Equation (5)). Yellow-colored circles mean the average among the 100 iterations. The control bias was defined as a vector from the average without limitation for the nondimensionalized biomass of bass y to the corresponding average.

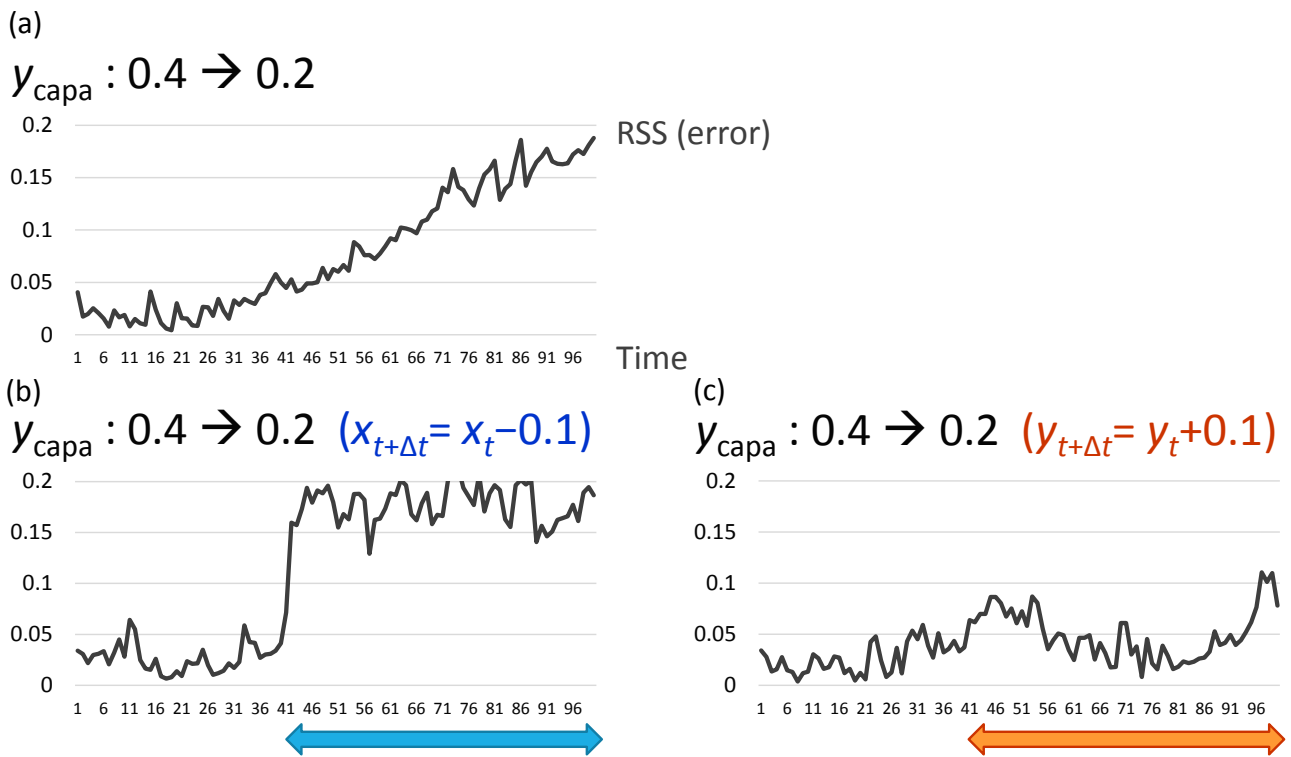


Figure 6. Numerical experiment results for the control performance of the bass-crayfish ecosystem with management actions: (a) Without the management action. (b) The nondimensionalized biomass of crayfish x was continuously reduced as $x_{t+\Delta t} = x_t - 0.1$ ($t > 40$). (c) The nondimensionalized biomass of bass y was continuously increased as $y_{t+\Delta t} = y_t + 0.1$ ($t > 40$), where t means the number of iteration in the calculation for the differential equations (Equation (5)). The horizontal and vertical axes mean the number of iteration in the calculation for the differential equations (Equation (5)) and deviation of x and y calculated by a root-sum-square of x and y from the average without limitation of the the nondimensionalized biomass of bass y . In (a), (b), and (c), the nondimensionalized biomass of bass y was limited equal or lower than 0.4 and 0.2 at $t \leq 40$ and $t > 40$, respectively. The colored-arrows in (b) and (c) indicate the period in which the management action was conducted.