A Mathematical Modelling for the Cheliped Regeneration with Handedness in Fiddler Crab

Hiromi Seno [a,*] and Mikiko Shigemoto [b]

[a] *Department of Mathematical and Life Sciences, Graduate School of Science, Hiroshima University, Higashi-hiroshima 739-8526, JAPAN*

[b] *Department of Information and Computer Sciences, Faculty of Science, Nara Women's University, Nara 630-8506, JAPAN*

Abstract

An enoumously developed giant cheliped with the other small one characterizes the adult male fiddler crab. Some experiments with artificial severances of cheliped indicate that such a handedness in the cheliped size is maintained even after the regeneration of severed cheliped. On the other hand, some experimental researches give some results about an unknown physiological system which controls the emergence and the regeneration of the handedness in the cheliped size. In this paper, with two hypothesized factors relevant to the regeneration of a severed cheliped, we propose a simple mathematical model to describe the experimental result about the cheliped regeneration with a handedness after the cheliped severance for the fiddler crab. Our model gives a suggestion about an underlying system for the cheliped regeneration in the fiddler crab or some other crustacean species.

Key words: handedness, fiddler crab, regeneration, mathematical model, differential equations

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1 Introduction

The most characteristic feature of male fiddler crab is an enormously developed giant cheliped and the other small one, while the female has two small equal-sized chelipeds (Crane, 1977; Mariappan et al., 2000). It depends on the

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[*] Corresponding author. *Phone & Fax:* +81-82 424 7394
Email address: `seno@math.sci.hiroshima-u.ac.jp` (Hiromi Seno).

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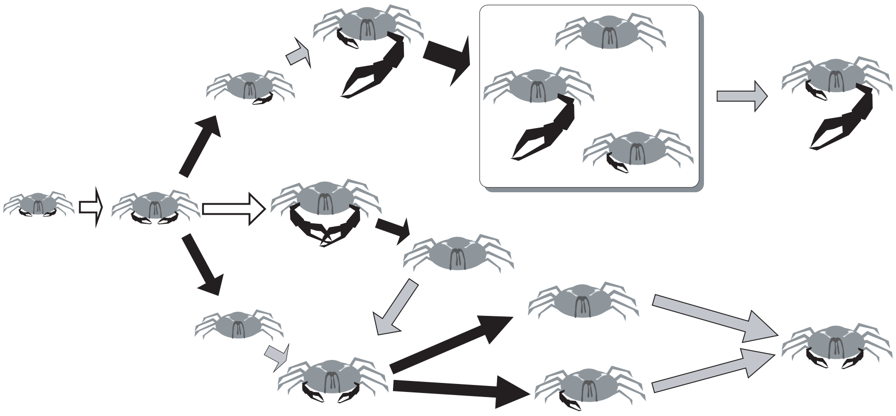

Fig. 1. Experimental result about the cheliped regeneration after the artificial severance by Yamaguchi (1977, 1978). White arrow indicates the growth, the black arrow does the operation of a cheliped severance, and the light dark arrow does the cheliped regeneration. For detail, see the main text.

individual which side of chelipeds is giant (Yerkes, 1901; Yamaguchi, 1977). Few male individuals have nearly equal-sized (both giant or small) chelipeds (Morgan, 1923; Yamaguchi, 1973).

Crustacean can regenerate its lost limb. Mechanism of such a limb regeneration has been attracting various biological researchers. von Hagen (1962) found that the male of *Uca tangeri* regenerates its larger cheliped, keeping the handedness, that is, the larger side being unchanged. Yamaguchi (1977, 1978, 2001) and Yamaguchi & Henmi (2001) examined the cheliped regeneration with some experiments for the fiddler crab *Uca lactea*, in which a cheliped is artificially severed and then the regenerated size is compared to the size of the original and the other unsevered cheliped (see Fig. 1). In the experimental results, after a cheliped of young male is severed, the regenerated cheliped appears smaller than the unsevered cheliped. Both chelipeds become giant for the male which has not experienced any severance of its cheliped. The cheliped severance of adult male with a handedness in the cheliped size does not affect its handedness even after the cheliped regeneration. That is, the originally larger side is still larger than the other even after the cheliped regeneration, independently of which side is severed. For the adult male with two giant chelipeds, if both chelipeds are severed, regenerated chelipeds become small.

Before the emergence of such a handedness in the cheliped size, the young male loses one of chelipeds which are originally of equal size (Morgan, 1923, 1924; Ahmed, 1976; Otani, 1993; Yamaguchi & Henmi, 2001). Then, the unsevered cheliped grows larger than the regenerated one (Weis, 1976, 1977; Ahmed, 1978; Yamaguchi & Henmi, 2001). Such a differentiated handedness is physiologically maintained in the more matured period even when another lost of a cheliped occurs (Vernberg & Costlow, 1966; Yamaguchi, 1973, 1977, 1978, 2001; Weis, 1976, 1977; Ahmed, 1978; Yamaguchi & Henmi, 2001).

In contrast, in case of snapping shrimps, the severance of a chela can cause the reversal of the handedness in the chela size (Wilson, 1903; Przibram, 1931; Mellon, 1981; Govind & Pearce, 1988; Govind et al., 1988; Govind, 1989; Young et al., 1994; Mariappan et al., 2000). If the larger chela is severed, then the smaller chela grows larger in turn, while the regenerated one does smaller than it. It is reported that some species of heterochelous crab and lobster show such reversal of the handedness, too (Cheung, 1976; Hamilton et al., 1976; Yamaguchi, 1977, 1995; Simonson & Steele, 1981; Simonson, 1985; Haefner, 1990; Mariappan et al., 2000).

Physiological system which controls the limb regeneration has something still unknown. Some molecular based researches have been revealing some factors, hormones/steroids and their receptors, which function in the regeneration process (Needham, 1965; Hopkins, 1989, 1993, 2001; Hopkins et al., 1999). Hopkins (2001) gives a suggestion about the hormonal mechanism in the early period of a limb regeneration in the crab *Uca* as illustratively shown in Fig. 2. He proposed that the epidermis in the regenerating blastema of *Uca pugilator* is analogous to the wound epidermis of vertebrates, and suggested that the release of growth factor(s) from the severed nerve and the production of compounds like a fibroblast growth factor (FGF) by the wound epidermis are very early events in crustacean limb regeneration, and that the effects of these growth factors may be modulated by endogenous retinoids. He also gave some suggestions about the role of ecdysteroids during blastema formation.

In this paper, with two hypothesized factors relevant to the regeneration of a severed cheliped, we present a simple mathematical model, to describe the experimental result about the handedness regeneration for the fiddler crab.

2 Model

2.1 Assumptions

To construct our mathematical model, we use the following assumptions about the physiological dynamics for the cheliped regeneration (see Fig. 3):

(1) A physiological factor **A** is always secreted by a certain source tissue. **A** inhibits its own production with a negative feedback;
(2) A signal of the cheliped severance stimulates the growth of a tissue **Z**. The tissue **Z** grows only after the first experience of a cheliped severance, so that it does not grow unless any cheliped is severed;
(3) The growth speed of **Z** is proportional to the concentration of **A**, while the growth becomes slower as the size of **Z** increases;

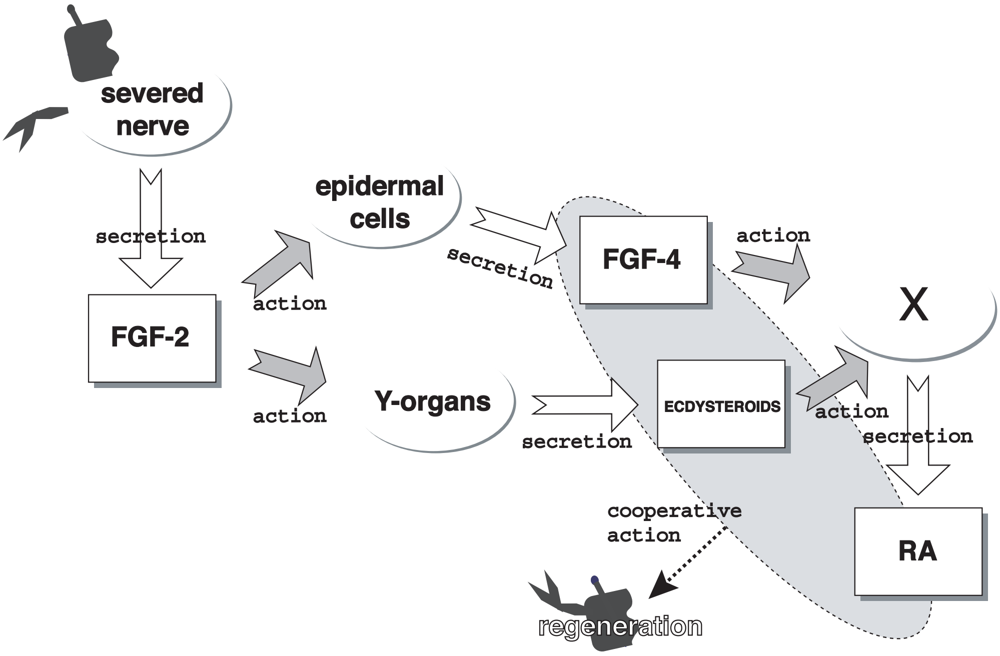

Fig. 2. Schematic explanation of the mechanism of a limb regeneration in the crab *Uca*, suggested by Hopkins (2001). FGF-2 denotes the fibroblast growth factor 2, FGF-4 the fibroblast growth factor 4, and RA the endogenous retinoic acid. The source (X) of RA has been unknown yet. Relationships indicated by 'action' are added by us.

(4) The tissue **Z** produces another physiological factor **B**, and its secretion rate increases as the size of **Z** gets larger;
(5) The physiological factor **B** inhibits its own production by the tissue **Z**, and does the production of the physiological factor **A** as well;
(6) Physiological factors **A** and **B** interact with each other, and then **B** loses its activity. Inactivated factor **B** never reactivates;
(7) The growth of regenerating cheliped is in a logistic manner with a saturation size;
(8) The saturation size of regenerating cheliped is independent of the size of the unsevered cheliped;
(9) The saturation size of regenerating cheliped is reduced by a cooperative action of **A** and **B**;
(10) Before the first severance of any cheliped, the cheliped size is the same between left and right.

Compared to the physiological mechanism suggested by Hopkins (2001) about a limb regeneration, the factor **A** could be regarded as corresponding to the ecdysteroids secreted by Y-organs. The signal of a cheliped severance could be to the secretion of the fibroblast growth factor 4 (FGF-4) by epidermal cells stimulated by the severance, and the factor **B** could be to the endogenous retinoic acid (RA). The tissue **Z** could be to the source tissue ('X' in Fig. 2) of RA. It may be possible that **Z** could be regarded as representing a gene

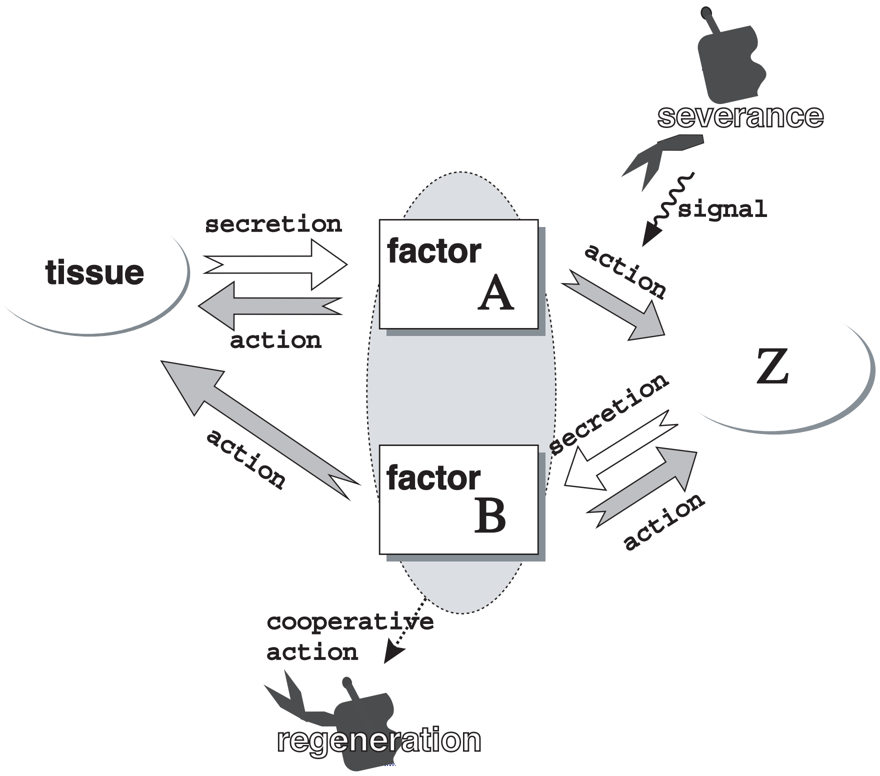

Fig. 3. Illustrative explanation of our mathematical modelling for the physiological system of the cheliped regeneration. For detail, see the main text.

product which is reflected to the concentration of a physiological factor **B**. In a sense, our modelling could be regarded as an aggregation of the unknown physiological system into a simple one.

2.2 Physiological dynamics

With the above assumptions, we consider the following mathematical model for the physiological dynamics about the cheliped regeneration:

$$\frac{da(t)}{dt} = \alpha \left\{ 1 - \frac{a(t)}{c_a} - (\theta_{\mathrm{L}} + \theta_{\mathrm{R}})\mu b(t) \right\} a(t); \tag{1}$$

$$\frac{dz(t)}{dt} = (\theta_{\mathrm{L}} + \theta_{\mathrm{R}})\gamma \left\{ 1 - \frac{z(t)}{c_z} \right\} a(t); \tag{2}$$

$$\frac{db(t)}{dt} = \beta \left\{ 1 - \frac{b(t)}{c_b} \right\} z(t) - (\theta_{\mathrm{L}} + \theta_{\mathrm{R}})\delta a(t) b(t), \tag{3}$$

where $a(t)$ is the concentration of physiological factor **A**, $b(t)$ that of physiological factor **B**, $z(t)$ the size of **Z** at time t. Every parameter is positive.

Parameter α is the intrinsic secretion rate of **A** from an unknown source, β that of **B** from the tissue **Z**. Saturation concentrations for **A** and **B** are respectively given by c_a and c_b. γ is the intrinsic growth rate of **Z**, and c_z the carrying capacity for its size. μ is the inhibition rate for the secretion of **A** due to **B**. δ is the inactivation rate of **B** due to an interaction between **A** and **B**. θ_{R} (resp. θ_{L}) is the regeneration initiation parameter which is zero before the *first* severance of the right (resp. left) cheliped, and changes to 1 after the first severance. In our modelling, the strength of a signal caused by the cheliped severance to promote the growth of **Z** doubles when both chelipeds are severed.

As for the initial condition, we assume that the physiological factor **A** is at its saturation: $a(0) = c_a$, and that the tissue **Z** does not exist: $z(0) = b(0) = 0$. Before the first severance, parameters θ_{R} and θ_{L} are both kept zero, while the physiological condition is kept the same as the initial. The state $(a, z, b) = (c_a, 0, 0)$ is an equilibrium state for the system of (1–3) with $\theta_{\mathrm{R}} = \theta_{\mathrm{L}} = 0$.

2.3 Growth of the cheliped size

In addition to the above physiological dynamics, we consider the following system that governs the temporal variation of the right cheliped size $r(t)$, the left cheliped size $l(t)$, the saturation size for the right cheliped growth $k_{\mathrm{R}}(t)$, and that for the left cheliped growth $k_{\mathrm{L}}(t)$:

$$\frac{dr(t)}{dt} = \sigma \left\{k_{\mathrm{R}}(t) - r(t)\right\} r(t); \tag{4}$$

$$\frac{dl(t)}{dt} = \sigma \left\{k_{\mathrm{L}}(t) - l(t)\right\} l(t); \tag{5}$$

$$\frac{dk_{\mathrm{R}}(t)}{dt} = -\theta_{\mathrm{R}}\eta a(t)b(t) \left\{k_{\mathrm{R}}(t) - r(t)\right\}; \tag{6}$$

$$\frac{dk_{\mathrm{L}}(t)}{dt} = -\theta_{\mathrm{L}}\eta a(t)b(t) \left\{k_{\mathrm{L}}(t) - l(t)\right\}. \tag{7}$$

Parameter σ is the intrinsic growth rate of the cheliped size, and η the strength coefficient for the cooperative action of **A** and **B** to suppress the saturation size of regenerating cheliped.

We assume that the cheliped size is sufficiently small at the initial condition: $r(0) = l(0) = x_0 < k_{\mathrm{L}}(0) = k_{\mathrm{R}}(0) = c_k$. Besides, just after the severance of a cheliped, the regeneration starts with the initial size x_0 again, independently of the original size before the severance.

Since $\theta_{\mathrm{R}} = \theta_{\mathrm{L}} = 0$ before the first severance, from (6) and (7), $k_{\mathrm{R}} = k_{\mathrm{L}} = c_k$. Meantime, from (4) and (5), the size of each cheliped is growing toward the saturation size c_k in a logistic manner. If no severance occurs, both chelipeds grow up to the same size c_k, which could be regarded as two giant chelipeds observed for few samples of fiddler crab.

We remark that, in our model composed of (1–7), the dynamics of (1–3) is independent of that of (4–7), whereas the latter is affected by the former.

2.4 Non-dimensionalized system

From (1–7), we can get the following non-dimensionalized system:

$$\frac{dA(\tau)}{d\tau} = \{1 - A(\tau) - (\theta_{\mathrm{L}} + \theta_{\mathrm{R}})MB(\tau)\}\, A(\tau); \tag{8}$$

$$\frac{dZ(\tau)}{d\tau} = (\theta_{\mathrm{L}} + \theta_{\mathrm{R}})\Gamma\, \{1 - Z(\tau)\}\, A(\tau); \tag{9}$$

$$\frac{dB(\tau)}{d\tau} = P\, \{1 - B(\tau)\}\, Z(\tau) - (\theta_{\mathrm{L}} + \theta_{\mathrm{R}})DA(\tau)B(\tau); \tag{10}$$

$$\frac{dR(\tau)}{d\tau} = S\, \{K_{\mathrm{R}}(\tau) - R(\tau)\}\, R(\tau); \tag{11}$$

$$\frac{dL(\tau)}{d\tau} = S\, \{K_{\mathrm{L}}(\tau) - L(\tau)\}\, L(\tau); \tag{12}$$

$$\frac{dK_{\mathrm{R}}(\tau)}{d\tau} = -\theta_{\mathrm{R}} EA(\tau)B(\tau)\, \{K_{\mathrm{R}}(\tau) - R(\tau)\}\, ; \tag{13}$$

$$\frac{dK_{\mathrm{L}}(\tau)}{d\tau} = -\theta_{\mathrm{L}} EA(\tau)B(\tau)\, \{K_{\mathrm{L}}(\tau) - L(\tau)\}\, , \tag{14}$$

with the following variable and parameter transformations:

$$\tau = \alpha t; A(\tau) = \frac{a(t)}{c_a};\ Z(\tau) = \frac{z(t)}{c_z};\ B(\tau) = \frac{b(t)}{c_b};$$

$$K_{\mathrm{R}}(\tau) = \frac{k_{\mathrm{R}}(\tau)}{c_k};\ K_{\mathrm{L}}(\tau) = \frac{k_{\mathrm{L}}(t)}{c_k};\ R(\tau) = \frac{r(t)}{c_k};\ L(\tau) = \frac{l(t)}{c_k};$$

$$M = c_b\mu;\ \Gamma = \frac{c_a\gamma}{c_z\alpha};\ P = \frac{c_z\beta}{c_b\alpha};\ D = \frac{c_a\delta}{\alpha};\ S = \frac{c_k\sigma}{\alpha};\ E = \frac{c_a c_b \eta}{\alpha}.$$

For a mathematical convenience, we hereafter analyze this non-dimensionalized system instead of the original one.

3 Analysis

3.1 Equilibrium state reached from the severance of a single cheliped

After the first severance of a single cheliped, only one of parameters θ_{R} and θ_{L} becomes 1, and the other remains 0. The dynamics given by (8–10) has three types of the equilibrium point $(A^*, Z^*, B^*) = (0, 0, +)$, $(0, +, 1)$, and $(+, 1, +)$, where the symbol '+' means an undetermined positive value. With the local stability analysis, we can easily find that the equilibrium point $(0, 0, +)$ is always unstable.

At most two different equilibrium points of type $(+, 1, +)$ exist if one of the following conditions is satisfied:

$$\begin{cases} 1 < M < \dfrac{(P/D+1)^2}{4P/D}; \\ \dfrac{P}{D} < 1, \end{cases} \tag{15}$$

or

$$M < 1. \tag{16}$$

When the equilibrium point exists unique, the standard local stability analysis shows that it is asymptotically stable. When different two exist, the smaller one is asymptotically stable while the larger is unstable.

In contrast, as for the equilibrium point $(0, +, 1)$, the local stability analysis shows that it is unstable if $M < 1$. In contrast, for $M > 1$, making use of the isoclines projected on the (A, B)-phase plane, we can suggest that it is globally stable, or exists locally stable with the other locally stable equilibrium point of type $(+, 1, +)$, that is, in a *bistable* situation (see Appendix).

3.2 Equilibrium state reached from the severance of both chelipeds

We have $\theta_{\mathrm{R}} = \theta_{\mathrm{L}} = 1$ after the severance of both chelipeds. As in case of the severance of a single cheliped, there are three types of the equilibrium point $(A^*, Z^*, B^*) = (0, 0, +)$, $(0, +, 1)$, and $(+, 1, +)$. Again the equilibrium point $(0, 0, +)$ is always unstable.

Local stability for each type of the equilibrium point is analogous to that in case of the severance of a single cheliped. As for the equilibrium point of type

Table 1
Classification of the parameter region according to the local stability of the equilibrium (A^*, Z^*, B^*). The "stable" means the asymptotical stability. See also Fig. 4.

Severance	(A^*, Z^*, B^*)	Region I	Region II	Region III
Single	$(+, 1, +)$	stable	stable	non-existent
	$(0, +, 1)$	unstable/stable	unstable/stable	stable
Both	$(+, 1, +)$	stable	non-existent	non-existent
	$(0, +, 1)$	unstable/stable	stable	stable

$(+, 1, +)$, at most two different equilibrium points exist if one of the following conditions is satisfied:

$$\begin{cases} \dfrac{1}{2} < M < \dfrac{(P/D+2)^2}{16P/D}; \\ \dfrac{P}{D} < 2, \end{cases} \tag{17}$$

or

$$M < \frac{1}{2}. \tag{18}$$

When the equilibrium point exists unique, it is asymptotically stable. When different two exist, the smaller one is asymptotically stable while the larger is unstable.

As for the equilibrium point $(0, +, 1)$, we can apply the arguments similar to those in the previous section, and find that it is unstable if $M < 1/2$. For $M > 1/2$, we can suggest that the equilibrium point becomes globally stable, or exists locally stable with the other locally stable equilibrium point of type $(+, 1, +)$: a bistable situation.

3.3 Classification of the parameter region

From the above results about the existence and the local stability of the equilibrium point of type $(+, 1, +)$, we can classify the parameter region into the following three (see Table 1 and Fig. 4):

Region I: For the severance of a single cheliped and of both chelipeds, the equilibrium point of type $(+, 1, +)$ exists locally stable.

Region II: The equilibrium point of type $(+, 1, +)$ exists unique and locally stable only in case of the severance of a single cheliped. In case of the

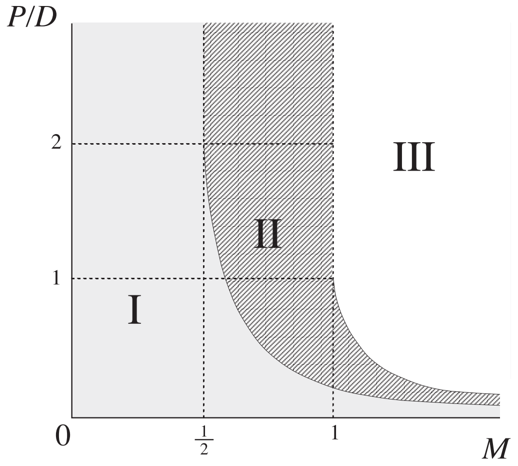

Fig. 4. Classification of the parameter region according to the local stability of the equilibrium (A^*, Z^*, B^*). Boundaries are given by (15–18). For detail, see Table 1 and the main text.

severance of both chelipeds, it does not exist. The equilibrium point of type $(0, +, 1)$ is globally stable only in case of the severance of both chelipeds.

Region III: The equilibrium point of type $(+, 1, +)$ does not exist, while that of type $(0, +, 1)$ is globally stable.

3.4 Emergence of the handedness

Before the first severance, both chelipeds grow with the same size. After the first severance for a single cheliped, the handedness in the cheliped size emerges as indicated in Fig. 5 by numerical calculations. At the equilibrium state, the regenerated cheliped is much smaller than the unsevered cheliped. Numerical calculations indicate that the equilibrium state is independent of when the first severance occurs. Only for the parameter region III, the concentration of **A** asymptotically diminishes after the cheliped regeneration process is initiated.

In the case when the first severance is for both chelipeds, the regenerating chelipeds grow toward a saturation size smaller than the original saturation size (Fig. 6). In this case, except for the parameter region I, the concentration of **A** asympototically diminishes.

3.5 Effect of repeated severances

We numerically investigate the variation of cheliped size due to some repeated severances and regenerations.

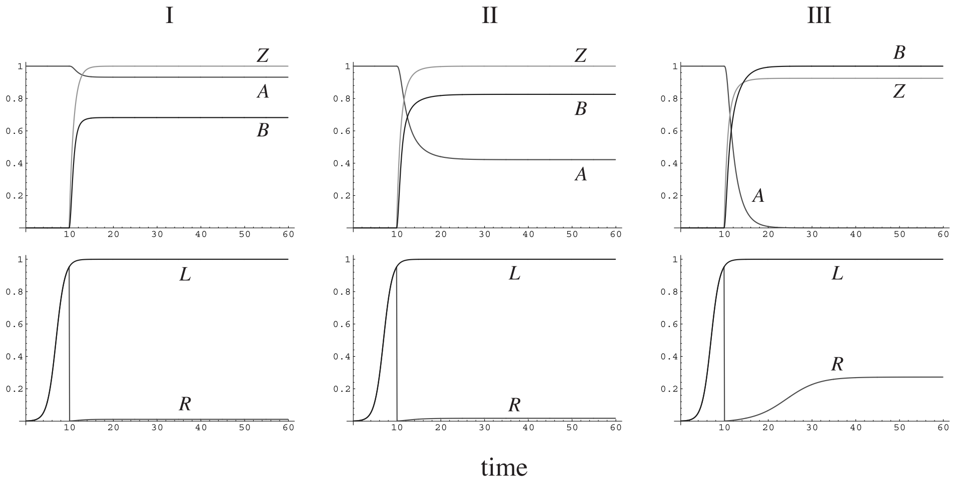

Fig. 5. Temporal variation of variables A, Z, B, R, and L after the first severance of the right cheliped. The severance occurs at time $\tau = 10$. $\Gamma = D = S = Q = 1.0$, $P = 2.0$, and $x_0 = 0.001$. $M = 0.1$ for the parameter region I, $M = 0.7$ for II, and $M = 1.5$ for III.

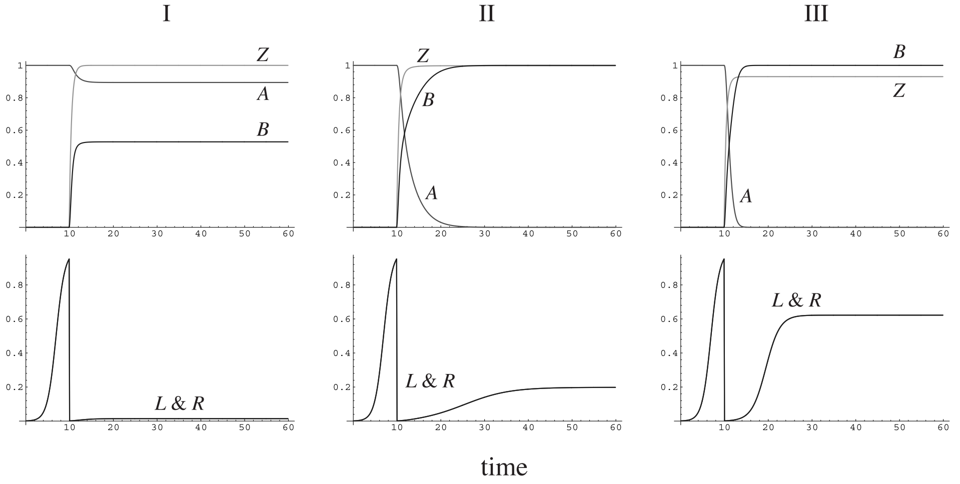

Fig. 6. Temporal variation of variables A, Z, B, R, and L after the first severance of both chelipeds. Parameter values for numerical calculations are the same as for those in Fig. 5.

Subsequent two severances of a single cheliped affect the regenerated size except for the case of the parameter region III (see Figs. 7 and 8). As for the parameter region III, if the second severance occurs sufficiently later than the first one does, the handedness emerged by the first severance can be exactly reproduced by the cheliped regeneration after the second severance, independently of which cheliped is severed at the second severance. In the case when the second severance occurs for the cheliped regenerated after the first severance, the regenerated cheliped size is the same as before, independently of the moment of the second severance. However, as indicated in Fig. 8, if the second severance occurs for the unsevered cheliped at the moment sufficiently near the first severance, the second severance affects which cheliped becomes

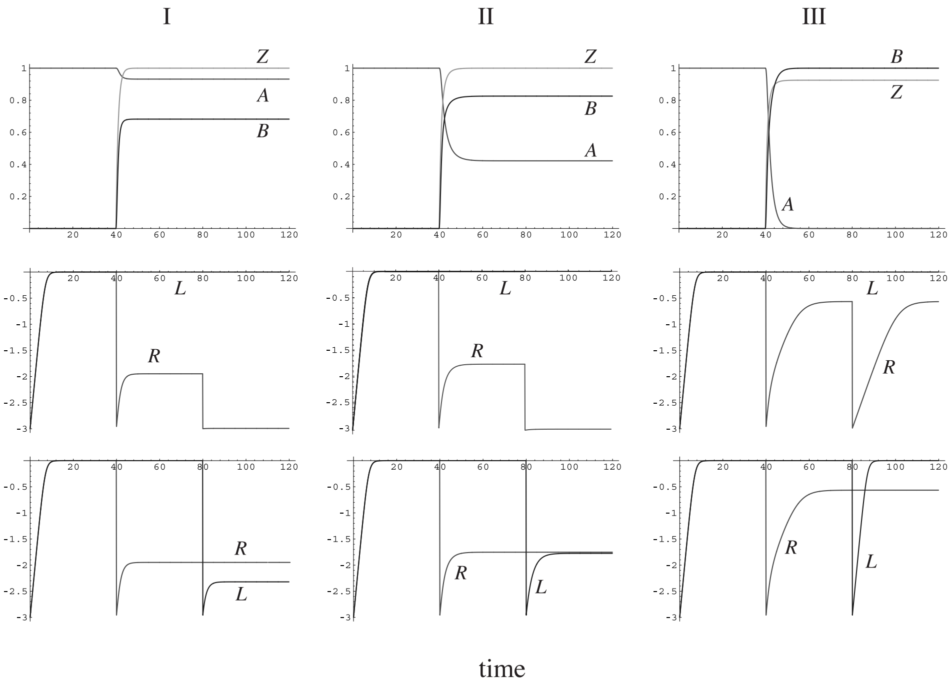

Fig. 7. Numerical calculations for the temporal variation of variables A, Z, B, R, and L with subsequent two severances of a single cheliped. Severances occur at time $\tau = 40$ and 80. The second row in the figure is about two severances of the same side of cheliped, and the third is about those for different sides. $\Gamma = D = S = Q = 1.0$, $P = 2.0$, and $x_0 = 0.001$. $M = 0.1$ for the parameter region I, $M = 0.7$ for II, and $M = 1.5$ for III. Values of R and L are plotted in logarithmic scale.

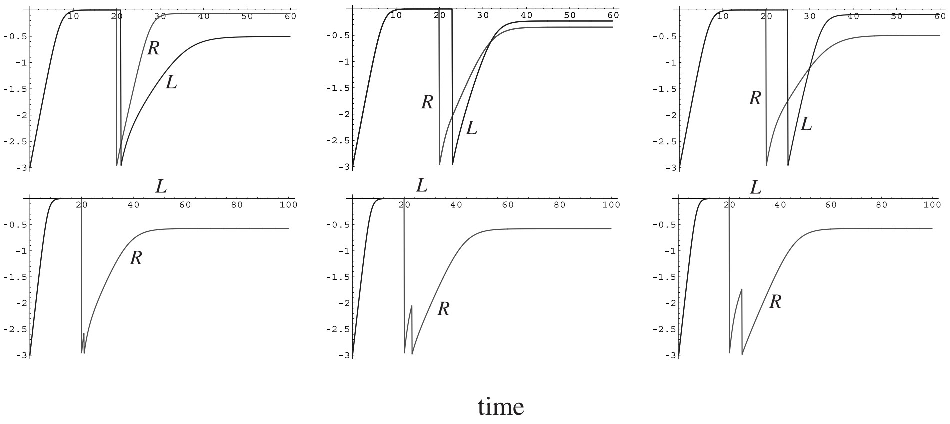

Fig. 8. Numerical calculations for the temporal variation of the cheliped size R and L for the parameter region III with two severances of a single cheliped. The second severance occurs relatively near the first one. Vertical axis is in logarithmic scale. The second row is about two severances of the same side of cheliped, and the third is about those of different sides. Temporal variation of A, Z, and B is independent of the moment of the second severance. $\Gamma = D = S = Q = 1.0$, $P = 2.0$, $x_0 = 0.001$, $M = 1.5$.

larger than the other at the saturation size.

In contrast, as shown in Fig. 7, for the parameter region I or II, when the cheliped regenerated after the first severance is severed again, the regenerated cheliped becomes smaller than before. If the second severance occurs for the larger cheliped which was not severed at the first severance, the regenerated cheliped cannot recover its original size. It becomes smaller than the other cheliped for the parameter region I and does almost the same with the other for the parameter region II. Therefore, for the parameter region I or II, the second severance significantly changes the handedness emerged by the first severance.

If we remove both chelipeds twice, then, for the parameter region II or III, the size of regenerated chelipeds is the same as before. For the parameter region I, such two severances make the cheliped size significantly smaller than before.

By numerical calculations, we find that these characteristics of the cheliped regeneration are qualitatively the same also in case of more frequent random/periodic severances. Especially, for the parameter region III, the handedness emerged after the first severance tends to be robustly maintained even after such repeated severances. In contrast, for the parameter region I or II, such repeated severances make the regenerated cheliped size smaller and smaller.

3.6 Result

With numerical calculations for each parameter region classified in the previous section, we lastly obtain the following result about the size of the cheliped regenerated after the severance:

Region I: Differently from the experimental result, after the severance of a cheliped, the handedness in the cheliped size is not necessarily recovered as before.

Region II: If the larger cheliped is severed at the second severance, the size of the regenerated cheliped is not recovered as it was. This is different from the experimental result shown in Fig. 1, although the qualitative result for the other cases of the severance appears corresponding to the experimental result.

Region III: The size of the regenerated cheliped qualitatively corresponds to the experimental result shown in Fig. 1.

For any parameter region, the cheliped regenerated after the severance of the smaller one never becomes larger than the other.

4 Concluding Remarks

With some hypotheses about the physiological system for the cheliped regeneration, we constructed a mathematical model in order to compare to the experimental result by Yamaguchi (1977, 1978) for the cheliped handedness in a fiddler crab. We analyzed the model in terms of the size of the cheliped regenerated after its severance, focusing the handedness in the cheliped size. Consequently, we found the parameter region that can qualitatively describe the experimental result, although, for the other parameter region, our model shows some features different from the experimental result.

Hypotheses for our modelling would be rather simple and general, because our aim is to present a mathematical model as simple as possible in order to emphasize a main structure of the unknown physiological system for the cheliped regeneration. We have not specified any substances in vivo for the physiological factors **A** and **B** in our model. The corresponding substances may depend on species. Our results different from the experimental result, that is, those for the parameter region I or II, may be applicable for another species. Our results imply that such a species cannot keep the handedness, and shows a reduction of the cheliped size by repeated severances and regenerations. For such a species, the handedness in the cheliped size would not be excessive in comparison with the fiddler crab.

From our results, we suggest that there would be a physiological factor (**A** in our model) which works in the juvenile period, like a juvenile hormone, before the first severance of a cheliped. The first severance of a cheliped would serve as an initiation of the secondary sexual characteristics, diminishing a juvenile hormone with growing a specific tissue or activating some gene product (**Z** in our model) for the secondary sexual characteristics. Disappearance of the juvenile hormone would be necessary for the handedness robust against additional severances. If the experiment of aritificial severances of the cheliped in the fiddle crab could be designed with accompanying investigation of the variation of hormon composition in vivo, our results would be useful as a comparison to the experimental result.

In the actual regeneration process, the growth of regenerating cheliped depends on the period of molting. Although our model does not include such an effect of the period of molting, we expect that our model would be able to grasp the main structure of the unknown physiological system for the cheliped regeneration in the fiddler crab.

In case of snapping shrimps, the severance of a chela can cause the reversal of the handedness in the chela size. Our present model cannot explain such a handedness reversal. Such a handedness reversal may require an interaction of the growth between right and left chelae. With some additional hypotheses or modifications in our model, we would be able to extend our model to explain such a handedness reversal, since the physiological system for the limb/cheliped/chela regeneration would be expected to have a common main structure in Crustacea. Such an extension would be one of the next steps of this theoretical study with a mathematical model.

Appendix

A Stability of $(A^*, Z^*, B^*) = (0, +, 1)$

In this appendix, for the system after the first severance of a single cheliped, we show a stability analysis for the equilibrium point (A^*, Z^*, B^*) of type $(0, +, 1)$.

By the standard linearization method, the eigenvalues for $(A^*, Z^*, B^*) = (0, +, 1)$ can be easily obtained as $1 - M$, 0, and $-PZ^*$. If $M < 1$, one eigenvalue is positive, so that the equilibrium point is unstable. If $M > 1$, two eigenvalues are negative, and one is zero. So hereafter we focus the case of $M > 1$.

Now, let us consider the trajectory of (A, B) projected on a plane $Z =$ const. On the plane, as shown in Fig. A.1, we consider the projected null clines for A and B, which are given by (8) and (10) with a constant Z. Although the null clines for A are independent of Z, the null cline for B depends on the value of Z. We find that only two cases indicated in Fig. A.1 can occur. One is that those null clines have the unique intersection $(0, 1)$, and the other is that they have three intersections, $(0, 1)$ and the other two with positive values. As illustrated in Fig. A.1, in the latter case, one of positive intersections is repulsive while the other two are attractive. In contrast, when those null clines have the unique intersection $(0, 1)$, it is attractive.

Actually, the value of Z is variable in time, governed by (9), so that the shape of the above-mentioned null cline for B is temporally variable. This means that, if Z converges to a positive value Z^* as $\tau \to \infty$, then the configuration of null clines for A and B on the plane $Z = Z^*$ should be alternatively one of those shown in Fig. A.1.

This argument suggests that, if $M > 1$, the equilibrium point (A^*, Z^*, B^*) of type $(0, +, 1)$ exists globally stable, or locally stable with the other locally stable equilibrium point of type $(+, 1, +)$.

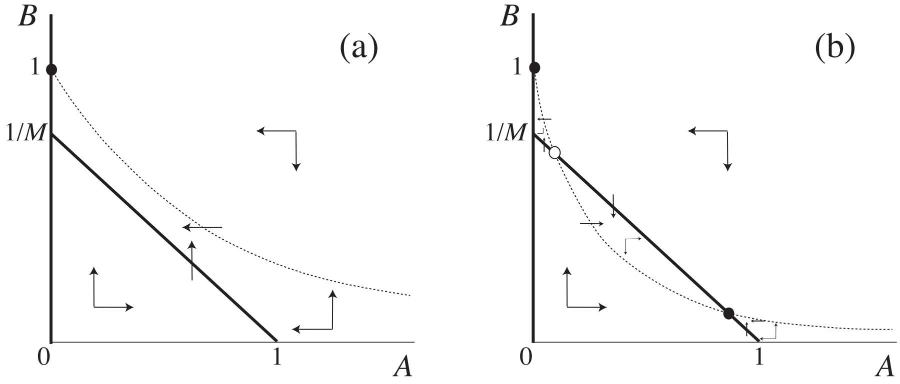

Fig. A.1. Phase plane for (A, B) projected on a plane $Z =$ const. Thick lines indicate the null clines for A, and the dotted curve does the null cline for B. The shape of the dotted curve depends on the value of Z. Black point indicates the locally stable equilibrium point, and white one does the unstable equilibrium point. (a) the equilibrium point is only $(A, B) = (0, 1)$; (b) three equilibrium points appear.

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