Persistence of Population with Age-dependent Sex Reversal

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論文概要

性転換を伴う生物個体群の存続性に関する数理モデル解析

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一部の動物では、小さいときは雌、大きくなると雄に性転換するもの、逆に、小さいときは雄、大きくなると雌に性転換するものが知られている。前者の例としてはホンソメワケベラ、キンギョハナダイという魚、後者の例としてはクマノミという魚が有名である。いずれの場合にも、自分の遺伝子を次世代により多く残すためであると考えられ、本研究では、後者を取り上げる。性転換がどのように起こるかによる個体群変動の相異を、性転換開始時期、性転換率、雄と雌の交配のしやすさの効果に着目して考察する。

個体群を、シングル雄、シングル雌、繁殖可能カップルの 3 つに大別し、時刻 t における齢 a の雄、齢 a' の雌の個体群密度分布関数をそれぞれ $v(a,t)$、$w(a',t)$、齢 a の雄、a' の雌からなる繁殖可能カップルの密度分布関数を $c(a,a',t)$ とする。シングルの雄の密度分布関数 $v_e(a,t)$、シングルの雌のそれ、$w_e(a',t)$ は、雄と雌それぞれの総密度分布から、カップルの密度分布を差し引いたもので与えられ、本論文中の (1)、(2) で表される。雄、雌の個体群密度分布関数の微小時間において起こる変動は、雌雄それぞれ自然死亡率 δ_v, δ_w と、年齢に依存する性転換率 $M(a)(= 0 \text{ for } a < a_c; m \text{ for } a_c \leq a)$ によるものと仮定する。$M(a) = 0$ の場合は、性転換が行われていないとき、$M(a) > 0$ の場合は、与えられた確率でランダムに行われているときを示す。a_c とは、性転換開始齢を示す。また、繁殖可能カップルの個体群密度に微小時間において起こる変動は、カップルの一方が死ぬ率 $\delta_v + \delta_w$、カップルを解消する率 D、新たにカップルが出来る率 S によるものと仮定する。S は、交配のしやすさであり、シングル雄の密度とシングル雌のそれを掛け合わせたもので表されるものと仮定している。最も単純な質量作用の仮定を採用した。さらに、出生率 λ、および出生時性比 β を加味することによって、それぞれの個体群密度分布ダイナミクスを、本論文中の式 (6-8) で与えられる偏微分方程式系で表す。

性転換が開始される齢 a_c の個体群存続性への影響に注目するため、性転換開始以前の齢にある雄の個体の成す部分個体群サイズを $X(t)$ とし、全雄、全雌、繁殖可能カップルの個体群サイズ $V(t)$、$W(t)$、$C(t)$ と合わせて、偏微分方程式系 (6 -8) から、4 次元の常微分方程式系 (21-24) を導くことができる。$X(t)$ に関する微分方程式 (22) 中の $v(a_c,t)$ については、偏微分方程式系 (6-8) についての特性曲線の方法を用いて、式 (25) で表される事が導かれる。

性転換がない場合には、個体群変動を表す常微分方程式系は式 (27-29) で表される。この系の解析より、絶滅平衡点は常に局所安定であることが導かれる。さらに、この系においては、雌雄の死亡率 δ_v と δ_w が等しいとき、時間無限大において、個体群性比が出生性比に漸近収束することが証明できる。この漸近収束性を用いた近似を用いて 2 次元に縮約した系の解の漸近挙動に関する解析を行った結果、非自明な平衡点はサドルであることも導くことができる。そして、数値計

算より、個体群は初期値に依存して絶滅に向かうか発散に向かうことがわかる。これらの解析より、カップルが少なく、メスも少ない時、個体群は絶滅に向かうが、カップルが少なくてもメスが多い時は個体群は絶滅しないことがわかる。つまり、個体群の存続については、雌の個体群サイズが重要である。

齢によらず常に性転換が起こり得る場合、個体群変動を表す常微分方程式系は式 (40-42) で表される。やはり絶滅平衡点は常に局所安定であることが導かれる。この場合、非自明な平衡点の存在条件を、Fig. 3(a) のように (δ_v, δ_w) 平面に示すことができる。Fig. 3(a) に示された結果より、性転換がない場合は、雌雄それぞれの出生率が、それぞれの死亡率よりも大きい場合に非自明な平衡点は存在するが、常に性転換が行われている場合、雄については、雄の出生率が、死亡率と有効性転換率の和より大きく、雌については、雌の出生率と雄からの有効性転換率の和が死亡率より大きいときに、非自明な平衡点が存在する。これらのことより、性転換が全く行われない場合と常に行われる場合の非自明な平衡点の存在条件を比較すると、非自明な平衡点の存在条件のうち、雄に関するものについては、雄から雌への性転換の存在によって、より厳しくなり、逆に雌に関するものについては、雌として生まれてくる個体のほかに、性転換によって雌になる個体が存在することにより、条件がより緩くなるといえる。

また、カップルの個体群サイズの時間変動が雌雄個体の個体群の時間変動に比べて十分に早いと仮定した場合、カップルの変動速度が無限大の数学的近似を用いて、近似的二次元系を考えることができ、それを用いて解析を行った結果、非自明な平衡点はサドルであることが導かれる。元の系 (40-42) についての数値計算により、個体群は初期値に依存して絶滅に向かうか発散に向かうこともわかる。この場合についても、個体群の存続については、雌の個体群サイズが重要である。

齢に依存する階段関数 (17) で性転換率が与えられる場合、個体群変動を表す常微分方程式系は式 (21-24) で表される。この系の解析より、やはり絶滅平衡点は常に局所安定であることが導かれる。さらに、非自明な平衡点の存在条件は、(51) で表される。この条件式 (51) より、雌の死亡率が、雌の出生率と、齢 a_c 以降の雄からの有効性転換率の和よりも小さく、雄の出生率が、雄の死亡率と、齢 a_c 以降の雌への有効性転換率の和よりも大きい場合に非自明な平衡点が存在する。

性転換率 m と性転換開始齢 a_c について、$\delta_w < (1-\beta)\lambda$、つまり、雌の死亡率が雌の出生率よりも小さい（雌の出生率が十分に大きく、雌個体群が存続しやすい）場合、個体群の存続のためには、性転換率が大きいほど、性転換開始齢が遅くならなければならないことが Fig. 7(a) に示された結果よりわかる。また、個体群の存続に関するパラメータ領域の境界が、ある a_c の値に漸近していることがわかり、その値よりも性転換開始齢が遅い場合には、性転換率によらず、存続が可能であることが示唆される。$\delta_w > (1-\beta)\lambda$、つまり、雌の死亡率が雌の出生率よりも大きい（雌の出生率が十分に小さく、雌個体群が存続しにくい）場合、Fig. 7(b) に示されるように、性転換開始齢が早すぎても遅すぎても個体群は絶滅する。従って、ある限られた範囲内の性転換開始齢 a_c の時にのみ、個体群は存続できる。個体群の存続に関するパラメータ領域の境界それぞれは、必ずある a_c の値に漸近しおり、一方の漸近値より大きい a_c（性転換開始齢がある閾値より遅い）の場合と、もう一方の漸近値より小さい a_c（性転換開始齢がある閾値より早い）の場合には、性転換率によらず個体群は絶滅するという結果である、と解釈できる。これらの閾値の特性については、$m \to \infty$ の場合のダイナミクスから調べることができるであろう。なお、雌が少ないときに性転換率も低ければ個体群は必然的に絶滅するが、それ以外の場合について、存続は、初期値に依存して定

まる。

また、m を固定し、a_c への依存性を考えた場合、a_c が小さくても大きくても、個体群は絶滅に向かい、ある中庸な範囲の値を取る場合にのみ存続する可能性があることが、Fig. 8 に示された結果より明らかである、一方、a_c を固定し、m への依存性を考えた場合、m がある閾値よりも大きいと、個体群は絶滅に向かうことが Fig. 9 に示された結果よりわかる。

$d_w < (1-\beta)\lambda$、つまり、雌の死亡率が雌の出生率よりも小さい（雌の出生率が十分に大きい）場合、個体群が存続するためには、カップリング係数がある閾値以上の値、即ち、十分にカップルが形成されやすく、性転換率がある閾値よりも小さいことが必要であることが、Fig. 10(a) に示された結果よりわかる。$d_w > (1-\beta)\lambda$、つまり、雌の死亡率が雌の出生率よりも大きい（雌の出生率が十分に小さい）場合、カップルの形成率が小さすぎるか、カップル形成率が十分に大きくても性転換率が相当に小さいならば、個体群は絶滅に向かう。個体群が存続するためには、十分にカップルが形成されやすい状況で、性転換率がある中庸な範囲の値にあることが必要であることが、Fig. 10(b) に示された結果よりわかる。いずれの場合においても、カップル形成率が大きくなると正味の出生率が大きくなるため、存続する可能性のある領域は広がる。

カップリング係数 r と性転換開始齢 a_c について、$\delta_w < (1-\beta)\lambda$、つまり、雌の死亡率が雌の出生率よりも小さい（雌の出生率が十分に大きい）場合、Fig. 11(a) に示された結果より、性転換開始齢が早すぎると、カップルが形成されやすくても、個体群は絶滅に向かい、個体群存続のためには、十分にカップルが形成されやすく、性転換開始齢がある閾値より遅いことが必要であることが分かる。$d_w > (1-\beta)\lambda$、つまり、雌の死亡率が雌の出生率よりも大きい（雌の出生率が十分に小さい）場合、Fig. 11(b) に示された結果より、個体群存続のためには、十分にカップルが形成されやすく、ある中庸な範囲の性転換開始齢が必要であることが分かる。つまり、性転換開始齢が遅すぎても早すぎても絶滅する。非自明な平衡点（サドル）(V^*, X^*, W^*, C^*) の大きさに対する性転換開始齢 a_c の影響について、$\delta_w < (1-\beta)\lambda$、つまり、雌の死亡率が雌の出生率よりも小さい（雌の出生率が十分に大きい）場合には、Fig. 12 に示した数値計算の結果より、性転換開始齢が相対的に早いと、非自明な平衡個体群サイズが大きくなることが分かる。非自明な平衡個体群サイズが大きい場合には、絶滅すると考えられる初期値の範囲が広く、個体群が存続する可能性が低いと考えられる。さらに、Fig. 12(b) に示した数値計算の結果には、非自明な平衡点が原点に最も近くなるような唯一の性転換開始齢が存在する事が示されている。これは、個体群の存続可能性が最も高くなるような性転換開始齢の存在を意味している。

また、$d_w > (1-\beta)\lambda$、つまり、雌の死亡率が雌の出生率よりも大きい（雌の出生率が十分に小さい）場合、Fig. 13 に示した数値計算の結果より、性転換開始齢が相対的に早すぎても遅すぎても、非自明な平衡個体群サイズが大きくなることが分かり、その場合には、やはり、絶滅すると考えられる初期値の範囲が広く、個体群が存続する可能性が低いと考えられる。さらに、Fig. 13(b) に示した通り、非自明な平衡点が原点に最も近くなるような唯一の性転換開始齢が存在する事が示されており、再び、個体群の存続可能性が最も高くなるような性転換開始齢の存在を意味している。

以上の結果より、雌の存続しやすさによって、個体群の存続条件を満たす性転換開始齢の範囲に相違は見られるが、いずれの場合においても個体群の存続の可能性が最も高くなるような唯一の性転換開始齢が存在していることが示唆された。

一般的に動物は自分の遺伝子を多く残す、つまり、多くの子孫を残すような適応戦略を取るように進化したと考えられているが、性転換を行う動物において、性転換のスケジュールを適応戦略とみなすと、個体が利己的に最適な性転換スケジュールをとったとしても、個体群レベルのダイナミクスを考えると、個体群の絶滅を誘引する結果を引き起こす場合があり得るかもしれない。

本論文では、個体群の存続性への性転換の影響を考えてきた。これまでの解析結果により、性転換の有無に関係なく、非自明な平衡点が存在しなければ個体群は絶滅し、存在すれば存続の可能性があるといえることがわかった。

性転換が行われない場合、その種が生存していくのに十分なエサや環境があり、生息範囲内において雄と雌が出会う頻度が高く、カップルが形成されやすい場合、非自明な平衡点が存在し、個体群が存続できる可能性がある。逆に、自然災害や環境変動により、生存するのに十分な環境条件が満たされず、雄と雌がカップルを形成しにくい状況であったり、または、不確定な生態的攪乱や人工的摂動などを含む何らかの事情で個体数が少なくなってしまった場合は、決定論的な動態によって個体群は絶滅に向かうと考えられる。

齢によらず常に性転換が起こり得る場合、雄の出生率が十分に高いときは、性転換率が高ければ、個体群が存続する可能性があると考えられる。性転換が行われるのは、性転換によって雌になったほうが有利である場合、すなわち一般的には、雌の個体数が相対的に少ない場合である。実際、本論文で研究した数理モデルについては、そのような場合に、非自明な平衡点が存在し、個体群は存続する可能性がある。

齢に依存する階段関数として性転換が起こる場合、雌の死亡率がその出生率よりも小さくても、雄から雌になる性転換によって、個体群が存続できる可能性がある事が本論文の数理モデル解析によっても示唆された。個体群の存続性については、カップル形成率、死亡率や出生率といった、明らかな個体群動態パラメータのほかに、性転換開始齢、性転換率といった個体の生理的特性を表すパラメータに対する依存性が無視できない。実際、本論文の数理モデル解析の結果において、性転換開始齢に依存して個体群の存続性に相違が見られることが示唆されている。

本研究は、性転換という生理的な戦略による、個体群の存続性への影響の存在可能性を示すための理論的研究であって、実際には、性転換を行うほとんどの魚類で、ハレムなどの社会的構造が繁殖に関わっていることがわかっており、そのような社会的構造下での性転換と個体群動態に関する数理的研究は今後の興味ある課題である。

1 Assumptions and Modelling

1.1 Dynamics of age distribution

We denote the age distribution function of male age a and that of female age a' at time t by $v(a,t)$ and $w(a,t)$ respectively. In addition, $c(a,a',t)$ gives the density of reproductive couple which consists of male with age a and female with age a' at time t.

We assume that the changes of $v(a,t)$ and $w(a,t)$ are occurred by the natural death and the sex reversal *from male to female*. On the other hand, the change of $c(a,a',t)$ is due to the separating and the coupling. The former occurs by the death of male or female of couple, or by the alive separation of them.

Now, we define the constant separating rate D and the density-dependent coupling rate S for reproductive couple. We assume that the coupling rate S depends on the densities v_e and w_e of single male and female, defined by

$$v_e(a,t) = v(a,t) - \int_0^\infty c(a,a',t)da' \tag{1}$$

$$w_e(a',t) = w(a',t) - \int_0^\infty c(a,a',t)da. \tag{2}$$

The integral of right side of (1) means the density of coupled male of age a at time t, and that of (2) does the density of coupled female of age a' at time t.

With these assumptions, our modelling for the changes of $v(a,t)$, $w(a,t)$ and $c(a,a',t)$ in sufficiently small period h are given by

$$\begin{aligned} &v(a+h,t+h) - v(a,t) \\ &\quad = -\delta_v h \cdot v(a,t) - M(a)h \cdot v(a,t) + o(h^2) \end{aligned} \tag{3}$$

$$\begin{aligned} &w(a'+h,t+h) - w(a',t) \\ &\quad = -\delta_w h \cdot w(a',t) + M(a')h \cdot v(a',t) + o(h^2) \end{aligned} \tag{4}$$

$$\begin{aligned} &c(a+h,a'+h,t+h) - c(a,a',t) \\ &\quad = -(\delta_v h + \delta_w h) \cdot c(a,a',w) - Dh \cdot c(a,a',w) \\ &\qquad +S(a,a';v_e,w_e)h + o(h^2), \end{aligned} \tag{5}$$

where δ_v and δ_w are the constant natural death rates for male and female respectively, and $M(a)$ the *age-dependent* sex reversal rate from male to female at age a.

From (3), (4), and (5), we can derive the following partial differential equations to give the dynamics of age distributions $v(a,t)$, $w(a,t)$ and $c(a,a',t)$, as shown in Appendix A:

$$\frac{\partial v(a,t)}{\partial t} + \frac{\partial v(a,t)}{\partial a} = -\delta_v v(a,t) - M(a)v(a,t) \tag{6}$$

$$\frac{\partial w(a',t)}{\partial t} + \frac{\partial w(a',t)}{\partial a'} = -\delta_w w(a',t) + M(a')v(a',t) \quad (7)$$

$$\frac{\partial c(a,a',t)}{\partial t} + \frac{\partial c(a,a',t)}{\partial a} + \frac{\partial c(a,a',t)}{\partial a'}$$

$$= -(\delta_v + \delta_w)c(a,a',t) - Dc(a,a',t) + S(a,a';v_e,w_e) \quad (8)$$

We assume that the initial age distributions for $v(a,t)$ and $w(a',t)$ are not everywhere zero, denoted by $v(a,0) = v_0(a), w(a',0) = w_0(a')$, whereas that for $c(a,a',t)$ is everywhere zero, $c(a,a',0) = 0$ $(0 \le a < \infty; 0 \le a' < \infty)$.

Since we assume that the reproduction is possible only by couples, the recruitment as the boundary conditions are given by

$$v(0,t) = \beta\lambda C(t) \quad (9)$$

$$w(0,t) = (1-\beta)\lambda C(t), \quad (10)$$

where $C(t)$ is the total number of couples at time t, defined by

$$C(t) \equiv \int_0^\infty \int_0^\infty c(a,a',t)dada', \quad (11)$$

and λ is the birth rate per couple, β the male ratio at birth. Hence, $\beta\lambda$ and $(1-\beta)\lambda$ indicate the number of male newborns per couple, and that of female. We assume that both λ and β are constant independently of time and parent's age. Besides, we assume that the newborn with age 0 cannot be coupled, so that

$$c(a,0,t) = c(0,a',t) = 0. \quad (12)$$

Additional boundary conditions can be new given by

$$v(\infty,t) = 0 \quad (13)$$
$$w(\infty,t) = 0 \quad (14)$$
$$c(\infty,a',t) = 0 \quad (15)$$
$$c(a,\infty,t) = 0, \quad (16)$$

since any individual cannot live forever.

1.2 Sex reversal rate

In this paper, we assume the following age-dependent sex reversal rate $M(a)$:

$$M(a) = \begin{cases} 0 & (0 \le a < a_c) \\ m & (a_c \le a < \infty). \end{cases} \quad (17)$$

After the critical age a_c, the sex reversal from male to female occurs at randam with a constant rate, m. If $a_c \to 0$, the sex reversal occurs at any age. On the other hand, if $a_c \to \infty$, it is the case without sex reversal at any age.

1.3 Coupling rate

In this paper, we assume that $S(a, a'; v_e, w_e) = r \cdot v_e w_e$, where r is a positive constant. This is the assumption of mass action between female and male to couple, that is, the coupling is assumed to occur under the complete mixing of females and males to give the random occurrence of coupling.

1.4 Dynamics of population size

From the age distribution functions, $v(a,t)$, $w(a,t)$ and $c(a,a',t)$, we can define the population size of male, $V(t)$, and that of female, $W(t)$:

$$V(t) \equiv \int_0^\infty v(a,t)da \tag{18}$$

$$W(t) \equiv \int_0^\infty w(a',t)da'. \tag{19}$$

Besides, for mathematical convenience, we define here the subpopulation size of male younger than age a_c:

$$X(t) \equiv \int_0^{a_c} v(a,t)da. \tag{20}$$

Integrating (6), (7) and (8), we can derive the following dynamical system of ordinary differential equations that govern the temporal variations of population sizes defined by (11), (18), (19) and (20) (see Appendix B):

$$\frac{dV(t)}{dt} = -\delta_v V(t) + \beta\lambda C(t) - m\{V(t) - X(t)\} \tag{21}$$

$$\frac{dX(t)}{dt} = \beta\lambda C(t) - \delta_v X(t) - v(a_c,t) \tag{22}$$

$$\frac{dW(t)}{dt} = -\delta_w W(t) + (1-\beta)\lambda C(t) + m\{V(t) - X(t)\} \tag{23}$$

$$\frac{dC(t)}{dt} = -(\delta_v + \delta_w + D)C(t) + r\{V(t) - C(t)\}\{W(t) - C(t)\}. \tag{24}$$

As for $v(a_c,t)$ appeared in (22), we can derive the following result with the method of characteristic curve for (6) (Appendix C):

$$v(a_c,t) = \begin{cases} \beta\lambda C(t-a_c)e^{-\delta_v a_c} & (t > a_c) \\ v_0(a_c - t)e^{-\delta_v t} & (t \leq a_c). \end{cases} \tag{25}$$

We assume that the initial population sizes $V(0)$, $X(0)$ and $W(0)$ are positive:

$$V(0) = \int_0^\infty v_0(a)da > 0$$

$$X(0) = \int_0^{a_c} v_0(a)da > 0$$

$$W(0) = \int_0^{\infty} w_0(a)da > 0.$$

On the other hand, since $c(a, a', 0) = 0$,

$$C(0) = \int_0^{\infty}\int_0^{\infty} c(a, a', 0)dada' = 0.$$

1.5 The condition for the population size

In our modelling, both population size of male and female are to be larger than that of couple:

$$\begin{cases} C^* < V^* \\ C^* < W^*. \end{cases} \tag{26}$$

2 Analysis

As the first step of our mathematical study, we separately consider three cases in terms of the value of the critical age a_c: 0, ∞, and finite positive.

2.1 $a_c \to \infty$

2.1.1 Dynamics of population sizes

Since this is the case when the sex reversal does not occur, the dynamics of population sizes can be written as the following three dimensional dynamical system derived from (21), (23) and (24):

$$\frac{dV(t)}{dt} = -\delta_v V(t) + \beta\lambda C(t) \tag{27}$$

$$\frac{dW(t)}{dt} = -\delta_w W(t) + (1-\beta)\lambda C(t) \tag{28}$$

$$\frac{dC(t)}{dt} = -(\delta_v + \delta_w + D)C(t) + r\{V(t) - C(t)\}\{W(t) - C(t)\}. \tag{29}$$

2.1.2 Extinction state at three-dimensional differential equations

The extinction state $(V^*, W^*, C^*) = (0, 0, 0)$ is always locally stable. This can be easily shown by the eigenvalue analysis for it. Indeed, the characteristic equation about the extinction state $(V^*, W^*, C^*) = (0, 0, 0)$ can be written as follows:

$$(\alpha + \delta_v)(\alpha + \delta_w)(\alpha + \delta_v + \delta_w + D) = 0, \tag{30}$$

where α is eigenvalue. Hence, $\alpha = -\delta_v$, δ_w and $-(\delta_v + \delta_w + D)$, that is, all are negative real.

2.1.3 Non-trivial equilibrium state

From (27), (28) and (29), we can see that at most one non-trivial equilibrium state exists:

$$(V^*, W^*, C^*) = \left(\frac{\beta\lambda}{\delta_v} C^*, \frac{(1-\beta)\lambda}{\delta_w} C^*, \frac{\delta_v \delta_w (\delta_v + \delta_w + D)}{r(\beta\lambda - \delta_v)\{(1-\beta)\lambda - \delta_w\}} \right) \tag{31}$$

From the condition (26) and the positiveness for (31), we can get the following condition for the existence of non-trivial equilibrium state (31):

$$\begin{cases} \beta\lambda & > & \delta_v \\ (1-\beta)\lambda & > & \delta_w. \end{cases} \tag{32}$$

This means that the non-trivial positive equilibrium state (31) exists if and only if the sex-specified birth rate of each sex is larger than the natural death rate.

2.1.4 Asymptotic sex ratio

If $\delta_v = \delta_w = \delta$, we can get the following from (27) and (28):

$$\frac{d}{dt}\{(1-\beta)V(t) - \beta W(t)\} = -\delta\{(1-\beta)V(t) - \beta W(t)\}. \tag{33}$$

Therefore, we can get immediately the following:

$$(1-\beta)V(t) - \beta W(t) = \{(1-\beta)V(0) - \beta W(0)\}e^{-\delta t}. \tag{34}$$

This means that, as $t \to \infty$, the sex ratio asymptotically converges to that at birth:

$$\frac{V(t)}{W(t)} \to \frac{\beta}{1-\beta} \quad (t \to \infty). \tag{35}$$

2.1.5 Asymptotic dynamics

From the above result about the asymptotic behavior of sex ratio, let us consider the following two dimensional dynamical system for $\delta_v = \delta_w = \delta$ instead of three dimensional one described by (27), (28) and (29) for $t \gg 1$:

$$\frac{dW(t)}{dt} = -\delta W(t) + (1-\beta)\lambda C(t) \tag{36}$$

$$\frac{dC(t)}{dt} = -(2\delta + D)C(t) + r\left\{\frac{\beta}{1-\beta} W(t) - C(t)\right\}\{W(t) - C(t)\}. \tag{37}$$

This system corresponds to that given by (28) and (29) with $V(t) \equiv \beta W(t)/(1-\beta)$ and $\delta_v = \delta_w = \delta$. Asymptotic behavior of the system given by (36) and (37)

asymptotically coincides with that of (C, W) of the system given by (27), (28) and (29).

In our analysis for the case when $a_c \to \infty$, in order to consider the asymptotic behavior as $t \to \infty$, we now focus the two dimensional system given by (36) and (37) when $\delta_v = \delta_w = \delta$.

Equilibrium state for the asymptotic two-dimensional system The extinction state $(C^*, W^*) = (0, 0)$ is always locally stable. This can be easily shown as described in the section 2.1.2. As for the non-trivial equilibrium state, from (36) and (37), we can see that at most one exists:

$$(C^*, W^*) = \left(\frac{\delta^2(2\delta + D)}{(\delta - \beta\lambda)\{\delta - (1-\beta)\lambda\}}, \frac{\delta(2\delta + D)(1-\beta)\lambda}{(\delta - \beta\lambda)\{\delta - (1-\beta)\lambda\}} \right). \tag{38}$$

From the condition (26) and the positiveness for (38), we can get the condition for the existence of non-trivial equilibrium state (38), substituting $\delta_v = \delta_w = \delta$ in (32): $\min\{\beta\lambda, (1-\beta)\lambda\} > \delta$.

On the other hand, the eigenvalue analysis proves that the non-trivial equilibrium state (38) exists unstable as a saddle point. Indeed, its characteristic equation can be written as follows:

$$\alpha^2 + \left[\frac{(2\delta + D)\{-\delta^2 + \beta(1-\beta)\lambda^2\}}{(\delta - \beta\lambda)\{\delta - (1-\beta)\lambda\}} + \delta \right] \alpha - \delta(2\delta + D) = 0, \tag{39}$$

where α is eigenvalue. From (39), we can see that, since the sum and the product of two roots for (39) are both negative, two eigenvalues are real with different signs. Fig. 1 shows some trajectories of (C, W) when the non-trivial equilibrium state (38) exists.

Since the population goes extinct or infinite, depending on the initial state as shown in Fig. 1 when the non-trivial equilibirium state exists, we now consider the separatrix which corresponds to the stable manifold for the non-trivial equilibrium state. Although the stable manifold could not be analytically obtained, we can numerically draw it as shown in Fig. 2. Numerical result indicates the followings:

1. When both $C(0)$ and $W(0)$ are sufficiently small, the population goes extinct.

2. When $C(0)$ has an intermediate value, there is such a case that only some intermediate value of $W(0)$ causes the extinction of population, and too small or too large $W(0)$ does the growth.

Supposing that the coupling dynamics is sufficiently faster than the temporal variation of male and female populations, we put $dC(t)/dt \approx 0$ as an approximation for the dynamics given by (27), (28) and (29), and get an approximated two-dimensional differential equations about V and W. For the approximated dynamical system, we can carry out the same analysis about the asymptotic states considered above, and get the qualitatively same result.

2.2 $a_c \to 0$

2.2.1 Dynamics of population size

Since this is the case when the sex reversal always occurs, the dynamics of population size can be written as follows from (21), (23) and (24):

$$\frac{dV(t)}{dt} = -\delta_v V(t) - mV(t) + \beta\lambda C(t) \tag{40}$$

$$\frac{dW(t)}{dt} = -\delta_w W(t) + mV(t) + (1-\beta)\lambda C(t) \tag{41}$$

$$\frac{dC(t)}{dt} = -(\delta_v + \delta_w + D)C(t) + r\{V(t) - C(t)\}\{W(t) - C(t)\}. \tag{42}$$

2.2.2 Extinction state

Extinction state $(V^*, W^*, C^*) = (0, 0, 0)$ is always locally stable. This can be easily shown by the eigenvalue analysis for it. Indeed, the characteristic equation about the extinction state $(V^*, W^*, C^*) = (0, 0, 0)$ can be written as follows:

$$(\alpha + \delta_w)(\alpha + \delta_v + m)(\alpha + \delta_v + \delta_w + D) = 0$$

, where α is eigenvalue. From this equation, $\alpha = -\delta_w, -(\delta_v + m)$, and $-(\delta_v + \delta_w + D)$, so that three eigenvalues are all negative real.

2.2.3 Non-trivial equilibrium state

From (40), (41) and (42), we can see that at most one non-trivial equilibrium state could exist:

$$\begin{cases} V^* = \dfrac{\beta\lambda}{\delta_v + m} C^* \\ W^* = \dfrac{1}{\delta_w}\left\{\dfrac{m\beta\lambda}{d_{11} + m} + (1-\beta)\lambda\right\} C^* \\ C^* = \dfrac{\delta_v + \delta_w + D}{r\left\{\frac{\beta\lambda}{\delta_v + m} - 1\right\}\left[\frac{1}{\delta_w}\left\{\frac{m\beta\lambda}{\delta_v + m} + (1-\beta)\lambda\right\} - 1\right]}. \end{cases} \tag{43}$$

From the condition (26) and the positiveness for (43), we can get the following condition for the existence of non-trivial equilibrium state (43):

$$\begin{cases} \beta\lambda > \delta_v + \dfrac{m}{\delta_v + m}\beta\lambda \\ \dfrac{m}{\delta_v + m}\beta\lambda + (1-\beta)\lambda > \delta_w. \end{cases} \tag{44}$$

The first inequality of (44) means the condition such that the male birth is larger than the decrease caused by the natural death and the sex reversal. The second means the corresponding condition for female population such that the increase caused by the new born and the sex reversal is larger than the natural death. If and only if these two conditions are satisfied at the same time, the non-trivial equilibrium state (43) exists. Fig. 3(a) shows the condition for the existence of non-trivial equilibrium state (43). Figs. 4(a, b) that whether the population goes extinct or growth depends on the initial condition.

Analyzing the characteric equation for the non-trivial eqilibrium state (43) of the system given by (40-42), we can obtain the condition for the local stability (see Appendix D).

2.2.4 Approximation with two-timing method

Now, we apply the two-timing method for the dynamics governed by (40-42) in order to consider its characteristic nature in detail. Supposing that the change of coupling dynamics is sufficiently faster than those of male and female populations, we put $dC(t)/dt \approx 0$ as an approximation for this dynamics given by (40-42). With $dC(t)/dt = 0$ at (42), we can get the followings from (40) and (41):

$$\begin{aligned}\frac{dV(t)}{dt} &= -\delta_v V(t) - mV(t) + \frac{\beta\lambda}{2}\{rV(t) + rW(t) + g\} \\ &\quad -\frac{\beta\lambda}{2r}\sqrt{f(V(t), W(t))} \qquad (45)\\ \frac{dW(t)}{dt} &= -\delta_w W(t) + mV(t) + \frac{(1-\beta)\lambda}{2}\{rV(t) + rW(t) + g\} \\ &\quad -\frac{(1-\beta)\lambda}{2r}\sqrt{f(V(t), W(t))}, \qquad (46)\end{aligned}$$

where

$$\begin{aligned}f(V(t), W(t)) &= r^2\left\{V(t) + W(t) + g\right\}^2 - 4r^2V(t)W(t) \\ &= r^2[\left\{V(t) - W(t) + g\right\}^2 + 4W(t)g] > 0 \qquad (47)\end{aligned}$$

and

$$g = \frac{\delta_v + \delta_w + D}{r}. \qquad (48)$$

Since the population goes extinct or infinite depending on the initial condition as shown in Fig. 5 when the non-trivial equilibirium state exists, we again consider the separatrix. We can numerically draw it as shown in Fig. 6. Numerical result indicates the followings:

1. When $V(0)$ and $W(0)$ are sufficiently small, the population goes extinct and when $V(0)$ and $W(0)$ are sufficiently large, the population will diverge.

2. When $W(0)$ has an intermediate value, there is such a case that sufficiently small value of $V(0)$ causes the extinction of population, and sufficiently large $V(0)$ does the growth.

Analyzing the characteric equation for the non-trivial equilibrium state which is given by (45) and (46), we can obtain the condition for the local stability (see Appendix E).

2.3 $0 < a_c < \infty$

This is the case when the sex reversal occurs at random with a constant rate after a given age a_c as shown in (17). Population dynamics is given by (21-24).

2.3.1 Extinction state

The extinction state $(V^*, X^*, W^*, C^*) = (0, 0, 0, 0)$ is always locally stable. The characteristic equation about the extinction state $(V^*, X^*, W^*, C^*) = (0, 0, 0, 0)$ can be written as follows:

$$(\alpha + \delta_v)(\alpha + \delta_w)(\alpha + \delta_v + m)(\alpha + \delta_v + \delta_w + D) = 0, \tag{49}$$

where α is eigenvalue. Hence, $\alpha = -\delta_v, -\delta_w, -(\delta_v + m)$, and $-(\delta_v + \delta_w + D)$, that is, four eigenvalues are all negative real.

2.3.2 Non-trivial equilibrium state

From (21-24), we can see that at most one non-trivial equilibrium state could exist as follows:

$$\begin{cases} X^* &= \dfrac{\beta\lambda(1 - e^{-\delta_v a_c})}{\delta_v} C^* \\ V^* &= \dfrac{\beta\lambda\{m(1 - e^{-\delta_v a_c}) + \delta_v\}}{\delta_v(\delta_v + m)} C^* \\ W^* &= \dfrac{1}{\delta_w} \left\{ \dfrac{m\beta\lambda\{m(1 - e^{-\delta_v a_c}) + \delta_v\}}{\delta_v(\delta_v + m)} - \dfrac{m\beta\lambda(1 - e^{-\delta_v a_c})}{\delta_v} + (1 - \beta)\lambda \right\} C^* \\ C^* &= \dfrac{\delta_v + \delta_w + D}{r\left(\frac{V^*}{C^*} - 1\right)\left(\frac{W^*}{C^*} - 1\right)}. \end{cases} \tag{50}$$

From the condition (26) and the positiveness for (50), we can get the following condition for the existence of non-trivial equilibrium state (50):

$$\begin{cases} \beta\lambda &> \delta_v + \dfrac{m}{\delta_v + m}\beta\lambda e^{-\delta_v a_c} \\ (1 - \beta)\lambda + \dfrac{m}{\delta_v + m}\beta\lambda e^{-\delta_v a_c} &> \delta_w. \end{cases} \tag{51}$$

The first inequality of (51) means the condition such that the male birth is larger than the decrease caused by the natural death and the sex reversal which follows the age-dependent function (17). The second means the corresponding condition for female population such that the increase caused by the new born and the sex reversal which follows the age-dependent function (17) is larger than the natural death. If and only if these two conditions are satisfied at the same time, the non-trivial equilibrium state (50) exists. Fig. 3(b) shows the condition for the existence of non-trivial equilibrium state (50).

Making use of numerical calculations, we get the results given by Fig. 7 about the parameter dependence of population extinction. From Fig. 7(a), we can result in the followings:

- When the sex reversal does not occur so often, the population does not go extinct even if the critical age a_c is rather small.
- As the sex reversal rate m gets larger, the population does not go extinct when a_c is larger than a critical value.
- Population goes extinct with sufficiently large sex reversal rate m when a_c is smaller than a critical value.
- When a_c is larger than critical value, the population does not go extinct for any m.

From Fig. 7(b),

- Population goes extinct when the age a_c is too small or too large, that is, too early or too late.
- Even if the age a_c has an intermediate value, the population goes extinct when the sex reversal rate m is too small, while it does not when m is larger than a critical value.
- When the age a_c is larger than a critical value and smaller than another critical age, the population would not go extinct with any sex reversal rate m.
- When the age a_c is smaller than a critical value, the population would go extinct except in case of having small sex reversal rate m.

From Figs. 4, we can see that different initial condition causes the dynamics diffrent.

From Figs. 8, we can see that too small and too large critical age causes the population goes extinct. From Figs. 9, we can see that too large sex reversal rate causes the population goes extinct.

2.3.3 Coupling and sex reversal rates

From our numerical calculations shown in Figs. 10(a, b), we can see the followings:

- As the coupling coefficient r gets larger, the population does not go extinct if the sex reversal rate m is sufficiently small.
- Even if r is rather large, the population goes extinct when the sex reversal occurs so often.
- For the population persistence, the coupling coefficient r has to be sufficiently large. With too small r, the population goes extinct.

2.3.4 Coupling coefficient the critical age a_c

As shown in Fig. 11(a), we can see the followings:

- As the coupling rare r gets larger, the population does not go extinct with the age a_c larger than a critical value.
- Population goes extinct when the coupling coefficient r is smaller than a critical value.
- When the age a_c is earlier than a critical, any coupling coefficient r causes the population extinct.

From Fig. 11(b),

- As the coupling coefficient r gets larger, the population does not go extinct when the age a_c has an intermediate value.
- Population goes extinct when r is smaller than a critical value. In this case, the critical value for r would be determined by m.
- When the age a_c is smaller than a critical value, the population goes extinct for any coupling coefficient r.
- When the age a_c is larger than a critical value, the population goes extinct for any coupling coefficient r.

2.3.5 Effect of the critical age on the equilibrium population sizes

Fig. 12 shows the case when $\delta_w < (1-\beta)\lambda$, which means that the female's population persistence is possible. As shown in Fig. 12(a), we can see that, if the critical age a_c is sufficiently small for the case when the non-trivial equilibrium exists, the non-trivial equilibrium population sizes are so large that the region of initial points to go extinct is much wide. Since the non-trivial equilibrium point is saddle with a separatrix for the region of initial points to go extinct, the possibility of population persistence can be regarded as rather low in such case (also see Figs. 1, 2, 5, 6, and Fig. 12(b)). The later the critical age a_c is, the population persistence is feasible. Further, from Fig. 12(b), we can see that such the unique and intermediate critical age exists as to make the equilibrium point the nearest to the origin so that it makes the population persistence the most possible.

On the other hand, Fig. 13 shows the case when $\delta_w > (1-\beta)\lambda$, which means that the female's population persistence is difficult. As shown in Fig. 13(a), we can see that, if the critical age a_c is too small or too large for the case when the non-trivial equilibrium exists, the non-trivial equilibrium population sizes are so large that the region of initial points to go extinct is much wide. Hence, in such case, the possibility of population persistence can be regarded as rather low (also see Fig. 13(b)). Lastly, an intermediate range of the critical age a_c could make the possibility of population persistence the higher. Further, from Fig. 13(b), we can see again that such the unique and intermediate critical age exists as to make the equilibrium point the nearest to the origin so that it makes the population persistence the most possible.

References

[1] 菊沢喜八郎, 1995. 『植物の繁殖生態学』蒼樹書房.

[2] 寺本英, 山口昌哉編, 1975 『岩波講座 現代生物科学 17　数理を通してみた生命』岩波書店.

Appendix A

For sufficiently short period h, we calculate the Taylor series expansion of $v(a+h, t+h)$ as follows:

$$v(a+h,t+h) = v(a,t) + \frac{\partial v(a,t)}{\partial t}h + \frac{\partial v(a,t)}{\partial a}h + o(h^2). \quad (52)$$

Hence, substituting (52) to (3), we can obtain the following:

$$\begin{aligned} \frac{v(a+h,t+h)-v(a,t)}{h} &= \frac{\partial v(a,t)}{\partial t} + \frac{\partial v(a,t)}{\partial a} + \frac{o(h^2)}{h} \\ &= -\delta_v v(a,t) - M(a)v(a,t) + \frac{o(h^2)}{h}. \quad (53) \end{aligned}$$

As $h \to 0$ for (53), we can get (6).

Appendix B

By integrating the left side of (6) from 0 to ∞ in terms of a and using (9), (13) and (18), supposing that the exchange between the integration in terms of a and the differentiation in terms of t is possible, we can get the following.

$$\begin{aligned} \int_0^\infty \frac{\partial v(a,t)}{\partial t}da + \int_0^\infty \frac{\partial v(a,t)}{\partial a}da &= \frac{\partial}{\partial t}\int_0^\infty v(a,t)da + v(\infty,t) - v(0,t) \\ &= \frac{dV(t)}{dt} - \beta\lambda C(t). \quad (54) \end{aligned}$$

By integrating the right side of (6) from 0 to ∞ in terms of a, using (17) and (18), we can get the following:

$$\begin{aligned} &-\delta_v \int_0^\infty v(a,t)da - \int_0^\infty M(a)v(a,t)da \\ &\quad = -\delta_v V(t) - \left\{0 \cdot \int_0^{a_c} v(a,t)da + m \cdot \int_{a_c}^\infty v(a,t)da\right\} \\ &\quad = -\delta_v V(t) - m\left\{\int_0^\infty v(a,t)da - \int_0^{a_c} v(a,t)da\right\} \\ &\quad = -\delta_v V(t) - m\{V(t) - X(t)\}. \quad (55) \end{aligned}$$

From (54) and (55), we can get (21). Similarly, (23) can be derived from (7), (10), (14), (17) and (19).

By integrating the left side of (6) from 0 to a_c in terms of a, using (9) and (20), we can get the following:

$$\begin{aligned}\int_0^{a_c}\left(\frac{\partial v}{\partial a}+\frac{\partial v}{\partial t}\right)da &= v(a_c,t)-v(0,t)+\frac{\partial}{\partial t}\int_0^{a_c}v(a,t)da \\ &= v(a_c,t)-\beta\lambda C(t)+\frac{dX(t)}{dt}. \qquad (56)\end{aligned}$$

By integrating the right side of (6) from 0 to a_c in terms of a, using (17) and (20),

$$-\delta_v\int_0^{a_c}v(a,t)da-\int_0^{a_c}M(a)v(a,t)da=-\delta_v X(t). \qquad (57)$$

From (56) and (57), we can get (22).

By integrating (6) and (7) from 0 to ∞ in terms of a and a', using (11), (18) and (19), we can get the followings:

$$\begin{aligned}\int_0^{\infty}v_e(a,t)da &= \int_0^{\infty}v(a,t)da-\int_0^{\infty}\int_0^{\infty}c(a,a',t)dada' \\ &= V(t)-C(t), \qquad (58)\\ \int_0^{\infty}w_e(a',t)da &= \int_0^{\infty}w(a',t)da-\int_0^{\infty}\int_0^{\infty}c(a,a',t)dada' \\ &= W(t)-C(t). \qquad (59)\end{aligned}$$

By integrating the left side of (8) from 0 to ∞ in terms of both a and a', using (11), (12), (15) and (16), we can get the following:

$$\begin{aligned}&\int_0^{\infty}\int_0^{\infty}\left(\frac{\partial c}{\partial a}+\frac{\partial c}{\partial a'}+\frac{\partial c}{\partial t}\right)dada' \\ &= \int_0^{\infty}\int_0^{\infty}\frac{\partial c}{\partial a}dada'+\int_0^{\infty}\int_0^{\infty}\frac{\partial c}{\partial a'}dada'+\int_0^{\infty}\int_0^{\infty}\frac{\partial c}{\partial t}dada' \\ &= \frac{d}{dt}\int_0^{\infty}\int_0^{\infty}c(a,a',t)dada' \\ &= \frac{dC(t)}{dt}. \qquad (60)\end{aligned}$$

By integrating the right side of (8) from 0 to ∞ in terms of a and a', we can get the following, using (11), (58) and (59):

$$\begin{aligned}&-(\delta_v+\delta_w+D)\int_0^{\infty}\int_0^{\infty}c(a,a',t)dada'+e\int_0^{\infty}v_e(a,t)da\int_0^{\infty}w_e(a',t)da' \\ &\qquad = -(\delta_v+\delta_w+D)C(t)+r\{V(t)-C(t)\}\{W(t)-C(t)\}. \qquad (61)\end{aligned}$$

From (60) and (61), we can get (24).

Appendix C

Now, $v(a_c, t)$ corresponds to the density of male with age a_c at time t. If $t \geq a_c$, it originates with the density $v(0, t - a_c)$ of male newborn at time $t - a_c$. This is because age increases by the same increment as time does, so that $v(a_c, t)$ originates with the density $v(a_c - p, t - p)$ for any p such that $0 < p \leq a_c$. Let us put $F(p) \equiv v(a_c - p, t - p)$ $(0 < p \leq a_c)$ for any fixed $t \geq a_c$, then the function $F(p)$ is assumed to be continuous and sufficiently smooth.

From our modelling, since any male younger than age a_c does not make the sex reversal, the temporal variation of density $v(a_c - p, t - p)$ from time $t - p$ to $t - p + h$ is only due to the natural death. Therefore, for sufficiently small period h,

$$v(a_c - p + h, t - p + h) - v(a_c - p, t - p) = -\delta_v h \cdot v(a_c - p, t - p) + o(h^2),$$

that is,

$$\frac{F(p - h) - F(p)}{h} = -\delta_v \cdot F(p) + \frac{o(h^2)}{h}.$$

As $t \to 0$, we can get the following linear differential equation about $F(p)$:

$$\frac{dF(p)}{dp} = \delta_v \cdot F(p) \quad (0 < p \leq a_c). \tag{62}$$

As the boundary condition for (62), we use the below, derived from (9):

$$F(a_c) = v(0, t - a_c) = \beta\lambda C(t - a_c). \tag{63}$$

The differential equation (62) of $F(p)$ with the condition (63) can be easily solved and the solution becomes

$$F(p) = v(a_c - p, t - p) = \beta\lambda C(t - a_c) e^{\delta_v (p - a_c)} \quad (0 < p \leq a_c),$$

thus lastly, with $p \to 0$,

$$v(a_c, t) = \beta\lambda C(t - a_c) e^{-\delta_v a_c} \quad (t \geq a_c). \tag{64}$$

On the other hand, if $t < a_c$, $v(a_c, t)$ originates with the density of male with age $a_c - t$ at time 0. Hence, with $v(a_c - t, 0) = v_0(a_c - t)$ for any fixed $t < a_c$, in the similar way as above for the case when $t \geq a_c$, we can obtain the following:

$$v(a_c, t) = v_0(a_c - t) e^{-\delta_v a_c} \quad (t < a_c). \tag{65}$$

These results (64) and (65) give $v(a_c, t)$ of (25).

Appendix D

We can get the following characteristic equation for the non-trivial equilibrium state (43) of the system given by (40-42):

$$\begin{aligned}\alpha^3 &+ \{2(\delta_v+\delta_w)+A+B+m+D\}\alpha^2 \\ &+ [(\delta_v+\delta_w+m)\{A+B+\delta_v+\delta_w+D\}+\delta_w(\delta_v+m)-(1-\beta)\lambda A-\beta\lambda B]\alpha \\ &+ \delta_w(\delta_v+m)\{A+B+\delta_v+\delta_w+D\} \\ &\qquad -\{(1-\beta)\lambda(\delta_v+m)+m\beta\lambda\}A-\delta_w\beta\lambda B=0, \qquad (66)\end{aligned}$$

where $A=r(V^*-C^*)$, $B=r(W^*-C^*)$. V^*, W^* and C^* satisfy (43). From (66), we can formally get the condition for stability, making use of the Routh-Hurwitz criterion:

$$\begin{cases} \delta_w(\delta_v+m)\{A+B+\delta_v+\delta_w+D\}-\{(1-\beta)\lambda(\delta_v+m)+m\beta\lambda\}A-\delta_w\beta\lambda B>0 \\ \{2(\delta_v+\delta_w)+A+B+m+D\} \\ \times[(\delta_v+\delta_w+m)\{A+B+\delta_v+\delta_w+D\}+\delta_w(\delta_v+m)-(1-\beta)\lambda A-\beta\lambda B] \\ -\delta_w(\delta_v+m)\{A+B+\delta_v+\delta_w+D\}-\{(1-\beta)\lambda(\delta_v+m)+m\beta\lambda\}A-\delta_w\beta\lambda B>0. \end{cases}$$

Appendix E

We can get the following characteristic equation for the non-trivial equilibrium state given by (45-46):

$$\begin{aligned}\alpha^2+\left[-(\delta_v+\delta_w+m)+\frac{1}{2}\{\beta\lambda A+(1-\beta)\lambda B\}\right]\alpha \\ +\left\{\frac{\beta\lambda}{2}A-(\delta_v+m)\right\}\left\{\frac{(1-\beta)\lambda}{2}B-\delta_w\right\} \\ -\frac{\beta\lambda}{2}B\left\{m+\frac{(1-\beta)\lambda}{2}A\right\}=0, \quad (67)\end{aligned}$$

where

$$\begin{cases} A=1-\dfrac{2r(V^*-W^*)+2(\delta_v+\delta_w+D)}{\sqrt{(\delta_v+\delta_w+D+rV^*+rW^*)^2-4r^2V^*W^*}} \\ B=1-\dfrac{2r(W^*-V^*)+2(\delta_v+\delta_w+D)}{\sqrt{(\delta_v+\delta_w+D+rV^*+rW^*)^2-4r^2V^*W^*}}. \end{cases}$$

V^*, W^* and C^* satisfy (43). From (67), we can get the condition for the local stability:

$$\begin{cases} -(\delta_v + \delta_w + m) + \dfrac{1}{2}\{\beta\lambda A + (1-\beta)\lambda B\} < 0 \\ \left\{\dfrac{\beta\lambda}{2}A - (\delta_v + m)\right\}\left\{\dfrac{(1-\beta)\lambda}{2}B - \delta_w\right\} - \dfrac{\beta\lambda}{2}B\left\{m + \dfrac{(1-\beta)\lambda}{2}A\right\} > 0. \end{cases}$$

Figure Captions

Fig. 1

Numerical trajectories for the two dimensional system given by (33) and (34). $\beta = 0.4; \lambda = 1.0; \delta = 0.3; D = 0.0; r = 1.0$.

Fig. 2

Manifolds for the non-trivial equilibrium (C^*, W^*) about the two dimensional system given by (33) and (34). Numerically obtained. $\beta = 0.4; \lambda = 1.0; \delta = 0.3; D = 0.0; r = 1.0$.

Fig. 3

(δ_v, δ_w)-dependence of the existence of non-trivial equilibrium. (a)Region A is for the case when $a_c \to 0$, and B for $a_c \to +\infty$. (b)For the case when $0 < a_c < +\infty$. p shows the value for δ_v which satisfies the equation $(\delta_v + m)(\delta_v - \beta\lambda) = -\beta\lambda m e^{-\delta_v a_c}$.

Fig. 4

Temporal variation of population sizes $(V(t), X(t), W(t), C(t))$. (a) $(V(0), X(0), W(0), C(0)) = (1.0, 0.865, 1.0, 0.0)$; (b) $(V(0), X(0), W(0), C(0)) = (1.0, 0.865, 0.3, 0.0)$. $\beta = 0.7; \lambda = 1.0; \delta_v = 0.3; \delta_w = 0.2; D = 0.0; r = 1.0; m = 0.2; a_c = 2.0$.

Fig. 5

Numerical trajectories for the two dimensional system given by (46) and (47). $\beta = 0.7; \lambda = 1.0; \delta_v = 0.1; \delta_w = 0.5; D = 0.0; r = 1.0; m = 0.1$.

Fig. 6

Manifolds for the non-trivial equilibrium (V^*, W^*) for the two-dimensional system given by (46) and (47). Numerically obtained. $\beta = 0.7; \lambda = 1.0; \delta_v = 0.1; \delta_w = 0.5; D = 0.0; r = 1.0; m = 0.1$.

Fig. 7

(m, a_c)-dependence of population extinction. Black points indicate the parameter set to cause the extinction, estimated by numerical calculations. $\lambda = 1.0; D = 0.0; r = 1.0; (V(0), X(0), W(0), C(0)) = (1.0, 1 - e^{-a_c}, 1.0, 0.0)$; (a) $\delta_w < (1 - \beta)\lambda; \beta = 0.6; \delta_v = 0.2; \delta_w = 0.1$;(b) $\delta_w > (1 - \beta)\lambda; \beta = 0.7; \delta_v = 0.1; \delta_w = 0.4$.

Fig. 8

Temporal variation of population sizes $(V(t), X(t), W(t), C(t))$ for $m = 5.0$. (a) $a_c = 2.0$; (b) $a_c = 5.0$; (c) $a_c = 10.0$. $\beta = 0.6; \lambda = 1.0; \delta_v = 0.2; \delta_w = 0.1; D = 0.0; r = 1.0$.

Fig. 9

Temporal variation of population sizes $(V(t), X(t), W(t), C(t))$ for $a_c = 1.5$. (a) $m = 0.5$; (b) $m = 5.0$; (c) $m = 10.0$. $\beta = 0.7; \lambda = 1.0; \delta_v = 0.1; \delta_w = 0.4; D = 0.0; r = 1.0$.

Fig. 10

(r, m)-dependence of population extinction. $\lambda = 1.0; D = 0.0; a_c = 1.0; (V(0), X(0), W(0), C(0)) = (1.0, 1 - e^{-a_c}, 1.0, 0.0)$. (a) $\delta_w < (1-\beta)\lambda; \beta = 0.6; \delta_v = 0.2; \delta_w = 0.1$; (b) $\delta_w > (1-\beta)\lambda; \beta = 0.78; \delta_v = \delta_w = 0.23$.

Fig. 11

(r, a_c)-dependence of population extinction. $\lambda = 1.0; D = 0.0; m = 1.5; (V(0), X(0), W(0), C(0)) = (1.0, 1 - e^{-a_c}, 1.0, 0.0)$. (a) $\delta_w < (1-\beta)\lambda; \beta = 0.6; \delta_v = 0.2; \delta_w = 0.1$; (b) $\delta_w > (1-\beta)\lambda; \beta = 0.7; \delta_v = 0.1; \delta_w = 0.4$.

Fig. 12

(a)a_c-dependence of the non-trivial equilibrium population sizes $V^*, X^*, W^*, C^*, V^* + W^*$. (b)$a_c$-dependence of the distance of equilibrium point from the origin. For $\delta_w < (1-\beta)\lambda; \beta = 0.5; \lambda = 1.0; \delta_v = 0.2; \delta_w = 0.3; r = 1.0; D = 0.0; m = 2.0$. The non-trivial equilibrium can exist for $2.0776 < ac$.

Fig. 13

(a)a_c-dependence of the non-trivial equilibrium population sizes $V^*, X^*, W^*, C^*, V^* + W^*$. (b)$a_c$-dependence of the distance of equilibrium point from the origin. For $\delta_w > (1-\beta)\lambda; \beta = 0.7; \lambda = 1.0; \delta_v = 0.1; \delta_w = 0.4; r = 4.0; D = 0.0; m = 1.5$. The non-trivial equilibrium can exist for $0.8961 < ac < 18.8167$.

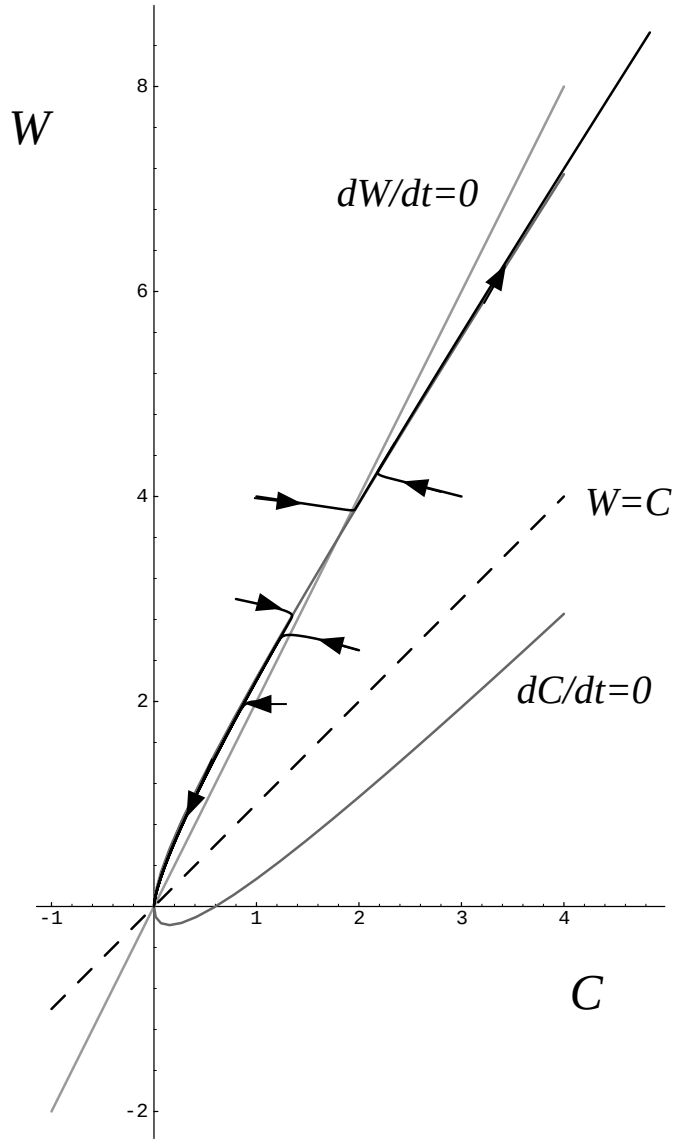


Fig. 1

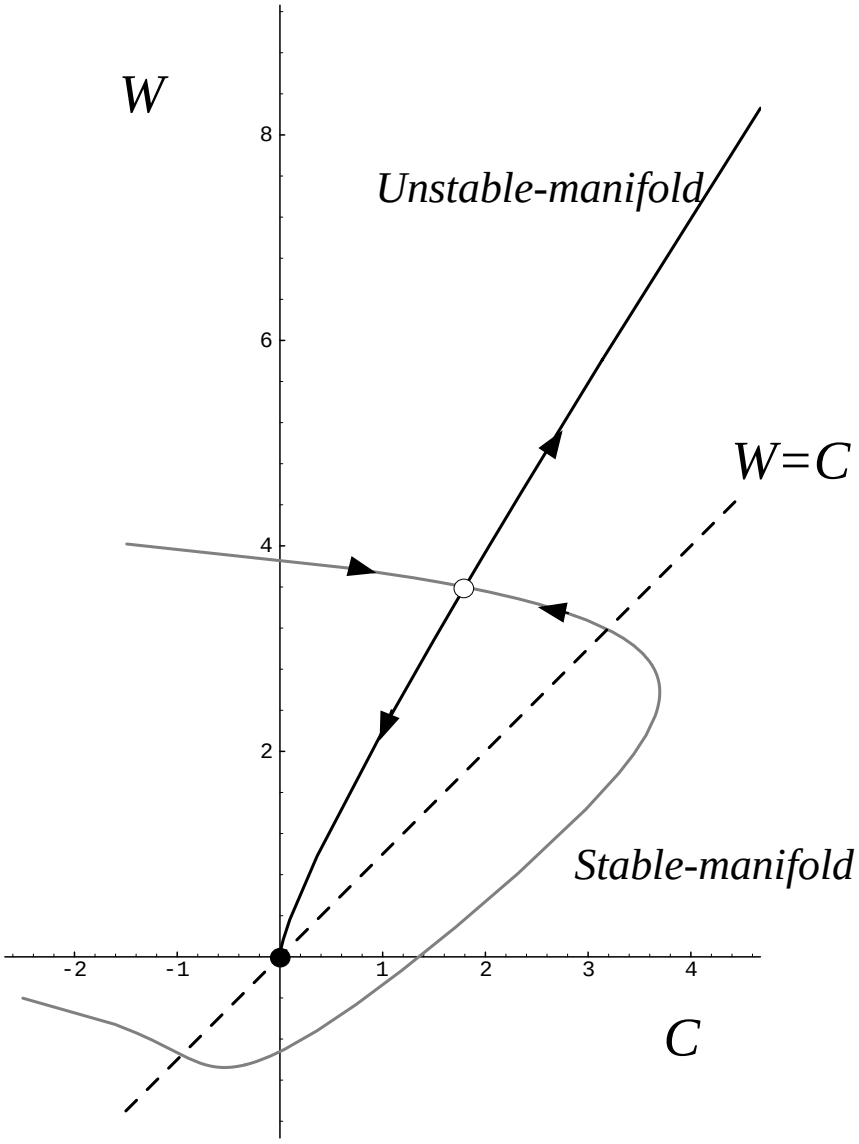
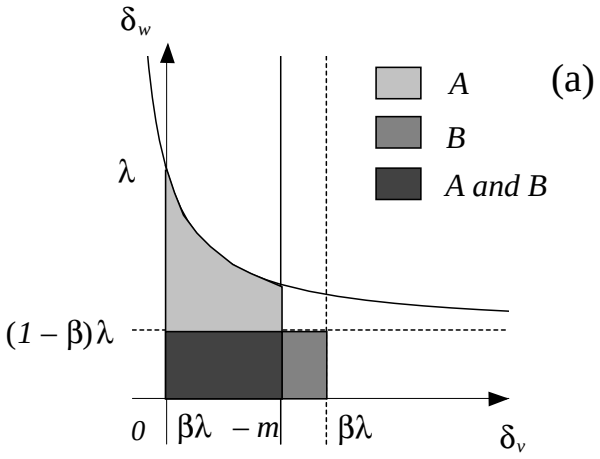
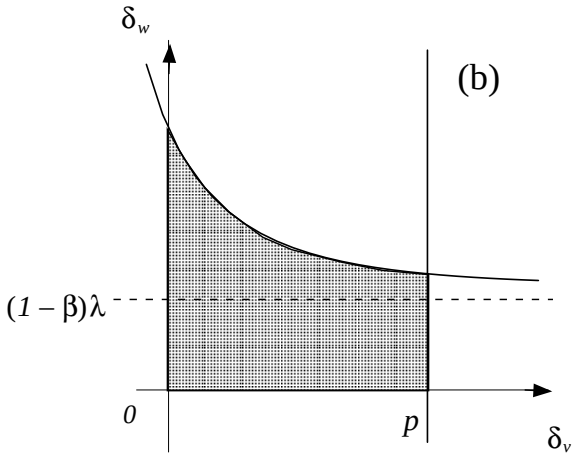


Fig. 2





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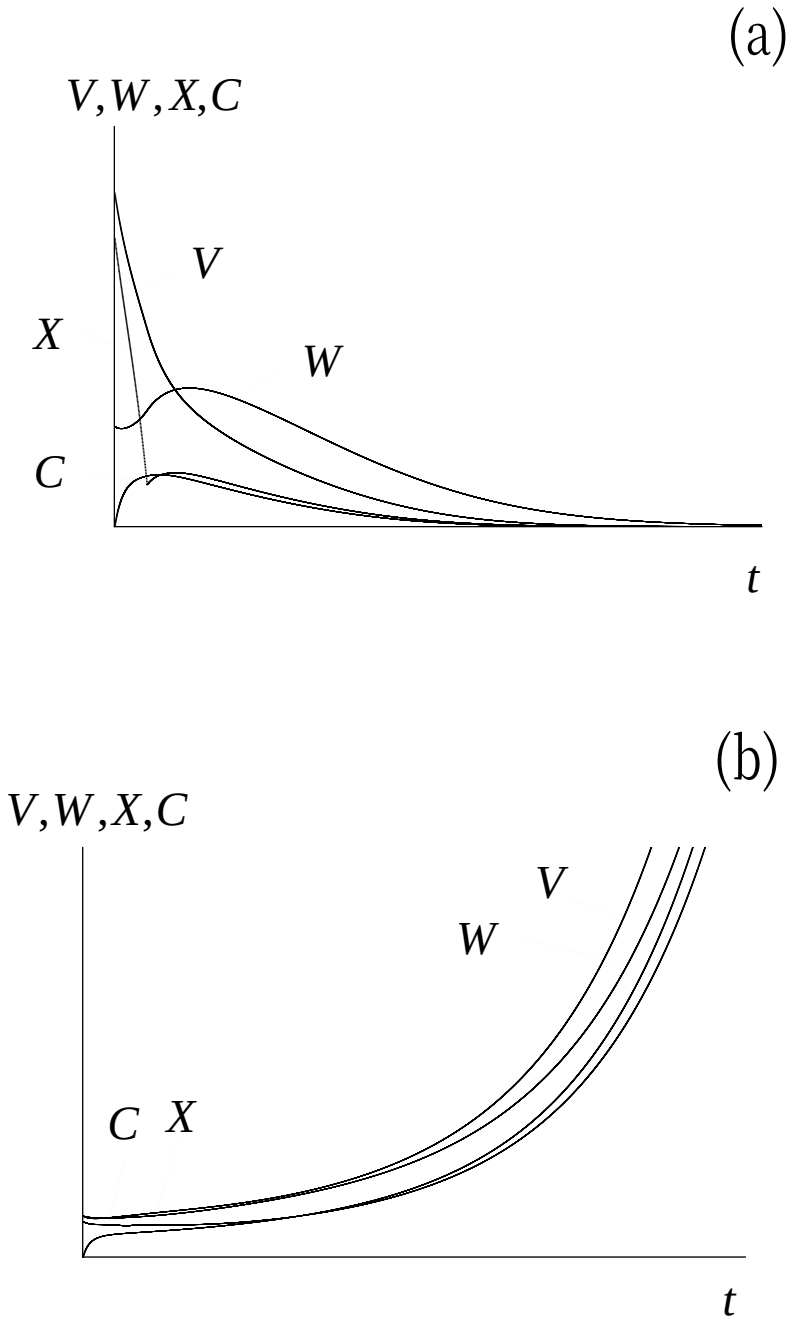

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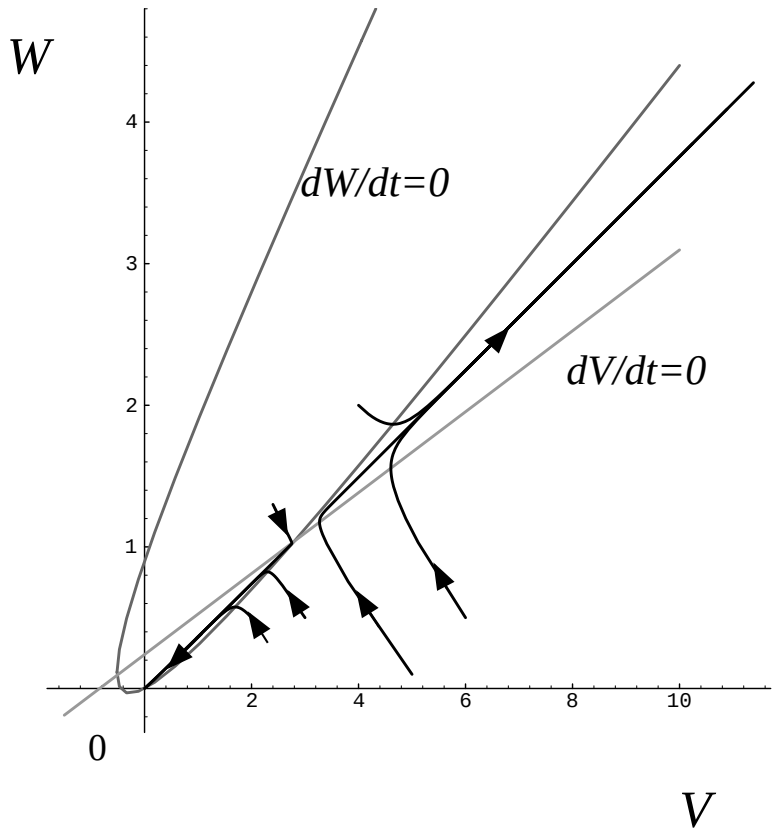

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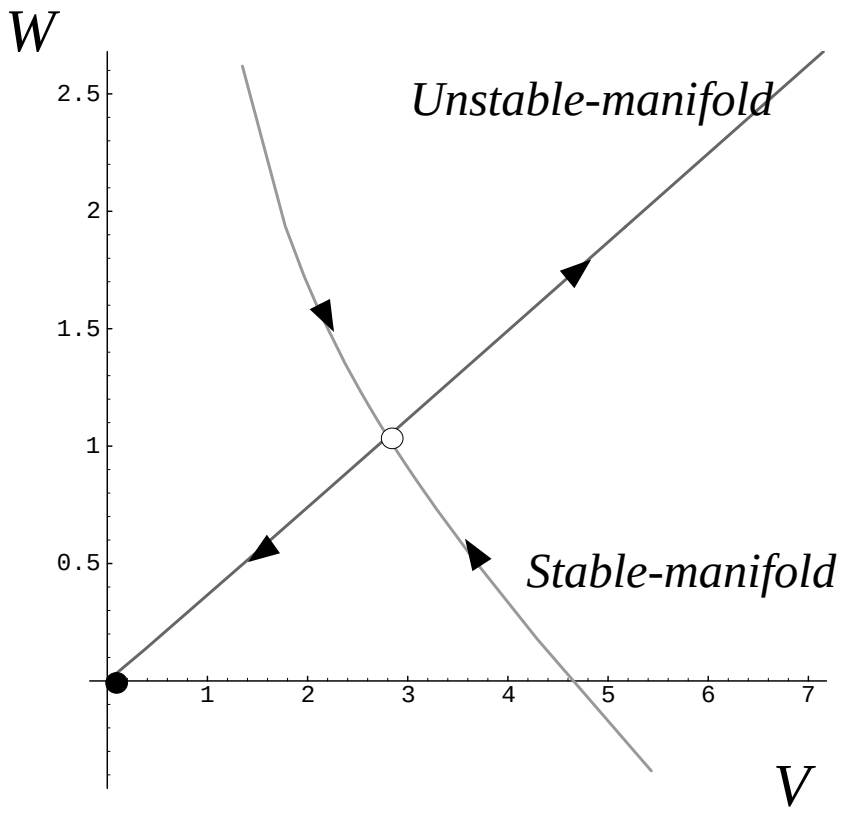

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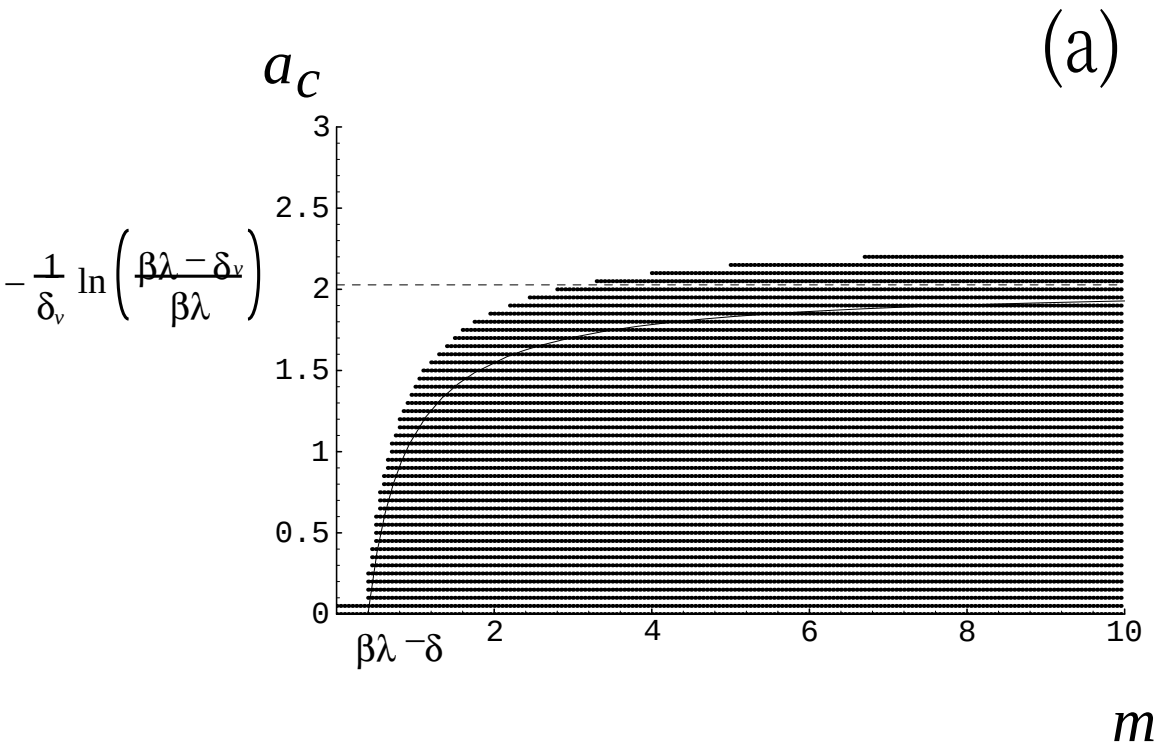

(a)
a_c
$-\frac{1}{\delta_v}\ln\left(\frac{\beta\lambda-\delta_v}{\beta\lambda}\right)$
3
2.5
2
1.5
1
0.5
0
2
4
6
8
10
$\beta\lambda-\delta$
m

Fig. 7(a)

(b)

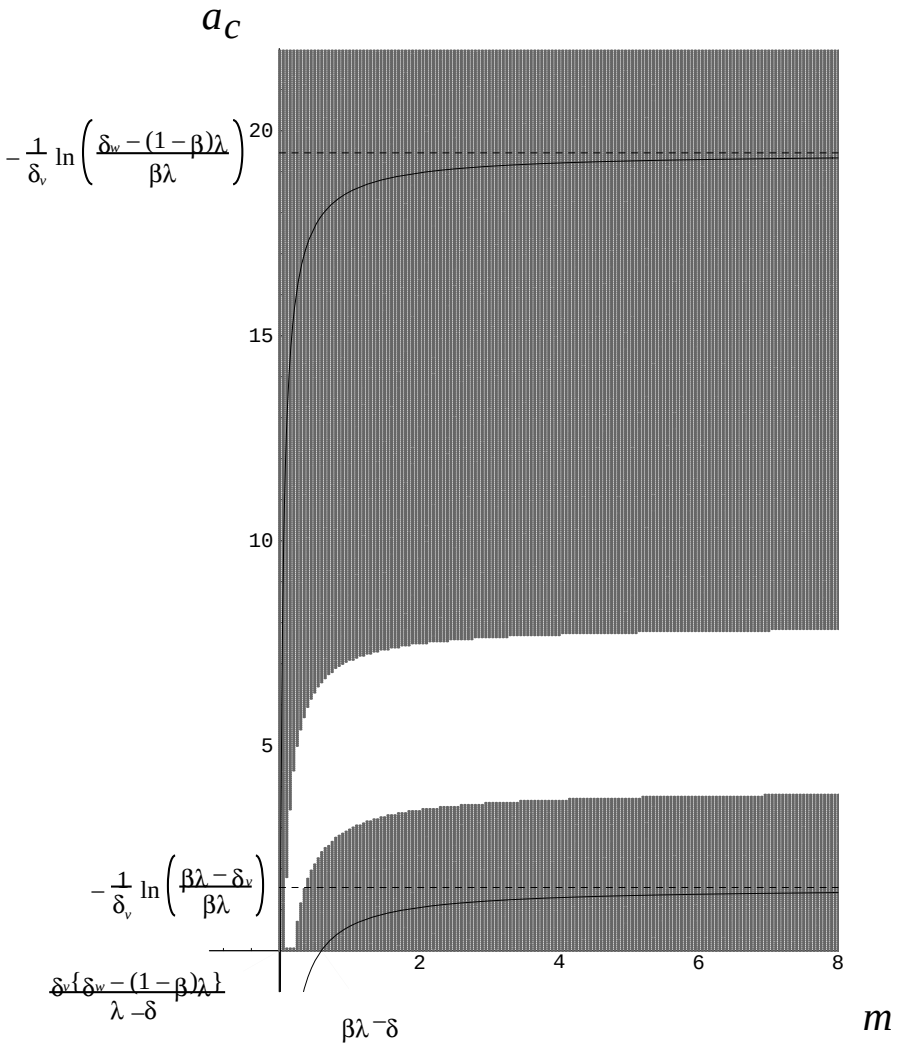
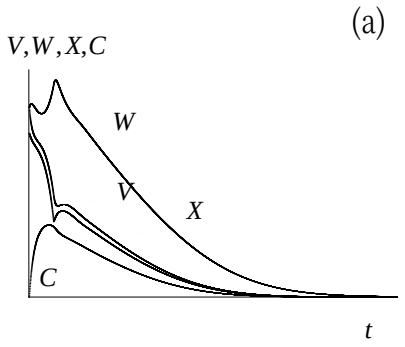
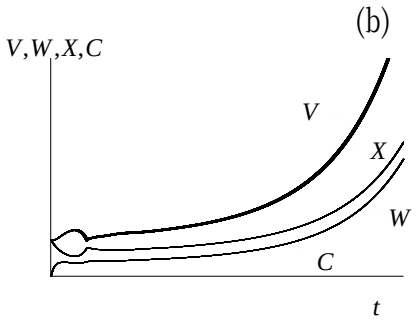

a_C
$-\frac{1}{\delta_v}\ln\left(\frac{\delta_w-(1-\beta)\lambda}{\beta\lambda}\right)$
20
15
10
5
$-\frac{1}{\delta_v}\ln\left(\frac{\beta\lambda-\delta_v}{\beta\lambda}\right)$
2
4
6
8
$\frac{\delta_v\{\delta_w-(1-\beta)\lambda\}}{\lambda-\delta}$
$\beta\lambda-\delta$
m

Fig. 7(b)





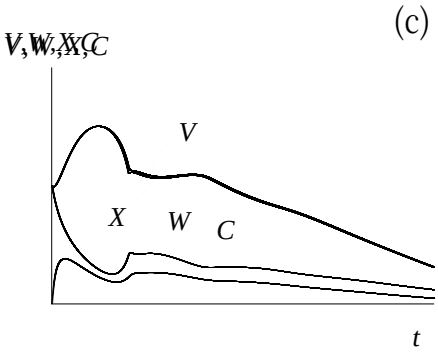
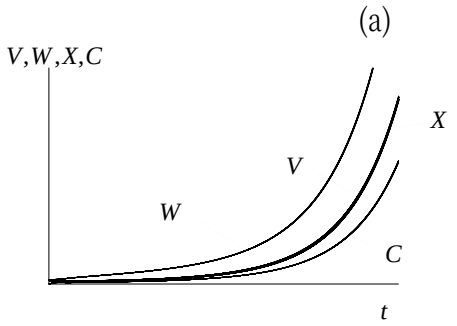
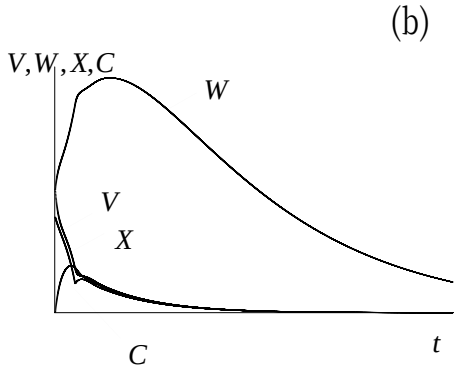


Fig. 8





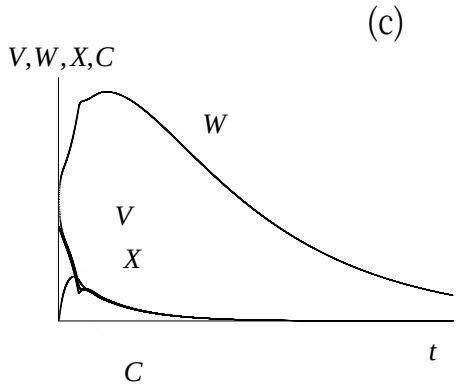
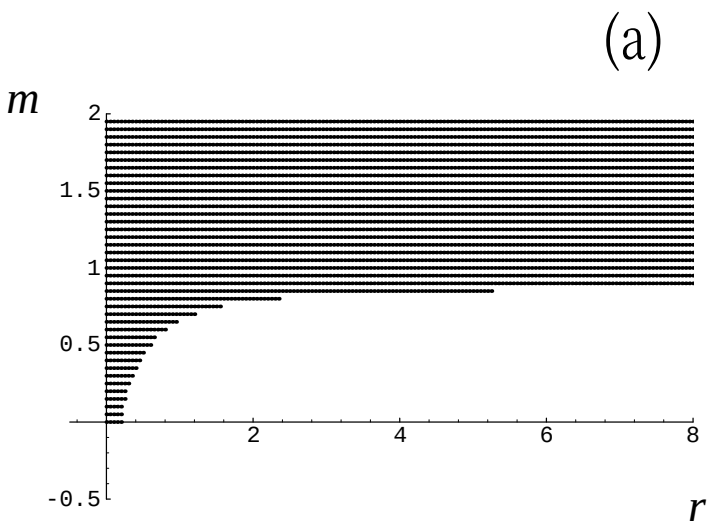


Fig. 9



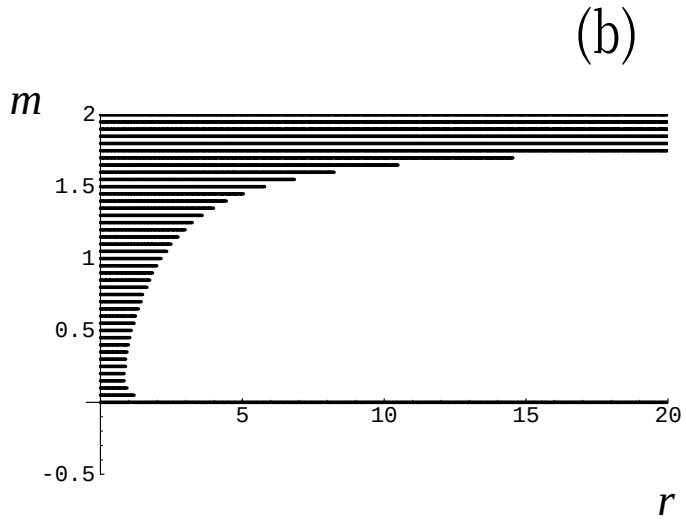
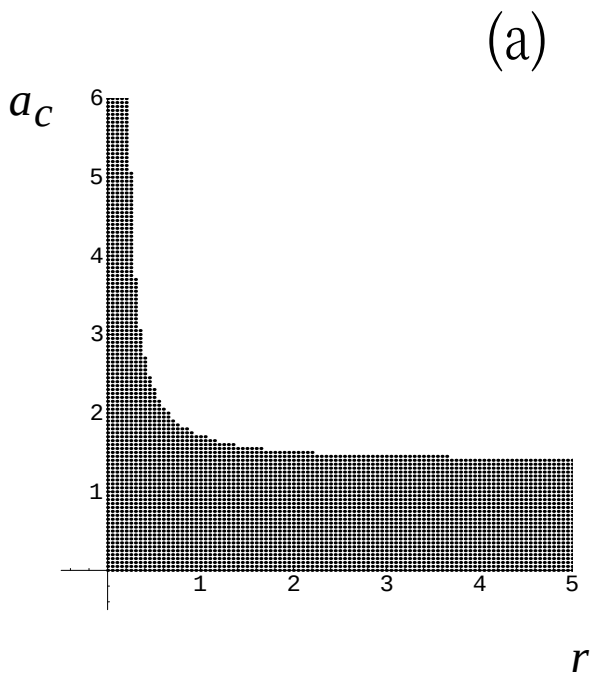


Fig. 10



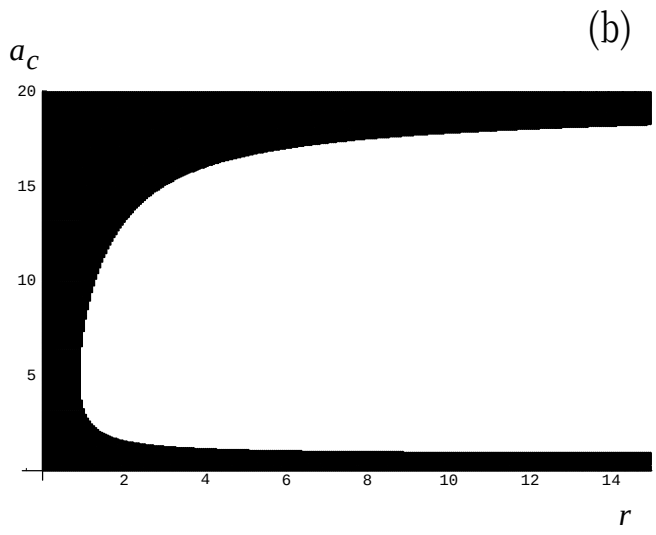
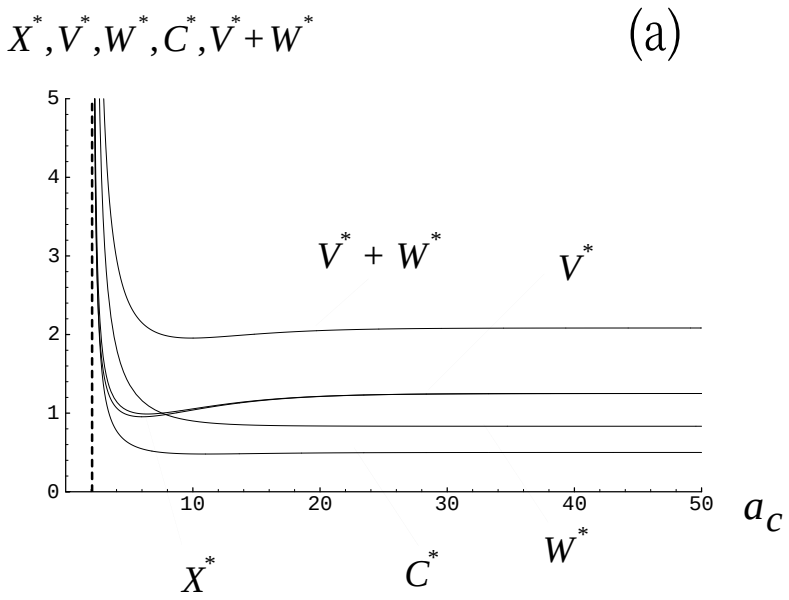


Fig. 11


$X^*, V^*, W^*, C^*, V^* + W^*$
(a)
5
4
3
2
1
0
10
20
30
40
50
$V^* + W^*$
V^*
W^*
X^*
C^*
a_C

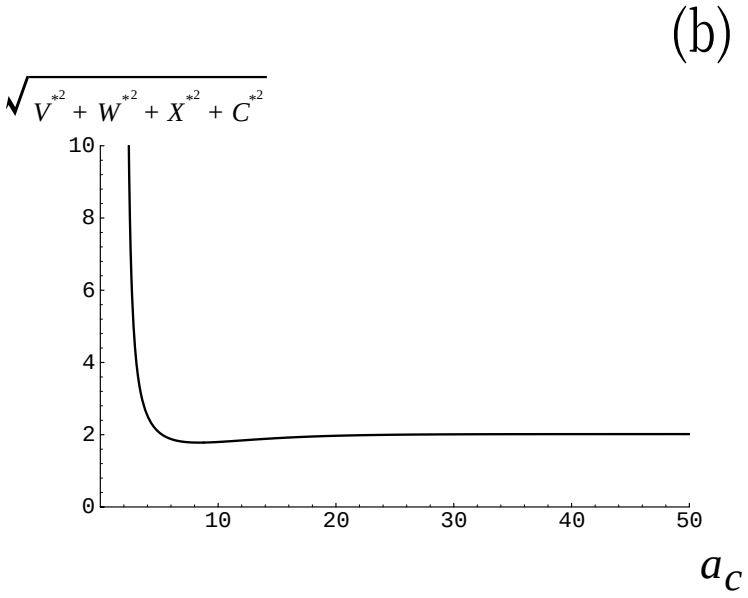
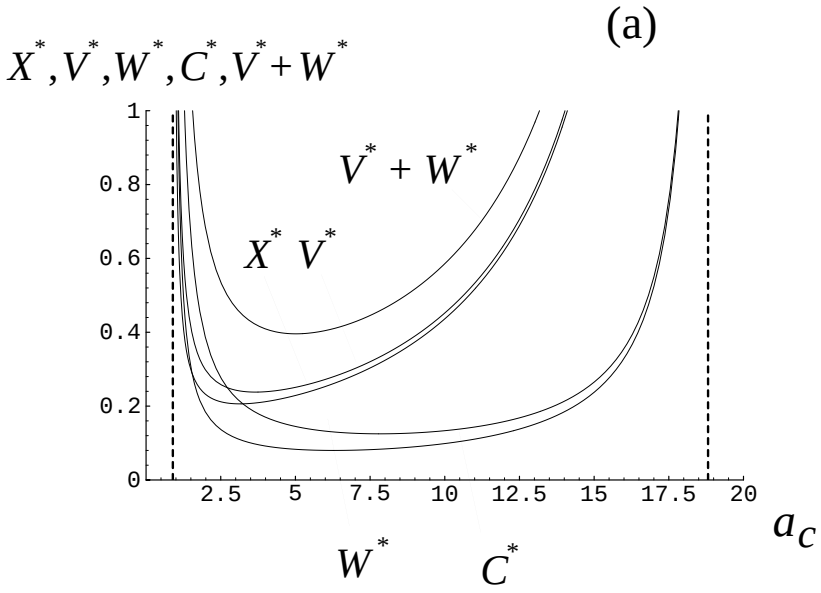

(b)
$\sqrt{V^{*2} + W^{*2} + X^{*2} + C^{*2}}$
10
8
6
4
2
0
10
20
30
40
50
a_C

Fig. 12


(a)
$X^*, V^*, W^*, C^*, V^* + W^*$
1
0.8
0.6
0.4
0.2
0
2.5
5
7.5
10
12.5
15
17.5
20
$V^* + W^*$
$X^* V^*$
W^*
C^*
a_C

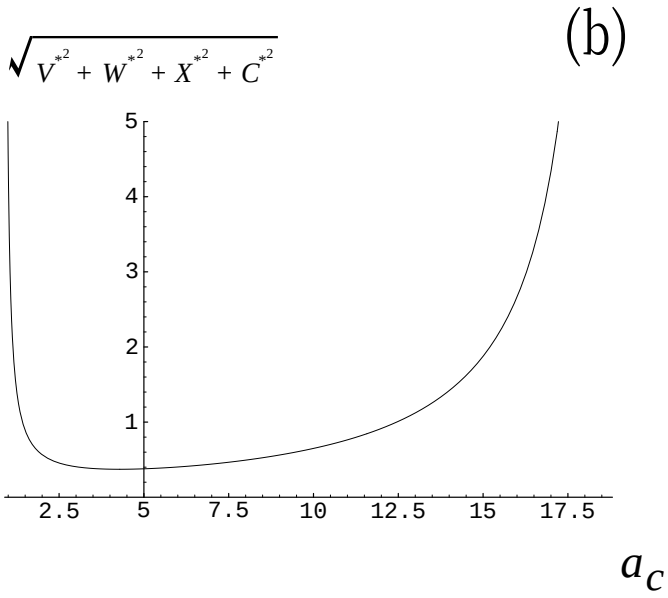

(b)
$\sqrt{V^{*2} + W^{*2} + X^{*2} + C^{*2}}$
5
4
3
2
1
2.5
5
7.5
10
12.5
15
17.5
a_C

Fig. 13