GSPT beyond the standard form

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Overview

- Geometric Singular Perturbation Theory
- Glycolythic Relaxation Oscillations
- Mitotic Oscillator
- Conclusion and Outlook

joint work with Ilona Kosiuk (MPI Leipzig)

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Singularly perturbed systems in standard form

$$\begin{array}{rcl} x' &=& \varepsilon f(x,y,\varepsilon) \\ y' &=& g(x,y,\varepsilon) \end{array}$$

x slow, y fast, $\varepsilon << 1$, fast time scale τ , $' = \frac{d}{d\tau}$ transform to slow time scale $t := \varepsilon \tau$

> $\dot{x} = f(x, y, \varepsilon)$ $\varepsilon \dot{y} = g(x, y, \varepsilon)$

- global separation into slow and fast variables
- singular behaviour with respect to one parameter

Limiting systems for $\varepsilon = 0$

layer problem

 $\begin{array}{rcl} x' &=& 0\\ y' &=& g(x,y,0) \end{array}$

• reduced problem $\dot{x} = f(x, y, 0)$ 0 = g(x, y, 0)

• critical manifold $S := \{g(x, y, 0) = 0\}$ S is a manifold of equilibria for layer problem.

reduced problem is a dynamical system on S.

Geometric Singular Perturbation Theory (GSPT)

critical manifold S normally hyperbolic, i.e. $\frac{\partial g}{\partial y}|_S$ hyperbolic $\Rightarrow S$ perturbs smoothly to slow manifold S_{ε} for ε small, \exists stable- and unstable manifolds $W^s(S_{\varepsilon})$, $W^u(S_{\varepsilon})$, invariant foliations,.... (Fenichel, 1979)

Refinements: Exchange Lemma, Fenichel Normal Form,... (C. Jones, N. Kopell, T. Kaper, P. Brunovsky,...)

Applications: analysis of periodic, heteroclinic, homoclinic, and chaotic dynamics; existence and stability of travelling waves,...

Extensions: blow-up method at non-hyperbolic parts of \boldsymbol{S}

Phenomena:

- relaxation oscillations
- canard solutions
- mixed-mode oscillations
- delayed bifurcations
- F. Dumortier, R. Roussarie,

M. Krupa, M. Wechselberger, P. Sz.,...

More difficulties

in many applications, e.g. from biology and chemistry, there is

- no global separation into slow and fast variables
- dynamics on more than two distinct time-scales
- singular or non-uniform dependence on several parameters
- several scaling regimes with different limiting problems are needed

Claim: GSPT and in particular the blow-up method is useful for such problems.

Strategy

- identify fastest time-scale and corresponding scale of dependent variables, rescale
- often the limiting problem has a (partially) non-hyperbolic critical manifold
- use (repeated) blow-ups to desingularize
- identify relevant singular cycles, etc.
- carry out perturbation analysis

case studies:

Autocatalator, Glykolythic Oscillations,

Mitotic Oscillator with I. Kosiuk (MPI Leipzig)

Glycolytic Oscillations

- model for glycolythic oscillations
- relaxation oscillations
- two parameter singular perturbation problem: $\varepsilon, \delta << 1$
- various scaling regimes
- $(\varepsilon,\delta)=(0,0)$ very degenerate
- geometric analysis based on blow-up method

Glycolytic Oscillations Model (GOM)

$$\begin{split} \dot{\alpha} &= & \mu \rho^{-1} - \rho^{-1} \phi(\alpha, \gamma) \\ \dot{\gamma} &= & \lambda \phi(\alpha, \gamma) - \gamma \end{split}$$

$$\phi(\alpha, \gamma) = \frac{\alpha^2 (\gamma + 1)^2}{L + \alpha^2 (\gamma + 1)^2}$$

- glycolysis: complicated biochemical reaction glucose → pyruvate
- simplified model
- substrate lpha, product γ
- parameters: μ, ρ, λ, L
- λ and L large
- L. Segel, A. Goldbeter, Scaling in biochemical kinetics: dissection of a relaxation oscillator
 J. Math. Biol. (1994)



• relaxation oscillation: α ,

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 $L = 5 \times 10^6, \quad \rho = 2.5, \quad \lambda = 40, \quad \mu = 0.15$



• L large, λ fixed: classical relaxation oscillations

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 $L = 5 \times 10^6, \quad \rho = 2.5, \quad \lambda = 40, \quad \mu = 0.15$



• L large, λ fixed: classical relaxation oscillations

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• L large, λ fixed: classical relaxation oscillations

• L, λ both large: more complicated

• small parameter $\varepsilon := \sqrt{\frac{\lambda}{L}}$

Scaling analysis

$$A \approx \left(\frac{2\sqrt{L}}{\lambda}, 1\right), B \approx \left(\frac{1}{2}\sqrt{\frac{L}{\lambda}}, 1\right), C \approx \left(\frac{1}{2}\sqrt{\frac{L}{\lambda}}, \lambda\right), D \approx \left(\frac{2\sqrt{L}}{\lambda}, \frac{\lambda}{2}\right)$$



Goldbeter & Segel:

$$\sqrt{\frac{\lambda}{L}} \ll \frac{1}{\sqrt{\lambda}} \ll 1 \qquad \Longrightarrow \qquad$$

relaxation cycle exists

rescaled variables:

$$\alpha = \sqrt{\frac{L}{\lambda}}a, \quad \gamma = \lambda b - 1$$

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Rescaled Equations

System (GOM) in (a,b) variables with $\rho = 1$

$$\begin{array}{rcl} a' &=& \varepsilon [\mu - \frac{a^2 b^2}{\delta^2 + a^2 b^2}] \\ b' &=& \frac{a^2 b^2}{\delta^2 + a^2 b^2} - b + \delta^2 \end{array} \qquad \qquad \varepsilon := \sqrt{\frac{\lambda}{L}}, \quad \delta := \frac{1}{\sqrt{\lambda}} \end{array}$$

multiplication with $\delta^2 + a^2 b^2 > 0$ gives

$$a' = \varepsilon [a^2 b^2 (\mu - 1) + \mu \delta^2] b' = a^2 b^2 (1 - b) + \delta^2 (a^2 b^2 - b + \delta^2)$$
(1)

• slow-fast system in standard form: a slow, b fast

• L large $\Rightarrow \varepsilon$ small for λ fixed; λ large $\Rightarrow \delta$ small

• Goldbeter-Segel condition: $\varepsilon \ll \delta \ll 1$

Slow-fast subsystems for $\varepsilon = 0$

layer problem

$$a' = 0 b' = a^2 b^2 (1-b) + \delta^2 (a^2 b^2 - b + \delta^2)$$
(2)

reduced problem

$$\dot{a} = a^{2}b^{2}(\mu - 1) + \mu\delta^{2}$$

$$0 = a^{2}b^{2}(1 - b) + \delta^{2}(a^{2}b^{2} - b + \delta^{2})$$
(3)

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Critical manifold

$$S^{\delta} = \{(a,b): \quad a^2b^2(1-b) + \delta^2(a^2b^2 - b + \delta^2) = 0\}$$



 $S^{\delta} = S_l \cup B \cup S_m \cup D \cup S_r, \quad \delta > 0$ singular cycle Γ_0^{δ} : four segments AB, BC, CD, DA

Critical manifold

$$S^{\delta} = \{(a,b): \quad a^2b^2(1-b) + \delta^2(a^2b^2 - b + \delta^2) = 0\}$$



 $S^{\delta} = S_l \cup B \cup S_m \cup D \cup S_r, \quad \delta > 0$ $\Rightarrow \text{ relaxation oscillations for } \delta > 0 \text{ fixed and } \varepsilon \text{ small.}$ Fold Point: (0,0) nonhyperbolic, blow-up method

Krupa, Sz. (2001)
$$\begin{aligned} x' &= -y + x^2 + \cdots \\ y' &= -\varepsilon + \cdots \end{aligned}$$



- asymptotics of $S_{a,\varepsilon} \cap \Sigma^{out}$
- map: $\pi: \Sigma^{in} \to \Sigma^{out}$ contraction, rate $e^{-C/\varepsilon}$

Critical manifold S^{δ} depends singularly on δ

$$S^{\delta} = \{(a,b): \quad a^2b^2(1-b) + \delta^2(a^2b^2 - b + \delta^2) = 0\}$$



Critical manifold S^{δ} depends singularly on δ

$$S^{\delta} = \{(a,b): \quad a^2b^2(1-b) + \delta^2(a^2b^2 - b + \delta^2) = 0\}$$



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Critical manifold S^{δ} depends singularly on δ

$$S^{\delta} = \{(a,b): \quad a^2b^2(1-b) + \delta^2(a^2b^2 - b + \delta^2) = 0\}$$



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$\delta = 0$, Critical manifold S^0

 $a^{2}b^{2}(1-b) = 0, \qquad a = 0, \quad b = 0, \quad b = 1$



The folded critical manifold S^{δ} collapses to the more singular "manifold" $S^0 = l_a \cup l_b \cup l_h$

Scaling Regimes



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Scaling Regimes:

Regime 1: $a = O(1), b = O(\delta^2)$



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Scaling Regimes:

Regime 1: $a = O(1), b = O(\delta^2)$, Regime 2: a = O(1), b = O(1)



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Scaling Regimes: Regime 3: $a = O(\delta), b = O(1)$

Regime 1: $a = O(1), b = O(\delta^2)$, Regime 2: a = O(1), b = O(1)



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Scaling Regimes: Regime 3: $a = O(\delta), b = O(1)$

Regime 1: $a = O(1), b = O(\delta^2)$, Regime 2: a = O(1), b = O(1)



in Regimes 1 - 3 results for $0 < \varepsilon \ll \delta \ll 1$

Scaling Regimes: Regime 3: $a = O(\delta), b = O(1)$

Regime 1: $a = O(1), b = O(\delta^2)$, Regime 2: a = O(1), b = O(1)



matching? overlap?

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For $\varepsilon = 0$, $\delta = 0$ exists very degenerate singular cycle singular cycle $\Gamma_0^0 := \sigma_1 \cup \sigma_2 \cup \sigma_3 \cup \sigma_4$



lines a = 0, b = 0 non-hyperbolic

line b = 1 hyperbolic

Main result

Theorem:

For $\mu < 1$ there exist $\delta_0 > 0$ and $\tilde{\varepsilon}_0 > 0$ such that system (1) has a unique attracting periodic orbit $\Gamma_{\varepsilon}^{\delta}$ for $0 < \delta \leq \delta_0$ and $0 < \varepsilon \leq \tilde{\varepsilon}_0 \delta$ with the properties

- $\Gamma^{\delta}_{\varepsilon}$ tends to singular cycle Γ^{δ}_{0} as $\varepsilon \to 0$ for $\delta \in (0, \delta_{0}]$,
- $\Gamma^{\delta}_{\varepsilon}$ tends to singular cycle Γ^{0}_{0} as $(\delta, \varepsilon) \to (0, 0)$.

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Proof: based on repeated blow-ups

Extended system

because of $\varepsilon \ll \delta \ll 1$ set $\varepsilon := \tilde{\varepsilon} \delta$

$$\begin{aligned} a' &= \tilde{\varepsilon} \delta[a^2 b^2 (\mu - 1) + \mu \delta^2] \\ b' &= a^2 b^2 (1 - b) + \delta^2 (a^2 b^2 - b + \delta^2) \\ \delta' &= 0 \end{aligned}$$

- three-dimensional vector field $X_{ ilde{arepsilon}}$ defined on \mathbb{R}^3
- $\tilde{\varepsilon}$ is the singular perturbation parameter causing the slow-fast structure
- family of 1-dim. critical manifolds S⁰
 corresponds to 2-dim. critical manifold S

Cylindrical blow-up of the non-hyperbolic line l_b



 $a = r\bar{a}, \quad b = \bar{b}, \quad \delta = r\bar{\delta}, \qquad (\bar{a}, \bar{\delta}, r, \bar{b}) \in \mathbb{S}^1 \times \mathbb{R} \times \mathbb{R}$

chart K₃: δ
= 1, corresponds to Regime 3
chart K₄: ā = 1, covers Regime 3 and Regime 2

Dynamics in K_4

slow-fast system, $0 < \tilde{\varepsilon} \ll 1$

$$r'_4 = \tilde{\varepsilon}g_1(b_4, \delta_4, r_4)$$

$$\delta'_4 = \tilde{\varepsilon}g_2(b_4, \delta_4, r_4)$$

 $b'_4 = f(b_4, \delta_4, r_4)$

slow variables r_4, δ_4 fast variable b_4



- invariant planes: $r_4 = 0$ and $\delta_4 = 0$
- \bullet critical manifold S partially desingularized
- S cusp-like along non-hyperbolic line l_a

Cylindrical blow-up of the non-hyperbolic line $l_{a,4}$



$r_4 = \bar{r}, \ b_4 = \rho^2 \bar{b}, \ \delta_4 = \rho \bar{\delta}, \quad (\bar{b}, \bar{\delta}, \rho, \bar{r}) \in \mathbb{S}^1 \times \mathbb{R} \times \mathbb{R}$

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Charts K_1 and K_2

chart
$$K_1$$
: $\bar{\delta} = 1$



chart K_2 : $\bar{b} = 1$

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Chart K_1 covers Regime 1 and parts of Regime 3



slow-fast for $\tilde{\varepsilon} \ll 1$, critical manifold S desingularized

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Chart K_2

covers Regime 1, Regime 2, and parts of Regime 3



slow-fast for $\tilde{\varepsilon} \ll 1$, critical manifold S desingularized

After two cylindrical blow-ups...



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Blown-up singular cycle Γ_0^0



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Blown-up critical manifold S and family of singular cycles Γ_0^δ



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Proof of main result

- Poincaré map $\Pi: \Sigma \to \Sigma$ for δ , $\tilde{\varepsilon}$ small
- S perturbs to slow manifold S_{ε} for $\tilde{\varepsilon}$ small
- folds, transition near hyperbolic line



Define sections Σ , Σ_b , Σ_a transversal to ω_2 , ω_5 , ω_1

- maps $\Pi_1: \Sigma \to \Sigma_b, \Pi_2: \Sigma_b \to \Sigma_a, \Pi_3: \Sigma_a \to \Sigma$
- $\Pi: \Sigma \to \Sigma$, $\Pi:=\Pi_3 \circ \Pi_2 \circ \Pi_1$
- attraction to slow manifolds, passage near folds, transition near hyperbolic line



Folds are treated by available results, which are proved by other blow-ups

- all maps are analyzed in the appropriate charts: Π_1 in K_4 , Π_2 in K_4 , and K_1 , Π_3 in K_2
- Π_1 and Π_2 are very similar: exp. strong contractions
- Π_3 desribes passage near a line of hyperbolic equilibria: at most algebraically expanding

 Π_1 maps Σ to an exponentially thin wedge $\Pi_1(\Sigma)$ exp. close to $S_{\varepsilon} \cap \Sigma_b$

• Π_1 restricted to a leaf $\delta = const.$ is a contracting with rate $e^{-c/\delta\tilde{\varepsilon}}$.



 Π maps Σ to an exponentially thin wedge $\Pi(\Sigma)$ exp. close to $S_{\varepsilon}\cap\Sigma$

- Π restricted to $\delta = const.$ contracts, rate $e^{-c/\delta\tilde{\varepsilon}}$.
- $\bullet \Rightarrow \exists$ fixed point of $\Pi,$ main result is proved



Summary

- identify fastest time-scale and corresponding scale of dependent variables, rescale
- often the limiting problem has a (partially) non-hyperbolic critical manifold

- use (repeated) blow-ups to desingularize
- identify relevant singular cycles, etc.
- carry out perturbation analysis

Mitotic Oscillator

enzyme reaction relevant for cell division cycle



- Cyclin triggers the transformation of inactive (*M*+) into active (*M*) cdc2 kinase by enhancing the rate of a phosphatase. A kinase with rate v2 reverts this modification.
- Cdc2 kinase phosphorylates a protease shifting it from the inactive (X+) to the active (X) form. The cyclin protease is inactivated by a further phosphatase.

A. Goldbeter, A minimal cascade model for the mitotic oscillator involving cyclin and cdc2 kinase. Proc Natl Acad Sci USA 88 (1991), 9107-9111.

Mitotic Oscillator (MO)

$$\frac{dC}{dt} = v_i - v_d X \frac{C}{K_d + C} - k_c C$$

$$\frac{dM}{dt} = V_1 \frac{1 - M}{K_1 + 1 - M} - V_2 \frac{M}{K_2 + M}$$

$$\frac{dX}{dt} = V_3 \frac{1 - X}{K_3 + 1 - X} - V_4 \frac{X}{K_4 + X}$$

Michaelis-Menten kinetics

C cyclin concentration, $M,\,X$ fractions of active kinase and cyclin protease, $1-X,\,1-M$ fractions of inactive cyclin protease and kinase.

 K_d , K_c , K_j , $j = 1, \ldots, 4$ - Michaelis constants

Sustained oscillations



T. Erneux and A. Goldbeter, *Rescue of the quasi-steady-state approximation in a model for oscillations in an enzymatic cascade* SIAM J. Appl. Math 67 (2006), 305-320.

Limit cycle

Periodic orbit in the cube $[0,1]^3 \subset \mathbb{R}^3$

partially close to X = 0, M = 1, X = 1, M = 0

Theorem: For ε small there exists a strongly attracting periodic orbit Γ_{ε} of system (1) which tends to a singular cycle Γ_0 as $\varepsilon \to 0$.



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Geometric Singular Perturbation Approach

(MO) as a singularly perturbed system of ODEs

$$\begin{aligned} X' &= [M(1-X)(\varepsilon+X) - \frac{7}{10}X(\varepsilon+1-X)]F_{\varepsilon}(M) \\ M' &= [\frac{6C}{1+2C}(1-M)(\varepsilon+M) - \frac{3}{2}M(\varepsilon+1-M)]F_{\varepsilon}(X) \\ C' &= \frac{1}{4}(1-X-C)F_{\varepsilon}(M)F_{\varepsilon}(X) \end{aligned}$$

obtained by multiplying (4) by the factor

 $F_{\varepsilon}(M)F_{\varepsilon}(X)):=(\varepsilon{+}1{-}M)(\varepsilon{+}M)(\varepsilon{+}1{-}X)(\varepsilon{+}X)$

e - singular perturbation parameter
 non-standard form of slow-fast systems on fast
 time-scale

Layer problem

$$X' = \left(M - \frac{7}{10}\right) F_0(M, X)$$
$$M' = \left(\frac{6C}{1 + 2C} - \frac{3}{2}\right) F_0(M, X)$$
$$C' = 0.25(1 - X - C)F_0(M, X)$$
$$F_0(M, X) := (1 - M)M(1 - X)X$$

In the layer problem all three variables evolve!

Critical manifold S consists of four planes M = 0, M = 1, X = 0, X = 1・ロト・日本・モト・モト ヨー うへぐ

 \exists single equilibrium point

Stability properties of the critical manifold S

Lemma. The layer problem has the following properties:

X = 0 is attracting for M < 0.7 and repelling for M > 0.7M = 1 is attracting for C > 0.5 and repelling for C < 0.5X = 1 is attracting for M > 0.7 and repelling for M < 0.7M = 0 is attracting for C < 0.5 and repelling for C > 0.5Equilibrium (X, M, C) = (0.5, 0.7, 0.5) is of saddle-focus type

non-hyperbolic lines and edges line C = 0.5in the planes M = 0 and M = 1line M = 0.7in the planes X = 0 and X = 1edges: (C, 0, 0), (C, 0, 1), (C, 1, 0), and (C, 1, 1) with $C \in [0, 1]$

Away from the nonhyperbolic lines and edges S perturbs to S_{ε}



Slow dynamics



relevant parts of the slow flow contract C = 2000

Periodic orbit

 $\exists \ \text{singular limit} \\ \text{cycle } \Gamma_0$

Slow motion:

in the attracting parts of the planes M = 0, X = 0, M = 1, X = 1

Exchange of stability at the edges

Fast jumps:

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from X = 0 to M = 1
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from X=1 to M=0

More details needed close to the edges!



Slow drift along the edge (0, 0, C)Extended system

$$X' = f_1(X, M, C, \varepsilon)$$
$$M' = f_2(X, M, C, \varepsilon)$$
$$f_2(X, M, C, \varepsilon)$$

 $C' = f_3(X, M, C, \varepsilon)$ $\varepsilon' = 0$

Edge (0, 0, C, 0) - very degenerate!

Very slow drift along the edges (X, M) = (0, 0) and (X, M) = (1, 1) - studied the **blow-up** method!



New phenomenon

$$M = 0 X = 0$$



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New phenomenon: "delayed" exchange of stability

$$M = 0 X = 0$$



Very slow drift along the edge (X, M) = (0, 0), where X = 0

Blow-up of the non-hyperbolic edge



Charts

For C fixed each point $\left(0,0,C\right)$ is blown-up to a sphere



 $(\bar{X},\bar{M},\bar{\varepsilon})\in\mathbb{S}^2$

Charts

 $K_1: \bar{\varepsilon} = 1$ (rescaling chart) $K_2: \bar{M} = 1$ $K_3: \bar{X} = 1$

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Blow-up of the non-hyperbolic edge



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Dynamics in chart K_1

Slow-fast system with respect to ${\ensuremath{\varepsilon}}$

$$\begin{aligned} X' &= -0.7X(1+M) + O(\varepsilon) \\ M' &= \left[\frac{6C}{2C+1}(1+M) - \frac{3}{2}M\right](1+X) + O(\varepsilon) \\ C' &= 0.25(1-C)(1+M)(1+X)\varepsilon + O(\varepsilon^2) \end{aligned}$$

slow variable C, fast variables M, X

Critical manifold curve of equilibria $X = 0, M = -\frac{4C}{2C-1}$ $C \in [0, 0.5)$, attracting



Dynamics of the blown-up system



For fixed C < 0.5equilibrium $X = 0, M = -\frac{4C}{2C-1}$ is a stable node!

From the analysis in chart K_2 :

for C = 0.5two equilibria collide!

 $\varepsilon = 0, \ 0 < C < 0.5$ - fixed

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Dynamics of the blown-up system





Exit point at C = 0.5still degenerate, second blow-up needed!

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Proof

- singular cycle Γ_0 :
 - slow motion in M = 0
 - very slow drift along edge (X, M) = (0, 0)
 - slow motion in X = 0
 - fast jump at M = 0.7from X = 0 to M = 1
- Poincaré map close to the singular cycle: strongly contracting



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Conclusion and Outlook

- case study 1: two-parameter singular perturbation problem, several scaling regimes
- case study 2: singular perturbation problem not in standard form
- \bullet singular behavior of critical manifold S is resolved by blow-up constructions
- use standard regular and singular perturbation results
- approach useful in other multi-parameter singular perturbation problems