Andronov bifurcations and sea shell patterns

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Tropical molluscs exhibit very complex pigmentation patterns on their shells. In this paper we intend to show that some of those patterns can be understood as the instability of limit cycles in spatially extended dynamical systems.

Reaction diffusion models exhibit a wide variety of patterns. The reactions are described by first order differential equations (ODE) which rule the time evolution of the various chemical concentrations \( C = (C_1, C_2 ....C_n) \)

\[
\frac{\partial C_i}{\partial t} = f_i(C, \mu)
\]

(1)

\( \mu = (\mu_1, \mu_2 ...., \mu_p) \) are \( p \) parameters which represent the temperature, the pressure, the reaction rates, etc. ... If one takes into account the diffusion of the chemicals, Eq. 1 becomes a set of partial differential equation (PDE)

\[
\frac{\partial C_i}{\partial t} = f_i(C) + D_i \nabla^2 C_i
\]

(2)

where the diffusion coefficients \( D_i \) are positive constants. A. Turing [1], in a famous work, introduces the idea that morphogenesis could be described by solutions of reaction-diffusion equations.

Although an ODE can possess complex solutions, the Poincaré geometrical theory tell us [3], in principle, how to classify the robust dynamical behaviors. The question of the robustness of the solutions of partial differential equations is completely open, mainly because of the lack of qualitative understanding of such dynamical systems. For example, there are no mathematical evidences that the solutions of reaction diffusion equations are more special than the solutions of any other PDE. This situation contrasts with the common observation that many of the solutions of those equations describe universal phenomena as for example fronts, patterns, defects, growth, ...In the 60’s R. Feynman, in his famous lectures [2] on Physics wrote : ”The next great area of awakening of human intellect may well produce a method of understanding the qualitative content of equations”.

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One way to generalize the idea of reaction-diffusion equations consists to study the continuous limit of coupled identical bifurcating elements. To each bifurcation corresponds a partial differential equation. These PDE generalize the normal forms of the bifurcation, when spatial variation are taken into account; they describe so to speak the spatial unfolding of the singular vector field.

The spatial unfolding of the pitchfork bifurcation, for example, is given by

\[ \partial_t u = u - u^3 + \nabla^2 u \]  

where \( u(\vec{r}, t) \) is a real valued function of space and time and \( \nabla^2 \) is the Laplacian operator. The spatial unfolding of the pitchfork bifurcation is a reaction-diffusion equation. This property is not true in general. Let us consider the bifurcation which leads to ”small” limit cycles (Andronov-Hopf bifurcation). When the bifurcation is supercritical, its normal form is given by

\[ \partial_t u = u - (1 + i\alpha)|u|^2u \]  

where \( u(t) \) is a complex valued function which describes the amplitude of the oscillation, \( u(t)\exp(i\omega_0 t) \), and \( \alpha \) is a constant which characterizes the oscillator. In spatially extended systems \( u \) also varies in space. It is a solution of the PDE

\[ \partial_t u = u - (1 + i\alpha)|u|^2u + (1 + i\beta)\nabla^2 u \]  

The parameter \( \beta \) is the dispersion constant, it measures the wave-vector dependance of the group velocity of the linear waves. The conservative limit of the Eq. 5 \((t \rightarrow -t, u \rightarrow \bar{u})\) is the well known nonlinear Schrödinger equation [4]

\[ \partial_t u = -i\alpha|u|^2u + i\beta\nabla^2 u \]  

The spatial unfolding of singularities leads to a large class of PDE which have been studied in many different contexts [5]. From a general view point, the spatial unfolding of a singular vector field leads to a PDE of the form

\[ \partial_t u = f(u, \nabla) \]  

which possesses the property that the differential equation

\[ \partial_t u = f(u, 0) \]

is the normal form of the unfolding of the singular vector field. The symmetry arguments restricts the form of the coupling terms. Space is assumed to be isotropic. Normal forms are useful when their finite order truncation describes universally the behavior of a nearly singular system. The criterion used to perform the truncation both combine asymptotic and robustness arguments. Let us consider as an example the spatial unfolding of the pitchfork bifurcation. First, \( u, \partial_t u, \nabla u \) are assumed to be small. Isotropy of space implies that the leading coupling term is \( \nabla^2 u \). Thus \( |\nabla u|^2u \) is smaller than \( \nabla^2 u \). The question of robustness is much more subtle,
since it is related with the structural stability of solutions of partial differential equations. Let \( u_T(\vec{r}, t) \) be a well identify solution of Eq.7 truncated to a given order. What happens if higher order terms are taken into account? Does this solution change just a little? No mathematical tool exists today to answer this question. In many cases a great deal of intuition is necessary to decide what terms are relevant and what terms are not. Two important questions arise naturally, when a bifurcation occurs in spatially extended systems. The first one concerns the stability of the spatially homogeneous solutions by respect to space dependent perturbations. The second question concerns the solutions which spontaneously break the space translations. When the bifurcations spontaneously break some symmetry, the topological defects are precisely solutions of this kind. In the case of the pitchfork bifurcation, the two bifurcated homogeneous solutions \( u = \pm 1 \) are stable by respect to small space dependant perturbations. The pitchfork bifurcation breaks the \( Z_2 \) parity symmetry \((u \rightarrow -u)\). Kink like stationary solutions exist in one space dimension:

\[
 u_\pm(x) = \pm \tanh(\frac{\sqrt{2}}{2}x)
\]

They are codimension one topological defects [5], whose existence is a direct consequence of the broken \( Z_2 \) symmetry. At the core of the defect solution \( u \) vanishes. In the case of the Andronov-Hopf bifurcation leading to a "small" limit cycle, the homogeneous solutions \( u = \sqrt{\mu} \exp(-i\alpha t + i\phi) \) are stable by respect to small space dependant perturbations only if \((1 + \alpha \beta) > 0\) [6]. The instability which occurs when \((1 + \alpha \beta) < 0\) leads to very complicated spatio-temporal behaviors which are far from being understood. In the reversible limit this instability is known as the self-focusing instability [4]. The codimension two topological defects exist in two space dimensions. When they are stable they take the form of spiral waves. Moving fronts are other spatio-temporal solutions which are common to many PDE [5]. In the simple case fronts are moving interfaces which separate homogeneous stationary solutions. This fronts separate stable and unstable domains, stable and stable domains or identical domains. Fronts between identical domains are actually spatially localized solutions which are known as solitary excitable waves in the context of dissipative dynamical systems. The fronts which separate stable and unstable domains have been studied mathematically in ref. [7]. The mathematical model considered corresponds actually to the spatial unfolding of the saddle node bifurcation which reads

\[
 \partial_t u = \pm 1 - u^2 + u_{xx} \tag{8}
\]

Using a simple change of variable, in the parameter range where the two solutions exist (case +1), this equation can be put in the simplest form

\[
 \partial_t v = v(1 - v) + v_{xx} \tag{9}
\]

Any positive initial condition which is different from zero on a compact set only, leads to the propagation of two contaminating fronts which connect the unstable solution \( v = 0 \) to the stable solution \( v = 1 \). Eq. 9 admits fronts with arbitrary velocity. The compactness of the initial condition leads to a strict selection mechanism. The selected front is the one which possesses the steepest profile without spatial oscillations [8]. In the presence of a small symmetry breaking term (imperfection), stationary kinks of the pitchfork bifurcation are transformed into fronts
which connect two stable domains. The motion of the fronts is such that the “most stable”
domain wins over the other [9]. The equation of the imperfect pitchfork bifurcation in one
dimension reads

$$ \partial_t u = u - u^3 + \eta + u_{xx} $$

(10)

where the parameter $\eta$ measures the breaking of the $Z_2$ symmetry. For $\eta$ small Eq. 10 possesses
two stable homogeneous stationary solutions. Fronts which separate domains corresponding to
these solutions propagate with a well define velocity. This velocity vanishes as $\eta \to 0$ where
they becomes stationary kinks. The question of fronts between homogeneous solutions reduces
itself to the problem of the existence of a heteroclinic connection for the dynamical system
obtained by looking for solutions of the form $u(\zeta)$, where $\zeta = x - ct$. For example in the case
of Eq. 15 the fronts obey to the differential equation

$$ u_{\zeta\zeta} + u - u^3 + \eta + cu_{\zeta} = 0 $$

(11)

The two homogeneous solutions of Eq. 10 becomes hyperbolic fixed point of the flow associated
with Eq.11. A front appears as a heteroclinic connection between these two fixed points. The
bifurcation leading to such a heteroclinic connection is a codimension one bifurcation which
can be reached for a given value of the velocity parameter $c$. The simplest example of excitable
front is found in the overdamped forced sine-Gordon equation which reads

$$ \partial_t u + \sin(u) = \Omega + u_{xx} $$

(12)

In the absence of the forcing $\Omega$, this equation possesses kink solutions which connects homoge-
nous solutions $2n\pi$ and $2(n \pm 1)\pi$. They are given by

$$ u_K = 4 \arctan(e^{\pm x}) + 2n\pi. $$

For $\Omega$ small these stationary solutions becomes propagating fronts which separate domains
$u_s + 2n\pi$ and $u_s + 2(n \pm 1)\pi$, where $\sin(u_s) = \Omega$ and move with a velocity which vanishes as
$\Omega \to 0$. The mathematical nature of these fronts is the same as the fronts connecting stable
domains. They correspond to a heteroclinic or a homoclinic bifurcation. Nevertheless the
physical interpretation of the motion is quite different. In the general case of fronts separating
stable domains, the difference in stability of the two domains leads to mechanism of propagation.
It is not the case for excitable fronts since there the two domains are identical or symmetrical.
For the over-damped forced sine-Gordon equation, the two domains are symmetrical since the
equation is invariant under the transformation $u \to u + 2p\pi$.

1 Andronov bifurcations in extended systems

In a famous work, Andronov and Pontryagin in 1937 [10] have described the codimension
one bifurcations leading to the appearance of limit cycles in planar dynamical systems (see Fig.
1). Thanks to the central manifold theorem [3], their results extend to arbitrary dimensions. In particular the simplest Andronov bifurcation is the well known Hopf bifurcation [12]. To some extend, this result was also known by Poincaré. The second Andronov bifurcation is the homoclinic bifurcation in which the limit cycle disappears as "it collides" with a fixed point. In the third Andronov bifurcation, the limit cycle disappears with the appearance of a pair of fixed points which appear through a saddle node bifurcation. The purpose of this paper is to discuss some spatio-temporal phenomena associated with the Andronov bifurcations when they occur in spatially extended systems [11].

Andronov-Poincaré-Hopf bifurcation in spatially extended system is described by Eq. 5. The stability of the bifurcated limit cycle depends upon the parameter $D_\phi = 1 + \alpha \beta$. A general perturbation of the limit cycle includes phase and amplitude perturbations. For homogeneous perturbations the amplitude perturbations have finite relaxation time, while the phase perturbations are marginal. For weakly homogenous perturbation the phase obeys to a diffusion equation given by [13]:

$$\partial_t \phi = D_\phi \phi_{xx}$$

(13)

For positive $D_\phi$ the limit cycle is stable with respect to non-homogeneous perturbation and develops a "phase instability" for negative $D_\phi$. This instability leads to a "frequency modulation" which eventually couples with the amplitude perturbations leading to a complex amplitude-phase dynamics which involves both phase singularities and large localized amplitude excursion [15]. This complicate state is far from being understood. It changes from "phase turbulence" to "amplitude turbulence" as the parameters $\alpha$ and $\beta$ are varied [14]. A typical $x - t$ diagram of Eq. 5 are shown on Fig. 2.

The spatio-temporal phenomena associated to the two other Andronov bifurcations are more difficult to study since the global bifurcations cannot be described by normal forms. Nevertheless higher codimension local bifurcations contain the nonlocal bifurcations in their unfolding. Such normal forms thus appear as simple models to study nonlocal bifurcation. For example the unfolding of the codimension two Bogdanov-Takens singularity contains naturally the Andronov homoclinic bifurcation. It corresponds to the nonlinear unfolding of a linear vector field with a non semi-simple double zero eigenvalue. Its normal form is given by:

$$u_{tt} + (\mu + \alpha u) u_t + \nu - u^2 = u_{xx} + \kappa u_{xxt}.$$  

(14)

In the parameter regime where the stationary solutions exist ($\nu > 0$), this equation can be reduced to the complex Ginzburg Landau equation:

$$\partial_T A = -\mu_2 A - (1 + i\alpha') |A|^2 A + (1 + i\beta') \nabla^2 A$$

(15)

where $\alpha' = (10/(3\alpha w) + \alpha w/3)$, and $\beta' = -1/w/\kappa$. The complex number $A$ measures the complex amplitude of the oscillation: $u = -\sqrt{\nu} + \epsilon \sqrt{\alpha}/w(Ae^{iux} + c.c.) + \epsilon^2 \alpha/(A^2 B e^{iux} + c.c. + C|A|^2)$, with $w^2 = 2 \sqrt{\nu}$, $B = (-1 + i\alpha w)/(3w^2)$, and $C = 2/w^2$. The small parameter $\epsilon$ is defined as $\mu = \alpha \sqrt{\nu} + \epsilon^2 \mu_2$. The bifurcation is supercritical if $\alpha > 0$. The homogeneous oscillation is stable when:
\[ D_\phi = 1 - \frac{\alpha}{3\kappa} \left( 1 + \frac{5}{\alpha^2 \sqrt{\nu}} \right) > 0. \]

This criterion of stability is valid only for limit cycle close to their onset. We notice, that for \( \alpha \) large enough or \( \nu \) small enough, the limit cycle is always unstable by respect to inhomogeneous phase perturbation. In fact, we have conjectured, that close to the homoclinic bifurcation, this limit cycle will be always unstable. This conjecture have been recently proven [16].

A very interesting spatio-temporal behavior is naturally associated with the spatial unfolding of the Andronov saddle-node bifurcation. Close to the bifurcation, in the parameter regime where stationary solution exists, the corresponding dynamical system exhibits "excitable" properties. Although the stable stationary solution is a global attractor (at least in the simple models of the Andronov bifurcation), small but finite perturbations above a given threshold can lead to very large amplitude excursion in the phase portrait. The stable manifold of the unstable fixed point acts as a separatrix for the initial conditions which converge in a simple manner to the stable fixed point and the initial conditions which converge towards the stable fixed point with a large amplitude transient. For obvious reasons this large amplitude transient is called the "excitation". When the bifurcation occurs in spatially extended systems, the excitation can propagate under the form of excitable waves [17].

2 Sea shell patterns

Pigmentation patterns observed on the shells of tropical molluscs exhibit very interesting features. A great deal of modelisation was achieved by H. Meinhardt using reaction diffusion equations [18]. These equations model various chemical reactions involved in the patterning formation processes. Our approach to this problem is somewhat different. We intend to give some mathematical hints about the robustness of those patterns, using very naive non-chemical models. The seashells of molluscs are a conical shell and are composed of calcified material. The growth of the shell is made by adding a new whorl to the shell. Before to add the whorl, the molluscs makes its mantle "taste" the growing edge of the shell and give the pigmentation \( P \) to the added accretion material by pigmentation cells placed at the extremity of the mantle. From this point of view the seashells just appears as a spatiotemporal diagram. In the continuous approximation \( P = P(x,t) \), the first attempt to model the dynamics of the pigmentation consists in writing the following equation for the pigmentation :

\[ \partial_t P = f(P) + D P_{xx} \quad (16) \]

where \( D \) measures the interaction between cells. The function \( f \) can be always written as \( f = -\partial V/\partial P \). A further simplification consists to assume the existence of two stable equilibria, noted \( A \) (pigmented cell) and \( C \) (non-pigmented cell or albinos state). They corresponds to different spatially homogeneous pigmentation patterns. A simple analytic expression for \( V \) may be given by

\[ V(P) = \frac{1}{2} P^2 + \frac{\mu}{3} P^3 + \frac{1}{4} P^4 \]
where $\mu$ is a positive parameter. Depending on the values of this parameter the dynamical system possess one ($A$ which corresponds to $P = 0$, for $\mu < 2$) or three fixed points ($A$, an unstable fixed point $B$, and $C$, for $\mu > 2$). The solutions of Eq. 16 converge to stationary solutions since this equation possesses the Lyapunov functional

$$L = \int (V(P) + \frac{1}{2} P^2) dx$$

which always decreases in the temporal evolution. Nevertheless transients are obviously dynamical and could be observed on sea shells which only live a finite time. For example, in the parameter regime $2.12 \ldots > \mu > 2$ an initial state which consists in patches of pigmented cells and albinos cells evolves to the homogeneously pigmented pattern through the propagation of fronts. In the $x-t$ diagram, this takes the form of a transitory triangular shaped pattern. The existence of the Lyapunov functional ruled out the possibility of temporal oscillations, which is a common feature of many sea shell textures [18]. As a matter of fact, the pigmentation can oscillate at a given position in $x$ as a function of time, i.e. as a function of the coordinate which measure the growth of the shell. In "mechanical" terms, inertia is missing in Eq. 16. The simplest generalization of this equation which allows the existence of oscillations is given by

$$\frac{\partial^2 P}{\partial t^2} + g(P) \frac{\partial P}{\partial t} = f(P) + D P_{xx} + \kappa \frac{\partial P_{xx}}{\partial t}$$

(17)

where a "dissipation function" $g(P)$ and a new parameter $\kappa$ which represents a diffusion constant have been introduced. The term $DP_{xx}$ is now associated with propagation, it is responsible for the existence of inertial waves. Sustained oscillations are possible only if $g(P)$ is negative for some interval of the pigmentation variable $P$. In order to model the dissipation, we choose the simple function

$$g(P) = -\nu + P^2$$

To summarize, our model depends now on three parameters. The relative stability as defined by the potential $V$ is associated with the parameter $\mu$. For $\mu$ larger than $\mu = 2$ the only stationary is $P = 0$. The fixed points $B$ and $C$ appear through a saddle-node bifurcation when $\mu = 2$. The parameter $\nu$ is associated with the "negative" dissipation. For positive $\nu$, the fixed point $P = 0$ looses its stability through the Andronov-Hopf bifurcation. Slightly above the bifurcation threshold, this bifurcation leads to a small stable limit cycle for the dynamical system obtained by dropping the spatial derivatives. For a critical value $\nu_h$, when $\mu > 2$, this limit cycle disappears through a homoclinic bifurcation. For this parameter value the stable and the unstable manifold of the fixed point $B$, merge. For a larger value of $\nu$, the fixed point $C$ itself looses its stability though an Andronov-Hopf bifurcation. Between $\nu_h$ and $\nu_c$ another homoclinic Andronov bifurcation occurs for $\nu = \nu_{hc}$. This bifurcation leads to a stable "large" limit cycle which encloses the three fixed points. For $\mu = 2$, the fixed points $C$ and $B$ disappear through a saddle node bifurcation. When this happens in the parameter range $\nu_{hc} > \nu > \nu_h$, a limit cycle appear through a saddle-node Andronov bifurcation. Our model thus contains the three Andronov bifurcations. It can be seen as a model to study spatio-temporal phenomena associated with the spatial unfolding of these bifurcations. The last parameter $\kappa$ is associated
with the diffusion. In the frame of this model, which can also be interpreted as the continuous
coupling of Van der Pol like electrical oscillators, we now describes few phenomena which are
relevant to understand some of the sea-shell patterns.

2.1 Cavitation like patterns

Near the onset of oscillations ($\nu > 0$) Eq. 17 reduces to the complex Ginzburg Landau
equation 5. The stability of the homogeneous oscillatory solutions depends on the sign of $1 + \alpha \beta$.
As expected large $\kappa$ stabilizes the homogeneous oscillatory solution. For large values of $\mu$ there
is only one stationary solution ($P = 0$) and the homogeneous oscillation is stable. The existence
of an Andronov homoclinic bifurcation is a sufficient condition of the instability of the limit
cycle. This bifurcation only occurs in the parameter range $\mu > 2$. As $\nu$ increases, two types of
spatio-temporal patterns are observed

- ”Phase patterns”. For $\nu$ close to zero, the phase instability leads to wavy patterns which
  are easily interpreted as the manifestation of the phase instability of the oscillatory ho-
  mogeneous pattern (see Fig 3.a).

- ”Cavitation patterns”[19]. For larger value of $\nu$, strong self-focalization of the chaotic
  oscillation leads to the nucleation of the homogeneous stationary solution $C$. Depending
  upon the values of $\mu$, the nucleated domains either retract or expand. The case where the
  domains disappear through the propagation of two fronts is particularly interesting. It
  leads to a sustained dynamical state in which new domains are permanently created. On
  the $x - t$ representation of such a state, one notices white triangles which corresponds to
  the retraction of the Albinsos domains (see Fig 3.b).

2.2 Patterns of excitable waves

When $\mu = 2$, the fixed points $B$ and $C$ disappear through a saddle-node bifurcation.
For $\mu \geq 2$, depending upon the value of $\nu$, the fixed point $C$ is a global attractor of the
planar vector field. Excitable solitary waves are then observed in the simulation of the partial
differential equation. For $\mu$ given, as $\nu$ increases, three types of spatio-temporal behavior are
observed

- ”Back fire patterns” [21]. This pattern is associated with the instability of the front
  which connects the fixed points $A$ and $C$. As the front moves, the $A$ domains left behind
  is unstable and leads to the nucleation of domains of the $C$ state (see Fig. 4.a).

- ”Normal” excitable wave patterns. This is the domain of parameter where excitable exists
  and are stable. Because of the finite spatial domain, excitable solitary waves generally
  disappear at the border, where they are absorbed. The nature of the interaction between
  a wave and the boundary depends upon the nature of the boundary conditions. In this
  paper, the free boundary conditions which have been considered are such that they lead
to the absorption of ”normal” excitable waves.

- ”Crossing patterns”[20]. The frontal collision of two excitable pulses generally leads to
  their disappearance. It has been recently shown that such a collision could actually leads
to the reflection of pulses. The transition from non-crossing to crossing has been described
in the context of the geometrical theory of dynamical system. In this parameter range, the partial differential equation, when it is solved with periodic of free boundary condition, exhibits sustained dynamical behaviors. For slightly larger value of $\nu$, the crossing patterns takes the form of a standing wave (see Fig. 4.b).

Acknowledgments

This work has been supported by the CNRS (France) and the EU through a TMR grant FMRX-CT96-0010. One of us (P.C.) thanks the support of the "Institut Universitaire de France".

Références


[16] Preprint INLN 1999


FIG. 1: Sketch of the three Andronov bifurcations
FIG. 2: Spatiotemporal diagrams of the modulus of the complex amplitude of Eq. . (a) Phase turbulence ($\alpha = 1$, $\beta = -1.5$. $0.9 < |A| < 1.2$) (b) Defect turbulence, ($\alpha = 2$, $\beta = -1.5$. $0 < |A| < 1.5.$) 

FIG. 3: (a) Phase like patterns ($\mu = 2.08$, $\nu = 0.05$, $-0.4 < u < 0.2$). (b) Cavitation like pattern ($\mu = 2.08$, $\nu = 0.2$, $-1.4 < u < 0.5$). The white color corresponds to small values of $u$, and time is running up.

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Fig. 4: Patterns of excitable waves. (a) Back-Fire pattern ( $\mu = 2.01$ and $\nu = 0.5$, $-1.4 < u < 0.5$). (b) Crossing pattern ( $\mu = 2.01$ and $\nu = 0.83$, $-1.4 < u < 0.5$). The white color corresponds to small values of $u$, and time is running up.