Pattern formation on skin of tropical fishes

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Abstract

The stripe patterns observed on skin of tropical fishes have been explained by applying reaction-diffusion principle. According to the principle proposed by Turing, simple dynamics include a few substances coupled by substance-diffusion can generate spatially periodic patterns. However, the basic reaction-diffusion model can't explain the fact that most of the fish stripes are either parallel or perpendicular to the body axis, where the direction may be different between species. We study a reaction-diffusion model including anisotropy in the diffusion term to explain specificity of the direction of the fish stripe. On the fish skin, each scale comes out to the direction of body axis.

It makes structural difference in epidermis between parallel and perpendicular direction to the body axis. The result depends on the ratio between anisotropy of diffusion of activator and that of inhibitor. When the anisotropy of activator is larger than that of inhibitor, the direction of stripe is likely to be parallel to the direction to which the activator diffuses faster. When the anisotropy of inhibitor is larger than that of activator, the direction of stripe is likely to be perpendicular to the direction to which the inhibitor diffuses faster. When the anisotropies are almost same between the two substances, the specificity of the stripe direction disappears. This result depends on neither other parameter value nor the form of the reaction term. From the result, we can make hypothesis that the mechanism of spatial transmission may be different between two substances in tropical fish skin.

Introduction

Many tropical fishes have stripe or dot patterns on their skin. The pattern reflects on distribution of activity of pigment cell in the epidermis. The patterns are different between species. Kondo and Asai showed that these fish patterns can be explained well by the "Reaction-diffusion" mechanism proposed by Turing, which says that the simple reaction including few substances spatially coupled by diffusion can induce periodic distribution of the substances at the equilibrium. The stripes patterns generated by the reaction-diffusion mechanism in two-dimensional space has stable periodicity, however, the direction of the stripe is not stable; that is variable depending on the initial distribution. On the other hand, the stripe on the fish skin has strong directionality; the directions of most of the fish stripes are either parallel or perpendicular to their body axis, and whether it is parallel or perpendicular depends on the species. In order to explain this directionality, we have to consider improved version of the reaction-diffusion model.

The actual fish epidermis has anisotropy in its structure. The scales come out in parallel to the body axis. The diffusion speed of substance in epidermis may be different between parallel direction and perpendicular direction to the body axis. In this study, we incorporate an anisotropy in diffusion of the substance.

We model the anisotropy of the diffusion as the following: the diffusion coefficient of each substance is a function of the direction of gradient of the substance at the position. We call the distortion of the shape of the diffusion range from a circle "anisotropy." We used three different reaction terms including two substances that have been shown to produce periodic spatial patterns by reaction-diffusion mechanism in previous study. One of them is not appropriate to be interpreted by "activator and inhibitor," which is often mentioned to understand reaction diffusion mechanism. The substance with larger diffusion coefficient in the reaction is not activated by the other substance and doesn't inhibit the other substance. Then we call the two substances in three models "less-diffusive-substance" and "more-diffusive-substance," respectively.

The results of the three models can be summarized as the followings: when the anisotropy of less-diffusive-substance is larger than that of more diffusive one, the direction of stripe is likely to be parallel to the direction to which the less-diffusive-substance diffuses faster. When the anisotropy of more-diffusive-substance is larger than that of less-diffusive-substance, the direction of stripe is likely to be perpendicular to the direction to which the more-diffusive-substance diffuses faster. This result is observed even if the difference in anisotropies between two substances is small. Only when the anisotropies are almost same between the two substances, the specificity of the stripe direction disappears. This result doesn't depend on other parameter values, and it is observed in the three different models using different reaction term. From the result, we can make hypothesis that the mechanism of spatial transmission may be different between two substances in tropical fish skin.

Model

1) RD system

Turing showed that two diffusive chemicals that react each other can evolve to a spatially heterogeneous patterns from spatially uniform pattern spontaneously. In general the system can be written as the followings:

$$\frac{\partial u}{\partial t} = \nabla^2 u + f(u,v) \tag{1a}$$

$$\frac{\partial v}{\partial t} = d\nabla^2 v + g(u,v) \tag{1b}$$

, where u and v indicate concentration of less-diffusive-substance and that of more diffusive concentration, respectively. The average diffusion of v is much larger than u, i.e. d is larger than 1. The reaction term f and g have to satisfy the condition for Turing's mechanism, which are not shown here. In the first model, we use the model proposed by Schnakenberg for studying a chemical reaction (Schnackenberg, 1979) as the reaction term f and g. That is shown as follows:

$$\frac{\partial u}{\partial t} = \nabla^2 u + \gamma(a - u + u^2 v) \tag{1c}$$

$$\frac{\partial v}{\partial t} = d\nabla^2 v + \gamma(b - u^2 v) \tag{1d}$$

, where a and b are the positive constants and γ indicates scale parameter.

2) The anisotropiy in diffusion

We assume anisotropy in diffusion of the substance. As there is the structural directionality in fish epidermis made by scales, it seems to be appropriate to assume directional dependency in diffusion speed. We assumed that the magnitude of flux of the substance at each point is a function of the angle of the gradient vector of the substance rather than just a constant. We modeled it as the followings:

$$D_\sigma(\theta_\sigma) = \frac{D_{\sigma 0}}{\sqrt{1 - \delta_\sigma \cos 2(\theta_\sigma - \varphi)}} \tag{2}$$

, where σ indicates u or v, $D_{\sigma 0}$ is the diffusion constant, θ_σ indicates the angular difference between gradient of the variable and the x-axis, and φ indicate the specific direction to which the substance diffuse faster. This anisotropy in diffusion is first modeled by Kobayashi. We call parameter δ_σ "anisotropy", which indicates the distortion of the diffusion range from a circle.

3)The model

We substituted anisotropy in the diffusion term of the Schnakenberg model. Then, we got the following model:

$$\frac{\partial u}{\partial t} = \nabla(D_u(\theta_u)\nabla u) + \gamma(a - u + u^2 v) \quad (3a)$$

$$\frac{\partial v}{\partial t} = \nabla(D_v(\theta_v)\nabla v) + \gamma(b - u^2 v) \quad (3b)$$

, where a and b are the positive constants and γ indicates the scale parameter .

Simulation and result

1) The effect of the anisotropy in diffusion

We calculated the model shown above by using some initial conditions where value of u and v are equilibrium values added the small disturbances randomly. The boundary condition is periodic. The obtained patterns are shown below.

1 . The results of anisotropy in diffusion of less-diffusive-substance u.

Fig 1a shows the result when u diffuse faster to the horizontal direction i.e. δ_v =0. When we changed the diffusive direction φ, the direction of the stripe is parallel to the diffusive direction of u. The directionality in the stripe pattern is stronger when we used large anisotropy δ_u .

2 . The results of anisotropy in diffusion of more-diffusive-substance v.

Fig 1b shows the result when v diffuse faster to the horizontal direction i.e. δ_u =0. When we changed the diffusive direction φ, the direction of the stripe is perpendicular to the diffusive direction of v. The directionality in the stripe pattern is stronger when we used large anisotropy δ_v .

3 . The anisotropy in diffusion in both substances

We incorporate the same anisotropy in both substances ($\delta_u = \delta_v$). In this case, the directionality disappears. We can't find any directionality in the obtained patterns even if the anisotropy is larger.

Then we changed the value of anisotropy of less-diffusive-substance and that of more-diffusive-substance, respectively. When the anisotropies of the two substances are different, we can see the directionality in the obtained stripe patterns. In such cases, the direction of the stripe is stable without depending on the initial distributions. The existence of the directionality and the direction of the stable stripe depend on relative value of the anisotropy of the two substances. Fig. 2

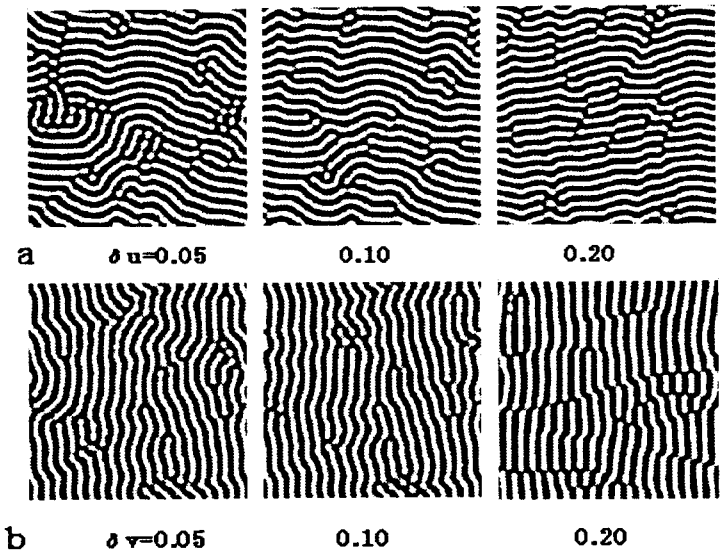

Figure1 The results when each substance diffuse faster to the horizontal direction. We showed the pictures when anisotropy of each substance are 0.05, 0.10 and 0.50. Parameters are a=0.025, b=1.550,d=20.0 and γ =10000 in (3a) and (3b). All computations were performed with periodic boundary condition in a square box of size:2.0*2.0 (grid:200*200). a shows the results when only u diffuse faster to the horizontal direction. b shows the results when only v diffuse faster to the horizontal direction.

shows the summarized result. We assumed that both of two substrates are more diffusive to the horizontal direction. From the result, we can say that if the anisotropy of less-diffusive-substance is larger, the direction of the stripe is parallel to the diffusive direction, however, if the anisotropy of more-diffusive-substance is larger, the direction of the stripe is perpendicular to the diffusive direction. This result can be easily understand, because the anisotropy of less-diffusive-substance is likely to make stripes parallel to the diffusive direction and the more-diffusive-substance is likely to make that to the perpendicular direction.

The above results are observed even when we changed the value of relative diffusion d, or the function of the anisotropy. It is also observed even after changing the reaction term. Then we believe this result is universal.

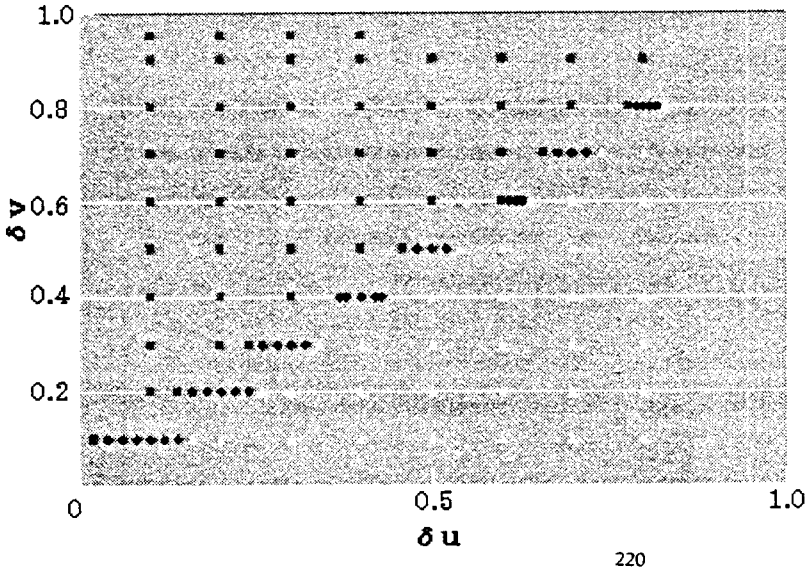

Figure 2 The diagram of parameter set of δ u and δ v. The parameter sets of ■ formed the perpendicular stripe to the diffusive direction. One of ▲ formed the pararelle stripe.One of ◆ formed stripe which had no specifcity of direction.

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