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Patterns on the Fish Skins Induced by Anisotropy in Diffusion

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Most of the stripes observed on fish skins are either parallel or perpendicular to their antero-posterior axis (Kondo & Asai, 1995). Some species have parallel stripes, some have perpendicular ones, and small number of species has random stripes, where the direction of the stripe is not fixed. For example, very close two species (*Genicanthus melanosphilos* and *Genicanthus watanabei*) show very different patterns; *G. melanosphilos* shows perpendicular and *G. watanabei* shows parallel stripes to the antero-posterior axis. On the other hand, the direction of stripes obtained by simple reaction diffusion systems is basically free. The stripes patterns generated by the reaction-diffusion mechanism in two-dimensional space has stable periodicity (Turing, 1952), however, the direction of the stripe is not stable; that is variable depending on the initial distribution. What makes the strong directionality in the actual fish skin?

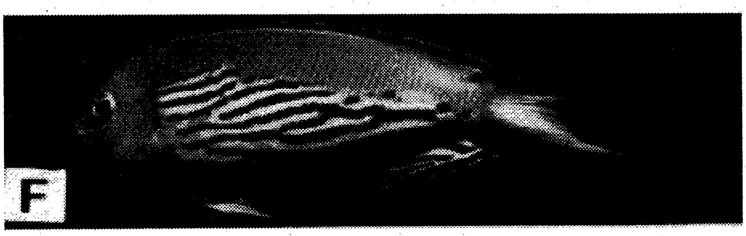

Figure 1. An example of parallel stripe to the antero-posterior axis (*G. watanabei*)

In fact, there is strong possibility that a fish skin has the property to make directionality in its structure. In the structure of fish skin, we can see that each scale comes out to the same direction along the antero-posterior axis. The epidermis is wrapping the scales and making zigzag form. As the zigzag structure doesn't exist along dorso-ventral axis, the structure is different between the antero-posterior axis and the dorso-ventral axis. This structural difference may make difference in speed of informational transfer between the two directions.

From the idea, we developed a modified reaction-diffusion model where the substances likely to diffuse faster to the special direction rather than simple homogeneous diffusion. By using the anisotropic diffusion-reaction model, we can explain the transition of the pattern in actual fish.

Model

The anisotropic property of the fish epidermis is modeled by incorporating the anisotropy into the diffusion term. The usual diffusion term is derived by assuming that the flux of substance is linear to the gradient of the substance. In this study, it is assumed that the diffusion coefficient is not a constant but a function of an angle between the gradient and a special direction. The special direction means the direction where the substances diffuse faster. In other word, we assumed that the flux would be enhanced if the direction of gradient of the substance is same as the special direction, and it would be reduced if the direction of gradient is perpendicular to the special direction.

The assumption is expressed mathematically in the following:

$$\frac{\partial u}{\partial t} = \nabla \cdot (D_u(\theta_u)\nabla u) + \gamma f(u,v) \tag{1a}$$

$$\frac{\partial v}{\partial t} = d\nabla \cdot (D_v(\theta_v)\nabla v) + \gamma g(u,v) \quad , \tag{1b}$$

where θ_u and θ_v indicate the angles of the gradient of the variables ($\theta_u = \tan^{-1}((\partial u/\partial y)/(\partial u/\partial x))$ and $\theta_v = \tan^{-1}((\partial v/\partial y)/(\partial v/\partial x))$), and $D_\sigma(\theta_\sigma)$ indicates the function of anisotropy in diffusion term. The form of the $D_\sigma(\theta_\sigma)$ used in the analysis is: $D_\sigma(\theta_\sigma) = \{1 - \delta_\sigma \cos 2(\theta_\sigma - \varphi)\}^{-\frac{1}{2}}$, where φ indicates the angle of most diffusive direction. We call the parameter δ_σ "anisotropy," which indicates the degree of distortion of the diffusion range from a circle. If the anisotropy is 0, the diffusion range is just a circle (normal diffusion), and if the value is large the distortion of diffusion range is large. We can choose different values of anisotropy for the two substances (δ_u and δ_v). On the other hand, the diffusive direction φ is assumed to be common between the two substances (because it comes from the structure of epidermis). This method to incorporate the anisotropy into the diffusion is first modeled by Kobayashi (Kobayashi, 1993), where he studied pattern formation the dendritic crystal growth like snow crystal.

The forms f and g indicate reaction terms. We use the form studied by Schnakenberg (Schnakenberg, 1972);

$$f(u,v) = A - u + u^2 v \tag{1c}$$

$$g(u,v) = B - u^2 v \qquad , \qquad (1d)$$

where A and B are positive constants. We also tried some different formulae later.

Result

We calculated the model (1a)-(1d) and derive patterns by using computer simulation. The used parameters values are ones that generate stripes in simple reaction-diffusion model. The boundary condition is periodic. The initial distribution is equilibrium value with small random fluctuation. To remove the effect of the boundary, the periodic boundary condition was chosen.

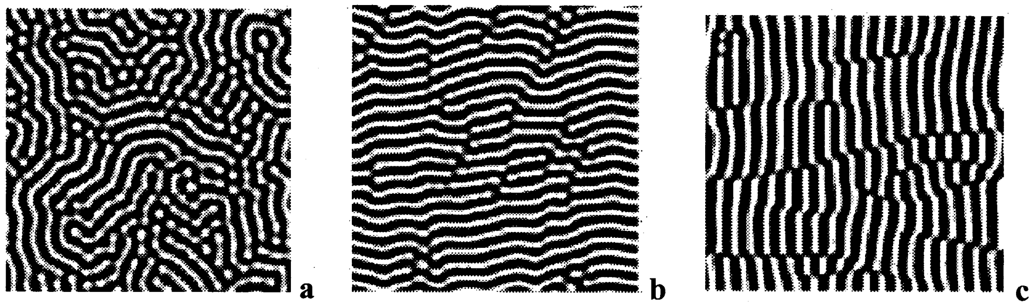

Figure 2 The obtained patterns by computer simulation

(1) The effect of positive same anisotropy

We incorporate the same positive value of anisotropy in both substances (i.e. $\delta_u = \delta_v$). Fig. 2a shows the simulation results, when the most diffusive direction is parallel to the x-axis (φ=0). We cannot find any directionality in this figure. This result was observed even if the value of the anisotropy is very large.

(2) The effect of anisotropic diffusion of less-diffusive-substance u

Fig. 2b shows the simulation results when the anisotropy of u is positive and that of v is 0. In the figure, the most diffusive direction is parallel to the x-axis (φ=0). The direction of the stripe becomes always parallel to the most diffusive direction of u, even if we changed the diffusive direction φ. The wave-length of the stripe is not influenced by δ_u.

(3) The effect of anisotropic diffusion of more-diffusive-substance v

Fig. 2c show the results when the anisotropy of v is positive and that of u is 0. The most diffusive direction is parallel to the x-axis (φ=0). In this case, the direction of the lines is likely to be perpendicular to the diffusive direction of v. We can remember that v corresponds to what is called inhibitor. Then we can intuitively understand the result that the direction of the stripes crosses the most diffusive direction of v.

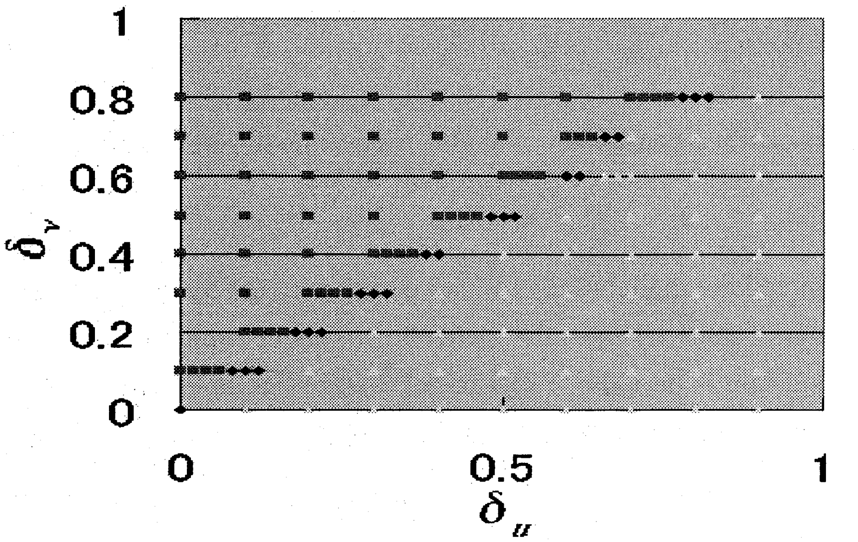

Figure 3 Summary of directionality of obtained stripes

Fig. 3 summarizes the directionality of stripe obtained patterns. The diffusive direction is fixed to be parallel to the x-axis. Each point indicates the direction of the observed stripe, horizontal, vertical, or not determined. To identify the direction is done by using a computer algorithm.

The result depends only on the relative magnitude of anisotropy of u and v. When δ_u is larger than δ_v, the direction of the stripe is horizontal; the direction is parallel to the most diffusive direction. When δ_v is larger than δ_u, the direction of stripe is perpendicular to the most diffusive direction. Only when the anisotropies of both substances are almost the same, the direction is not determined.

We tested several different conditions. We changed the value of parameter in reaction term, value of diffusion coefficient d, the function of anisotropy in diffusion term and also the form of the reaction term. The result does not depend on these changes. The same figure was obtained from all the trials we tested. We can say that this result is very general.

References

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