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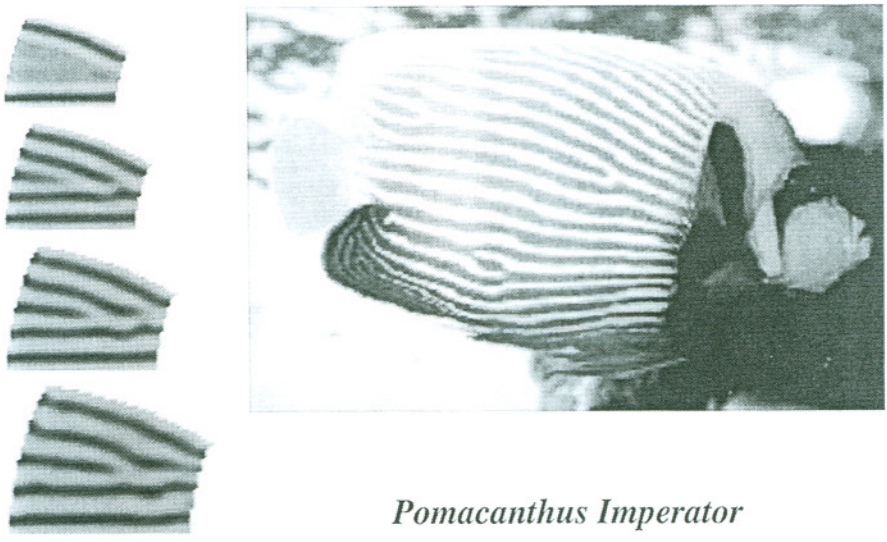

Pomacanthus Imperator

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Spatial Patterning in Modified Turing Systems: Application to Pigmentation Patterns on Marine Fish

J. L. ARAGÓN[1], C. VAREA[1], R. A. BARRIO[1] and P. K. MAINI[2]

[1]*Instituto de Física, UNAM, Apartado Postal 20-364, 01000 México, D.F., Mexico*
[2]*Centre for Mathematical Biology, Mathematical Institute, University of Oxford, 24-29 St. Giles, Oxford, OX1 3LB, U.K.*

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Abstract. In this paper we extend the study of Turing models to investigate the rôle of boundary conditions, parameter modulation, domain growth, and coupling of models. Our numerical simulations show that such modifications lead to patterns that cannot be reproduced by the standard model. By comparing our results with pigmentation patterning on marine fish we conclude that such models may have wider application than originally imagined.

1. Introduction

In 1952, the mathematician Alan M. Turing (TURING, 1952) proposed a theory for morphogenesis. He showed that a system of reacting and diffusing chemicals could evolve from initial near-homogeneity into a spatial pattern of chemical concentration (the phenomenon of "diffusion-driven instability"). He proposed that this spatially heterogenesis chemical (or morphogen) concentration pattern could serve as a pre-pattern to which cells would respond by differentiating accordingly, resulting in the formation of structure reflecting the underlying chemical pre-pattern. Turing systems have been proposed as possible mechanisms for generating patterns in a wide range of embryological applications (see MURRAY, 1993, for a comprehensive review). Although the existence of Turing patterns in biology is still a controversial issue, they have been found in chemistry (see MAINI *et al.*, 1997, for a review).

In this paper we extend the study of Turing systems to look at the rôle of boundary conditions, domain growth, and the coupling of Turing models. In Section 2 we present the three models we will consider and, in Section 3, we present a sample of our numerical simulations and compare the resultant spatial patterns with pigmentation patterns observed on certain marine fish. Conclusions are presented in Section 4.

2. Model Equations

The model equations are simple Turing systems of two chemicals, corresponding to models widely used to simulate biochemical processes. We choose three models (we refer the reader to the papers by VAREA *et al.* (1997) and BARRIO *et al.* (1998), for full details):

$$\frac{\partial u}{\partial t} = D\delta\nabla^2 u + \alpha u\left(1 - r_1 v^2\right) + v\left(1 - r_2 u\right)$$

$$\frac{\partial v}{\partial t} = \delta\nabla^2 v + \beta v\left(1 + \frac{\alpha r_1}{\beta} uv\right) + u\left(\gamma + r_2 v\right) \tag{1}$$

$$\frac{\partial u}{\partial t} = D\nabla^2 u + \beta - \kappa u - uv^2$$

$$\frac{\partial v}{\partial t} = D\delta\nabla^2 v + \kappa u + uv^2 - v \tag{2}$$

$$\frac{\partial u}{\partial t} = D\nabla^2 u + \beta_u - \rho_u \frac{v^2 u}{1 + \phi v^2}$$

$$\frac{\partial v}{\partial t} = D\delta\nabla^2 v + \beta_v - \kappa_v v + \rho_v \frac{v^2 u}{1 + \phi v^2}. \tag{3}$$

In each case, $u(\bar{x}, t)$, $v(\bar{x}, t)$ denote the concentrations of chemicals u and v at spatial position $\bar{x}$ and time t; D, δ, α, β, r_1, r_2, κ, β_u, β_v, ρ_u, ρ_v, κ_v and ϕ are parameter values.

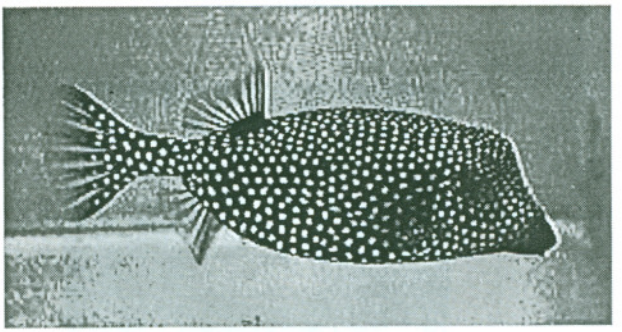
The models were solved on a two-dimensional domain subject to various types of boundary conditions for different parameter values. In some cases one adds a linear term hu where h is a constant different from zero only at a certain boundary. This term represents a possible source of chemical u. These sources can be interpreted as a biological mechanism by which a certain chemical responsible for the pigmentation is enhanced at the edge (VAREA *et al.*, 1997). This idea has close parallels with the mechanism of stripe formation in the *Drosophila* embryo, which is caused by a high concentration of the *Bicoid* protein along the anterior side (JOHNSTON and NÜSSLEIN-VOLHARD, 1992).

In the following section we present a series of numerical simulations and compare the results with pigmentation patterns on fish.

3. Numerical Results and Applications

All the models mentioned above exhibit the phenomenon of diffusion driven instability, that is, parameter regimes can be chosen such that the spatially uniform steady state is stable in the absence of diffusion, but can be driven linearly unstable by diffusion. In such parameter regimes, the solution may evolve to a bounded spatially non-uniform steady state. A great deal of analysis has been carried out on Turing systems with zero-flux boundary conditions on square domains, and the rôle of the non-linearities in pattern selection has been widely explored (see for example, ERMENTROUT, 1991; NAGORCKA and MOONEY, 1992).

In this paper we extend these studies to non-standard systems. First we consider the rôle of boundary sources of one of the chemicals; second we investigate how patterns change due to domain growth; third we study the effects of spatially varying parameters; fourth we examine interacting coupled models. We illustrate our results by the eight simulations below (the model equations were solved using a simple Euler scheme on grids of 100×100 sites).



Ostracion meleagris

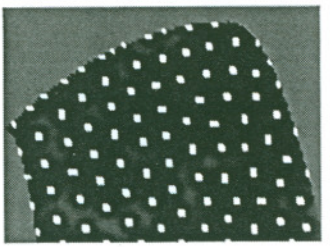
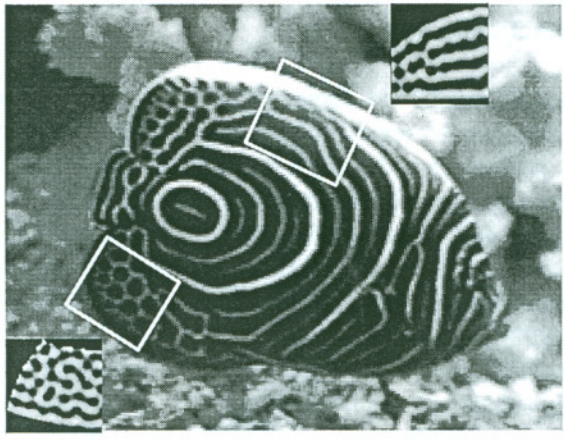
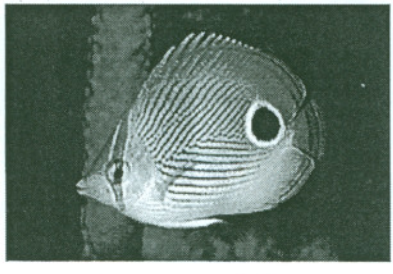


Fig. 1. Numerical simulation of model (1) with zero-flux boundary conditions and a source $h = 0.1$ of u on the upper boundary. The parameters were $D = 0.122$, $\delta = 2$, $\alpha = 0.398$, $\beta = -0.4$, $r_1 = 0.02$ and $r_2 = 0.2$. Observe the similarity with the pattern exhibited by the puffer fish *Ostracion meleagris*.



Pomacanthus imperator

Fig. 2. The juvenile coat of the angel fish *Pomacanthus Imperator* presents a complicated array of aligned stripes and cells similar to the results of numerical calculations from model (2). The insets comparing the theoretical patterns with the fish pigmentation are reproduced from VAREA *et al.* (1997) Figs. 3d and 4d, and correspond to our model (2).



Chaetodon capistratis

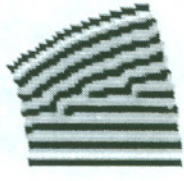


Fig. 3. Numerical simulation of model (3) on a "fish-like" domain and with an extreme value of the sources ($h = 0.5$) of u at the top and bottom boundaries. The zero-flux boundary condition was used on the other boundaries. The parameters used were $\delta = 0.025$, $\rho_u = 0.02$, $\rho_v = \kappa_v = 0.01$, $\beta_u = 0.02$, $\beta_v = 0$, $\phi = 0.1$, and $D = 0.01$. Compare with the pattern exhibited by the butterfly fish *Chaetodon capistratis*.

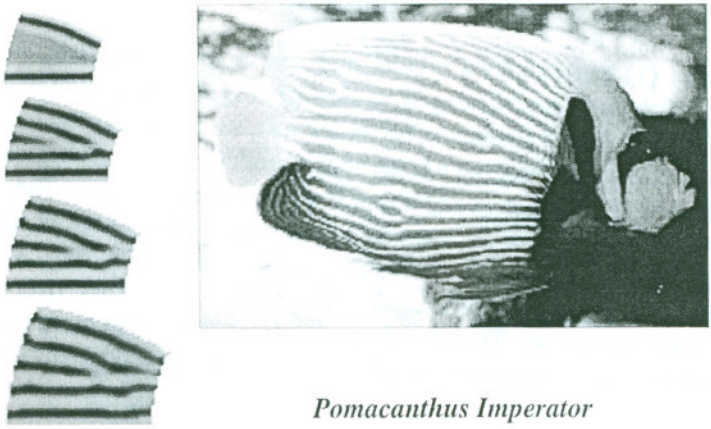


Fig. 4. Modeling the growth of the coat of the adult form of *Pomacanthus Imperator* using model (3) with parameter values as in Fig. 3, but with D changing steadily during the calculation to simulate the growth of the domain. See Fig. 5 in VAREA *et al.* (1997).

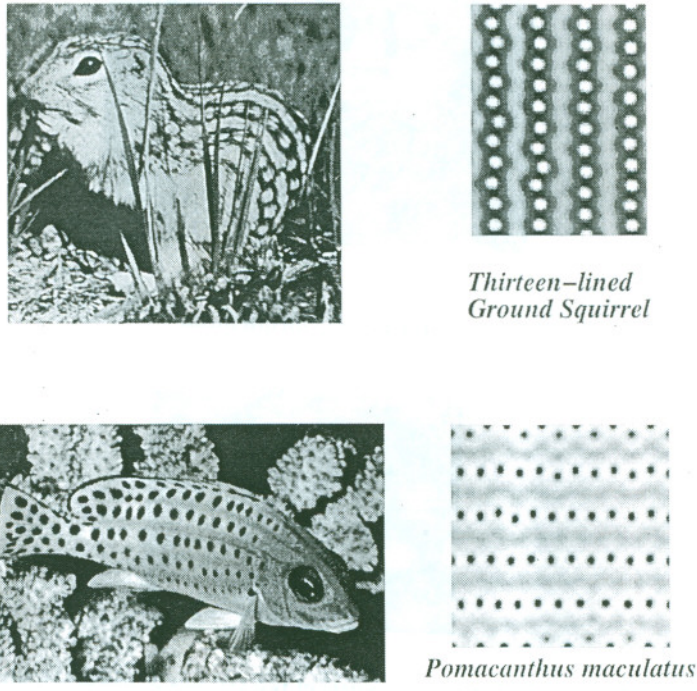


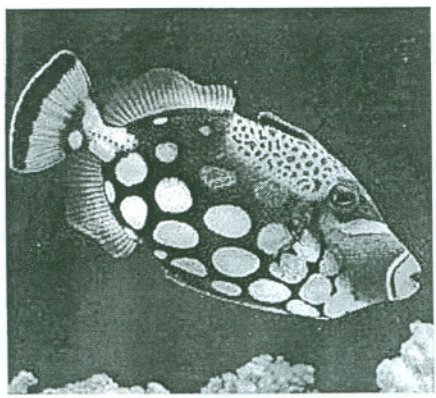
Fig. 5. Pattern obtained from solving model (1) on a rectangular domain with zero-flux boundary conditions for parameter values $D = 0.182$, $\delta = 2$, $\alpha = 0.5$, $\beta = -0.578$, $r_1 = 1.5$, and $r_2 = \cos(\pi y/10)$. This type of parameter modulation produces an alternate pattern of stripes and spots, similar to those observed in the thirteen-lined ground squirrel, and in the fish *Pomacanthus maculatus* (reproduced from FRANK (1973)).

1. Model (1) can exhibit a regular and sparse spotted pattern, similar to that observed on the fish *Ostracion meleagris*, as shown in Fig. 1. All the fish images presented in this paper, except that of *Pomacanthus maculatus*, were taken from our own tank.

2. Model (2) with sources of u at the edges, produces patterns very similar to those found near the tail of the juvenile angel fish *Pomacanthus imperator* (Fig. 2).

3. When the strength of the sources is increased, a new pattern of stripes appears that resembles the skin of the butterfly fish *Chaetodon capistratis* (Fig. 3).

4. The adult form of *Pomacanthus imperator* has stripes that conserve the wavelength as the fish grows. Therefore in some places of the skin there are dislocation-like patterns where a stripe bifurcates. The bifurcation point travels horizontally as the fish



Balistoides conspicillum

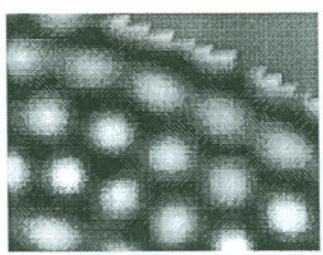
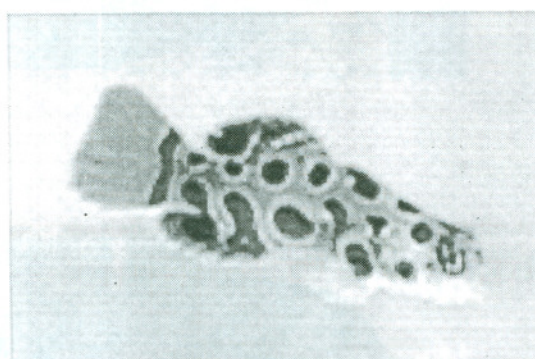


Fig. 6. Numerical simulation of a coupled system of two versions of model (1), where one submodel (in variables (u', v')) feeds into the other submodel (in variables (u, v)) by enhancing the linear production rate of u with the term $q_1 u'$ ($q_1 = -0.55$). The resultant system was solved on a "fish-like" domain with zero-flux boundary conditions for v, u', and v', with a source of strength $h = 0.005$ for u at the top boundary, and zero-flux everywhere else. Parameter values are $\delta = 2$, $r_1 = 3.5$ and $r_2 = 0.2$ for both models, $D = 0.516$, $\alpha = 0.899$, and $\beta = -0.91$ for the unprimed model, and $D' = 0.122$, $\alpha' = 0.398$, and $\beta' = -0.4$ for the primed model. The patterns produced are similar to those observed on *Balistoides conspicillum*.

grows to produce new stripes (KONDO and ASAI, 1995). This was modeled in a growing fish-like domain with sources at the horizontal borders and using model (3) (Fig. 4).

5. In model (1), the coefficient of the quadratic term (r_2) was modulated sinusoidally along the horizontal direction, producing an alternate pattern of spots and stripes that mimics the skin of the thirteen-lined squirrel and the marine fish *Pomacanthus maculatus* (see Fig. 5). This pattern cannot be produced by the standard Turing model (BARD, 1981; COCHO, 1987). In such a simulation, the question naturally arises as to how the spatial modulation of r_2 is set up. This could be due to feedback from another Turing model operating on a faster time scale. This motivates our study of coupled Turing systems, and the following three simulations present a sample of the complex patterns that can arise from such interactions.

6. We coupled linearly two models of form (1) with parameters chosen so as to enhance modes of different wavelengths in each sub-model, and with a small source of u at the upper border of a fish-like shaped domain. The pattern is a defective hexagonal



Synchiropus picturatus

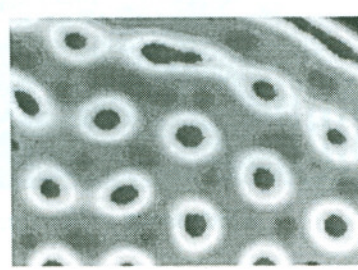
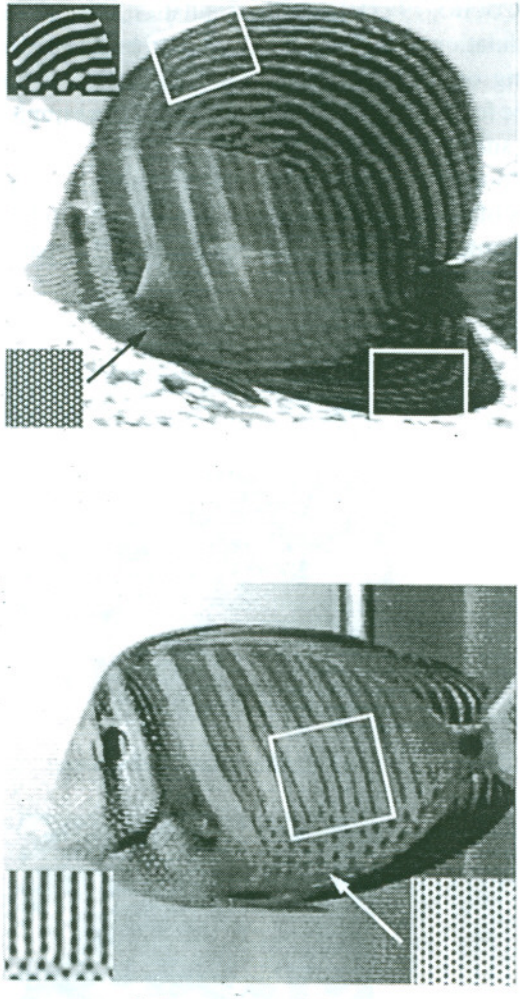


Fig. 7. Numerical simulation of a coupled system of two versions of model (1), where one submodel (in variables (u', v')) feeds into the other submodel (in variables (u, v)) by enhancing the production of u with a cubic term $q_3 u' v^2$, with a corresponding degradation term in the v equation ($q_3 = 0.55$). The equations were solved on a "fish-like domain" with a source of $h = 0.1$ at the top boundary. All the other parameters are the same as in Fig. 6. The resulting pattern is compared with the observed on *Synchiropus picturatus*.

lattice of dots aligned near the border, similar to the skin of the puffer fish *Balistoides conspicillum* (Fig. 6).

7. When two models of form (1) are coupled with a cubic interaction, complex patterns of dots arise resembling the skin of *Synchiropus picturatus* (Fig. 7).



Zebrasoma veliferum

Fig. 8. Patterns obtained with a coupled system of two versions of model (1) can give complicated configurations of stripes and spots, as the ones found on the skin of *Zebrasoma veliferum*. The three square insets in the figure show numerical calculations obtained with a cubic coupling $q_3 = 0.55$ between the two submodels (see Fig. 7 caption for explanation), and the "fish-like" inset was obtained with a source of u on the top boundary of strength $h = -0.1$. All the other parameters are listed in BARRIO *et al.* (1998).

8. Exploring further the coupling interactions in model (1) we find combined patterns of stripes and spots as the one found in the surgeon fish *Zebrasoma desjardinii* (Fig. 8).

4. Conclusions

We studied various Turing systems under different conditions with the aim of simulating the skin patterns of marine fish and other animals. We have shown that various modifications of the standard Turing system give rise to patterns that are not exhibited by the standard system. This allows us to extend the application of Turing theory to the complex spatial patterning observed in certain marine fish.

It is still an issue of controversy as to whether Turing patterns actually occur in biology. A number of other models have been proposed and most of them rely on the coupled mechanism of short-range activation and long-range inhibition. Due to this mechanistic similarity, it is believed that this class of models, although based on different detailed biological hypotheses, produce similar patterns. As Turing systems are representative of this more general class of model, we conclude that activator-inhibitor systems may have wider applicability than first thought.

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