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On the orientation of stripes in fish skin patterning

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Abstract

This paper is focused on the study of the stripes orientation in the fish skin patterns. Based on microscopic observations of the pigment cells behavior at the embryonic stage, the key aspects of the pigmentation process are implemented in an experimental reaction–diffusion system. The experiment consists of a photosensitive Turing pattern of stripes growing directionally in one direction with controlled velocity. Different growth velocities of the system rearrange the stripes in the same three possible orientations observed in the skin of the colored fishes: parallel, oblique, and perpendicular. Our results suggest that the spreading velocity of the pigment cells in the fish dermis selects the orientation in the patterning processes.

Keywords: Pattern formation; Turing; Reaction–diffusion; Growth

1. Introduction

Pigmentation processes and formation of patterns in the skin of living systems are a very active area of research [1–3]. These natural symmetry-breaking phenomena are often considered a key step to understand cellular interactions that yield to complex structures during axial segmentation and embryogenesis [4–7]. Despite the increasing number of studies in the field, the underlying mechanism that yields to the arising of stripes and spots in the skin of animals is still unknown [8].

Chemical systems of autonomous pattern formation has been proposed as the responsible mechanism for these symmetry-breaking processes in living organisms, from axial segmentation to cerebral cortex formation and skin pigmentation [9–14]. The hypothesis is that chemical species involving autocatalytic steps, called morphogenes, may control the cell differentiation in early stages of embryo development. These morphogenes can form pre-patterns due to a reaction–diffusion mechanism, first predicted by Alan M. Turing [15]. Once the chemical structure is established, cells may rearrange and differentiate following these pre-patterns. But half a century after Turing prediction, there is still no clear evidence of such morphogenes of activation and inhibition in any natural system (see [16] as a possible candidate).

Turing idea involves two interacting chemical species (called activator and inhibitor) diffusing at different rates. Under the appropriate chemical concentrations a periodic steady pattern arises, breaking the symmetry of a homogenous system and developing spots in hexagonal configuration or stripes in labyrinthine configuration. After their first experimental observation [17], there have been many attempts to explain natural symmetry breaking using the Turing mechanism [18].

An illustrative example is the pigmentation of skin in tropical fishes. Based on the similitude of the spatial configuration and the relaxation dynamics of defects [19,20], several authors claimed that a reaction–diffusion mechanism is the responsible for the non-homogenous distribution of pigment cells in the fish skin [21,22]. Numerical studies in domains with different shapes show that Turing stripes are influenced in the vicinity of the physical boundaries of the systems in the same fashion as stripes in the fishes [23].

But nowadays, there are still many open questions that Turing's idea does not solve. One important issue is related with the orientation of the pattern in the fish skin. Stripes in a typical Turing system appear to be randomly oriented with no

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preferential direction (see Fig. 1). On the contrary, stripes in the fish body are well organized and oriented. In fact, there exist only three main orientations for the arrangement of the pattern. Examples for these three configurations can be observed in Fig. 2.

The most common configuration is stripes oriented parallel to the head-to-tail axis, as in *Pomacanthus imperator* in Fig. 2a. Other possible configuration is composed of stripes ordered in oblique manner, with constant orientation (around 45° and/or −45°) respect to the head-to-tail axis, as in Fig. 2b. Finally, stripes perpendicular to the head-to-tail axis are also commonly observed (see Fig. 2c).

These three configurations compile the majority of the species of striped fishes, and only very rare exceptions can be found with the stripes oriented in another fashion. It is also known that other rearrangement of stripes in adult states can be caused by either a chemical irritant or injury to the fish's body [24]. In addition, the pattern is not completely steady and the pigment cells can rearrange as the fish grows, so in adult fishes, the stripes can be different that in young states [21].

Some studies propose the diffusion anisotropy in the skin of fishes as a mechanism for the orientation of the stripes [25,26], but anomalous diffusion does not explain why only these three major orientations are allowed to develop. Oblique configuration (Fig. 2b) cannot be easily explained due to diffusion anisotropy. In addition, the fact that different individuals of the same specie can exhibit the three configurations is also not included in the anomalous diffusion hypothesis [27].

Whether the Turing mechanism is the responsible of the symmetry breaking or not, there have to exist some other issue which selects among only these three possible orientations. In this paper, we propose that the way in which pigment cells migrate in the fist stages of embryo development is the responsible of these three configurations. The process of pigmentation is schematized in a simplified model. Then the model is implemented in an experimental pattern formation system, which develops steady stripes due to the Turing instability. The experimental Turing pattern arises under controlled growth velocity in the same three main configurations as the arrangement observed in the fish stripes. Our results suggest a key role in the velocity of growth of the natural pattern formation in the orientation of the stripes.

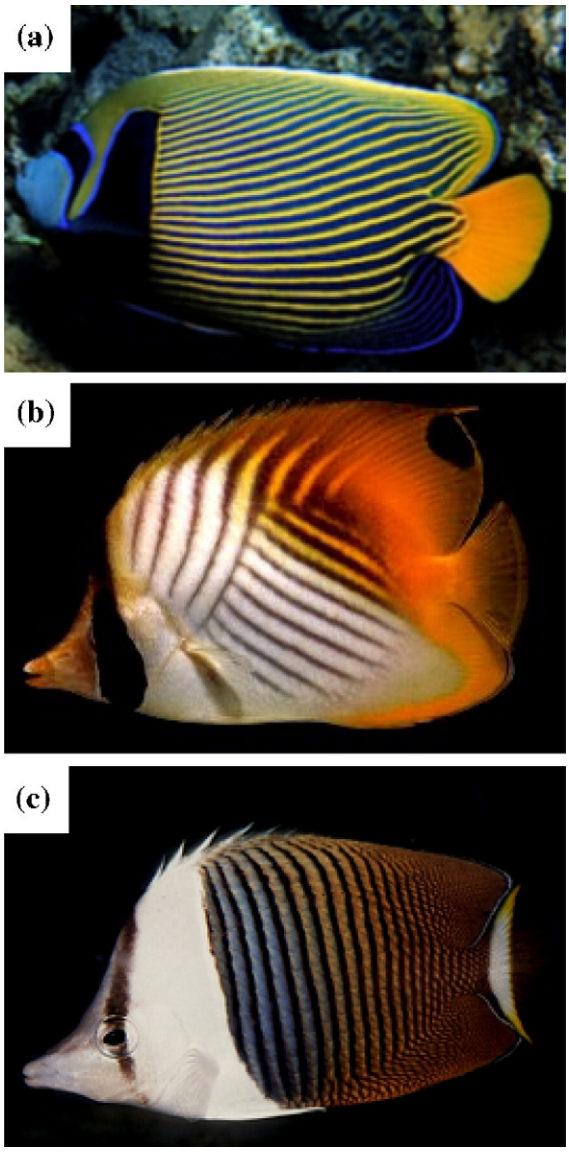

Fig. 2. Examples of patterns of pigment cells in the dermis of tropical fishes: (a) *Pomacanthus imperator*; (b) *Chaetodon mesoleucus*; (c) *Chaetodon auriga* (pictures courtesy of R. Fenner).

Fig. 1. Spontaneous labyrinthine Turing pattern in the chlorine dioxide–iodine–malonic acid (CDIMA) reaction–diffusion system. The typical labyrinthine configuration contrasts with the oriented pattern in fish skin.

2. The model

The process of fish skin pigmentation takes place during the early stages of development, when cells start to differentiate. Most of the studies were performed in zebrafish *Danio rerio*, a small fish from the minnow family (Cyprinidae) considered as an emerging model to understand vertebrae development and genetics [24,28–30]. Zebrafish exhibits stripes in the dermis, and it is transparent during the embryo stage, which facilitates the observation and study of the process of pigmentation.

During this process, the cells responsible for the pigmentation (also called chromatophores) arise from two distinct

embryonic sources: those that comprise the outermost layer of the retina derive from the optic cup, while those of the dermis and epidermis originate from the neural crest [31]. In the case of zebrafish *D. rerio*, the pigmentation in the dermis consists of black melanophores (a melanin-containing cell especially of fishes, amphibians, and reptiles), yellow xanthophores, and iridescent iridophores [29,7,31].

In zebrafish, the embryonic and early larval pigment pattern consists of several stripes of melanophores and iridophores, whereas xanthophores are scattered widely over the flank. This simple series of melanophore stripes developed during larvae stage remains unchanged for the first 2 weeks [32]. In the mature stage, the pattern is commonly composed of four black stripes horizontally oriented in the head-to-tail direction, but diverse mutations of the *D. rerio* can result in a completely different arrangement, as perpendicular stripes or even spots [30].

Although the mechanism responsible for the organization of cells in stripes is still unknown, it has been recently confirmed that the alternating light and dark horizontal stripes develop, in part, owing to interactions between melanophores and xanthophores [33].

The importance of the migration pathways for the pigment cells has been also recently discovered. Once formed, neural cells migrate throughout the embryo along two major migratory pathways, called ventromedial and dorsolateral. It has been observed that cells that migrate in the lateral way, i.e., from head-to-tail direction, develop only into chromatophores. The differentiation occurs during or even before migration. Cells migrate in a directional fashion in the head to tail direction, forming four thin stripes that result in the stripes in the mature stage [30,6,33].

Diverse experiments in *D. rerio* mutants evidence that the way that chromatophores migrate strongly affects the final configuration of the pattern. When the pigment cells migrate in an uncorrelated non-directional manner, no pattern arises and the melanophores are homogeneously distributed in the fish dermis [34]. The pattern only arises when the melanophores region grows from head to tail covering the fish dermis at the expenses of the melanophores-free region in the dermis.

On the other hand, it has been reported that the stripe patterns are also constrained ecologically [27]. External influence in the pattern configuration has been observed in certain species of colored fishes, as in East African cichlid fish. The same fish, under different environmental conditions, can develop different pattern configurations. The evolution of vertical patterns is associated with structurally complex habitats, such as rocky substrates or vegetation. The evolution of horizontal stripes is associated with a piscivorous feeding mode. Horizontal stripes are also associated with shoaling behavior. Also, under some circumstances, oblique stripes have been observed [27].

Summarizing, coordinated directional movement of melanophores seems to be extremely relevant in the establishment of the stripes. Also, feeding conditions, presumably related with growth velocity, play an important role in the pattern configuration. Based in these two statements, we will implement in a reaction–diffusion system these two main characteristics in the process of fish patterning. We will perform experiments in a Turing pattern formation system with directional growth and possibility to vary the growth velocity, mimicking the patterning process in fish embryo.

3. Experimental setup

The experiment consists in a two-dimensional photosensitive Turing system, which under homogeneous conditions develops stripes without preferential ordering (see Fig. 1). The system is allowed to growth directionally in one direction with different velocities. Fig. 3 shows the simplified mechanism for the pigmentation, and the corresponding scheme for the experimental setup.

We have used the chlorine dioxide–iodine–malonic acid (CDIMA) reaction in the Turing regime [35,36,17]. Experiments were carried out in a one side continuously fed reactor [37,38]. Structures are formed in a circular agarose gel layer (2% agarose, thickness of 0.3 mm, diameter of 20 mm). Between the gel and the feeding chamber, an Anapore membrane (Whatman, pore size of 0.2 mm, impregnated with 1% agarose) and a nitrocellulose membrane (Schleicher and Schuell, pore size of 0.45 mm) were introduced.

The reactor is maintained at 4 ± 0.5 °C, to allow the patterns to develop with good contrast. The reagents of the CDIMA reaction were continuously pumped into the reactor with the following feed-stream concentrations: $[I_2]=0.45$ mM, [malonic acid]$=1$ mM, $[ClO_2]=0.1$ mM, $[H_2SO_4]=10$ mM, [poly(vinyl) alcohol]$=10$ g/l. Using these input concentrations the system exhibits stationary labyrinthine stripes with a wavelength of $\lambda=0.54\pm0.01$ mm.

To introduce the effect of growth into the system, we have used the photosensitivity of the CDIMA reaction [39]. Basically, sufficiently high values of the external illumination intensity inhibit the arising of the structure. We have designed an experiment in which a domain able to develop Turing pattern grows in a given direction with a well-controlled velocity. This growth is caused by the displacement of a boundary separating an illuminated region from a shadowed one [40] (see Fig. 3d to e).

The moving boundary is produced by focusing a moving image from a commercial video projector (Hitachi, CP-X327) connected to a computer onto the gel. This setup allows to impose a constant controlled velocity for the boundary of the decreasing white zone (no pattern in the steady state regime) at the expense of the increasing black zone (allows pattern formation in the hexagonal regime). Images were recorded by a CCD camera connected to a computer.

The experimental procedure is as follows: The whole medium is initially illuminated, so the starting situation is a steady state all over the system. Then the shadowed domain starts growing from left to right with constant speed, where the pattern starts to arise.

The growth velocity in the experiments was in all cases below the Turing spreading velocity (estimated as $V_{spon}=1.8\pm$

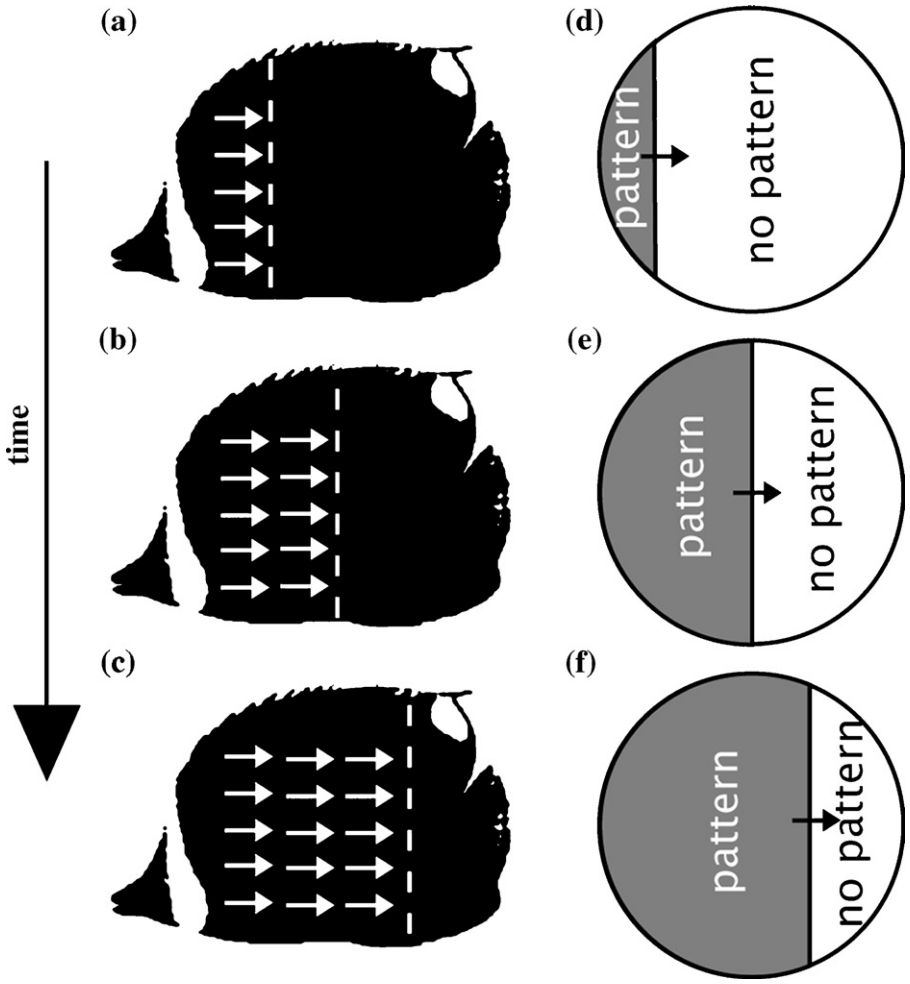

Fig. 3. Scheme of the process of patterning in fish skin: (a to c) pigment cells traveling throughout the embryo skin; (d to f) scheme of the experimental procedure.

0.1 mm/ h for the chemical concentrations here used), i.e., in the so-called absolutely unstable regime [41,42]. Experiments in the convective unstable regime are ongoing and will be the subject of a future communication.

4. Results

For low values of the growth velocity, the stripes develop organized parallel to the velocity axis. The pattern arises close to the moving boundary of illumination as stripes growing in length with the same velocity as the boundary. Fig. 4 is a snapshot of the pattern during an experiment with a velocity value in this range.

When the growth velocity is very low (around 0.1 mm/h), the stripes are almost perfectly oriented in the horizontal axis, with very few dislocations. As the growth velocity increases, the number of dislocations and defects on the orientation of the pattern also increases. Also note that close to the boundaries the alignment of the stripes is slightly disrupted.

When the velocity increases, a few spots arise in the system. For the concentrations here used, spots are not stable, and the system has to recover the stripes configuration. The process of recovering the stripes can be slow, depending on how far the system is from the spots solution in the parameter space. Surprisingly, the recovered pattern of stripes is organized in oblique configuration with respect to the velocity axis.

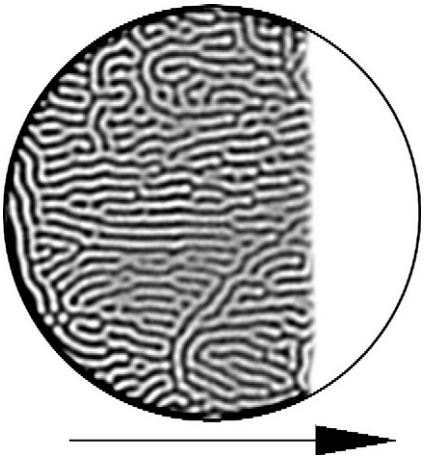

Fig. 4. Snapshot of the pattern oriented in horizontal way. $V = 0.28 \pm 0.1$ mm/h. The arrow indicates the direction of the movement of the boundary.

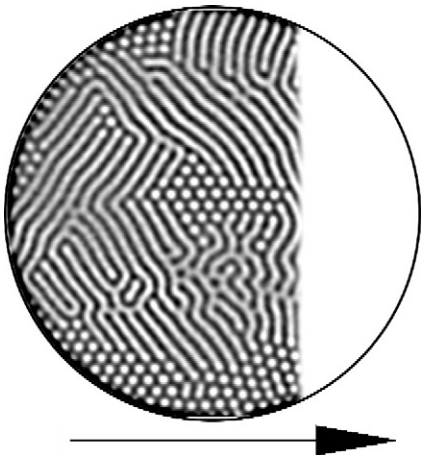

Fig. 5. Snapshot of the pattern oriented in oblique configuration. $V=0.55\pm0.1$ mm/h. The arrow indicates the direction of the movement of the boundary.

The formation mechanism for these stripes is via nucleation of neighboring spots, which are organized in rhombic configuration. For such reason, the stripes tend to be oriented at 45° and/or −45° respect to the growth axis. Although, depending on the growth velocity, the orientation of the oblique stripes can vary slightly. Fig. 5 is a snapshot of the experiment for a velocity value inside this regime. Some spots can still be observed in the system, which slowly recovers the oblique stripe pattern.

Finally, increasing values of the growth velocity yield to a different stripes orientation. A new stripe arises periodically in the system as the boundary moves. These stripes are mainly oriented perpendicularly to the growth axis. Nonetheless, some spots are also able to appear, inducing oblique stripes in some areas of the system, as it can be observed in Fig. 6.

The growth velocity modulates the wavelength of the stripes in this regime, but there is not a simple dependence between both values and this process deserves further analysis.

This regime of stripes perpendicular to the growth axis is extended until the boundary velocity reaches values out of the absolutely unstable domain, i.e., in the convective unstable domain. Here the behavior became more complex, with competing modes and different mechanism of orientation and wavelength selection. The convective unstable domain in Turing patterns will be the subject of future communications.

5. Discussion

This simplified model for the pigmentation process reproduces the three main configurations observed in the fish dermis. Parallel stripes in Fig. 4 can be identified with the orientation of stripes in *Pomacanthus imperator* in Fig. 2a. The oblique configuration in Fig. 5 is similar to the organization of stripes in the *Chaetodon* mesoleucus in Fig. 2b. Finally, high velocity values of the growing pattern produces perpendicular stripes, in the same fashion as the *Chaetodon auriga* in Fig. 2c.

Only these three different orientations for the stripes can be observed in both systems. In the reaction–diffusion experiments, the domains of parallel and perpendicular stripes appear to be considerably larger than the domain of oblique stripes. This is in coincidence with the fact that parallel and perpendicular stripes are more commonly observed in tropical fish patterns than oblique patterns. The fact that spots arise in the system rearranging into stripes in some cases is also consistent with experimental observations in pigment pattern formation in some species of tropical fishes [25].

More detailed analysis about growth in one-dimensional and two-dimensional experimental and numerical Turing patterns can be found in [40]. A mechanism of wavelength selection in one-dimensional media appears to be the reason of the two-dimensional orientation selection. The same result can be obtained in numerical simulations performed with the Lengyel–Epstein model for the CDIMA reaction [40].

In all cases here reported, the pattern arises near the moving boundary, and remains steady once the boundary is sufficiently far. The final stripes orientation is independent on the initial condition. To test the dependence of the pattern orientation with the initial condition, experiments and simulations were performed in systems with variable growth velocities. The results evidence that the final configuration is independent on the initial pattern [40].

Similar effects have been observed in other systems and numerical models, which suggest that this effect is independent on the mechanism responsible of the symmetry breaking and the formation of the pattern [43,44]. Whether the responsible for the symmetry breaking is the Turing or some other mechanism, the orientation of patterns depending on the growth velocity appears to be very general.

To check these predictions, we propose experiments in fish embryo, where the nutrients or external temperature can control the velocity of the melanophores during early days of pigmentation. The final pattern in the skin may be influenced by the external parameter, in the same fashion as the velocity of the boundary influences the stripes in the reaction–diffusion system.

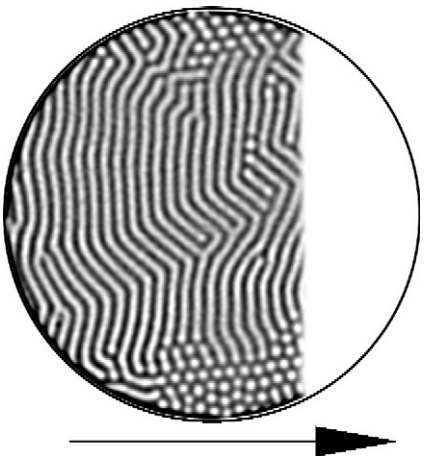

Fig. 6. Snapshot of the pattern oriented in perpendicular configuration. $V=1.05\pm0.1$ mm/h. The arrow indicates the direction of the movement of the boundary.

6. Conclusions

In this paper, we have focused on the orientation of the stripes in the skin of tropical fishes. Based on experimental observations of how the pigmentation occurs, we schematized the process and proposed a simplified model. The experimental system used develops spontaneously stripes that are allowed to grow in one direction. The effect of the ecology is introduced by varying the growth velocity. The three possible orientations observed in the chemical system correspond with the configurations observed in the skin of the majority of tropical fishes. These results suggest an important role of the growth velocity in the early stages of development for the formation of cellular structures, and open the possibility of future experiments where the growth velocity can be varied, controlling the shape of the tissue during embryogenesis.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.bpc.2006.06.014.

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