The interplay between phenotypic and ontogenetic plasticities can be assessed using reaction-diffusion models

The case of *Pseudoplatystoma* fishes

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Abstract Every morphological, behavioral, or even developmental character expression of living beings is coded in its genotype and is expressed in its phenotype. Nevertheless, the interplay between phenotypic and ontogenetic plasticities, that is, the capability to manifest trait variations, is a current field of research that needs morphometric, numerical, or even mathematical modeling investigations. In the present work, we are searching for a phenotypic index able to identify the underlying correlation among phenotypic, ontogenetic, and geographic distribution of the evolutionary development of species of the same genus. By studying the case of *Pseudoplatystoma* fishes, we use their skin patterns as an auxiliary trait that can be reproduced by means of a reaction diffusion (RD) model. From this model, we infer the phenotypic index in terms of one of the parameters appearing in the mathematical equations. To achieve this objective, we perform extensive numerical simulations and analysis of the model equations and link the parameter variations with different environmental

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and physicochemical conditions in which the individuals develop, and which may be regulated by the ontogenetic plasticity of the species. Our numerical study indicates that the patterns predicted by a set of reaction diffusion equations are not uniquely determined by the value of the parameters of the equation, but also depend on how the process is initiated and on the spatial distribution of values of these parameters. These factors are therefore significant, since they show that an individual's growth dynamics and apparent secondary transport processes, like advection, can be determinant for the alignment of motifs in a skin pattern. Our results allow us to discern the correlation between phenotypic, ontogenetic, and geographic distribution of the different species of *Pseudoplatystoma* fishes, thus indicating that RD models represent a useful taxonomic tool able to quantify evolutionary indexes.

Keywords Reaction-diffusion · *Pseudoplatystoma* fish · Skin pattern

1 Introduction

Multiple expressions of evidenced traits represent the expression of heritable genetic variation among individuals within each species and also represent adaptive evolution by natural selection [1].

Phenotypic changes induced by the environment together with ontogenetic plasticity have been recognized as important strategies by which organisms maximize fitness in environments with time and spatial variations [2, 3]. Thus, assessing the degree to which organisms may respond to environmental heterogeneity with *ontogenetic and phenotypic plasticity* is useful in examining ecologic and evolutionary models that cope with geographic distribution of biodiversity of several species.

Because phenotypic traits may vary in terms of phenotypic plasticity and ontogenetic drift [3], it is convenient to have a theoretical framework, criterion, or strategy that may allow researchers to evaluate in which cases, and in which degree, the interplay between these two types of trait plasticities are responsible for species differentiation. This criterion can, in principle, be formulated in terms of a phenotypic index based on morphological traits [4].

In this work, we adopt a viewpoint coming from systems theory [5, 6] in the sense that we will propose a transdisciplinary approach based on an abstract modeling of the phenomena. In particular, we propose that a phenotypic index can be inferred to assess the interplay between the phenotypic plasticity and the so-called ontogenetic plasticity. This inference emerges from the fact that mathematical models that are able to reproduce the variation of a trait depend on the values of one or several parameters of the corresponding model equations. These parameters may be used as a quantitative phenotypic index that may be correlated with the geographical distribution of several species.

With the aim to illustrate this general viewpoint of the question, we have selected the case of Teleostei fishes because they exhibit a great diversity of pigmentation patterns that characterize the eight recognized species [7]. More interestingly, some of these species are distributed in different rivers of South America and some of them have sympatric distributions [7]. The differences between species have been defined by means of its body shape, skeletal anatomy, vertebral numbers and, of fundamental importance for the present work, through the auxiliary trait associated to their pigmented skin patterns.

The inference of phenotypic expressions of the pigmented patterns in the *Pseudoplatystoma* fishes by means of mathematical and computational modeling can be done on the basis of a model that is able to reproduce the characteristic patterns observed in the skin of Teleostei fishes. This can be done by using a reaction–diffusion (RD) mechanism.

Historically, the work by Kondo and Asai was the first suggesting that a RD mechanism of the Turing-type could explain the formation of skin patterns [8]. The mechanism proposed by these authors supposes that the patterns emerged as a consequence of a cellular differentiation between regions of preponderance of one or other chromatophore at the skin cells [9, 10], and that transport and fixation processes should take place before the manifestation of the pattern [9, 11, 12]. The existence of biological patterns has been confirmed by numerical solution of the RD equations by many authors, see for instance Refs. [13–18].

Of particular interest for our work is the so-called BVAM reaction–diffusion model that has been used to reproduce essentially four types of motifs appearing in fishes [19]. These basic pattern motifs can be obtained by variation of a single parameter of the reaction terms in the set of equations, see Fig. 1. In this reference, it was first suggested the possibility that this parameter can be related to the patterns in *Pseudoplatystoma* fishes. This fact suggests that this parameter can, in principle, be considered as the phenotypic plasticity index we previously mentioned. However, in order to reproduce and track down the ontogenetic origin of the traits of the eight existing species of *Pseudoplatystoma* fishes, it is necessary to consider several other aspects that are not included in the reaction model. For simplicity sake, these factors can be introduced through: (1) the variation of initial conditions, (2) non-homogeneous transport coefficients, and (3) non-homogeneous kinetic coefficients. It is convenient to mention that other choices have been proposed in the literature like, for instance, anisotropic reaction–diffusion parameters [20–23], growing domain [14, 24, 25] curvature effects [26–28], sources [29] and noise [30, 31].

Thus, our proposal goes beyond the usual approach and scope of obtaining patterns from a given set of parameters of a RD model with standard initial and boundary conditions (see for example, Refs. [32–36]). Instead, we are searching for phenotypic indexes able to track

Fig. 1 Top: Some species of *Pseudoplatystoma* Bleeker catfish. From top to bottom. Left: *P. reticulatum* and *P. fasciatum*. Right: *P. tigrinum* and *P. corruscans*. Bottom: Several patterns predicted by the BVAM model after increasing the parameter δ in (1a) and (1b): A) $\delta_1 = 0.0$, B) $\delta_2 = 0.6$ C) $\delta_3 = 0.71$ D) $\delta_4 = 0.72$. The other parameters are $\epsilon = 0.65$, $\zeta = 0.165$, $\gamma = -2.5$, $D_0 = 0.344$ and $\eta = 0.15$. The domain is a square of size $L = 80$ with periodic boundary conditions

down the underlying correlation of phenotypic, ontogenetic, and geographic distribution of the evolutive development of several species having similar traits.

The article is organized as follows: In Section 2, we present the BVAM model and the basic patterns that can be derived from it using standard boundary and initial conditions. In Section 3, we introduce different boundary and initial conditions for a reaction scheme, with the same configuration of the space of parameters, in order to show how the original patterns become modified by these different external conditions. Furthermore, we will explore the effect of advection on the patterns and the spatial dependence of the kinetic parameters of the reaction in the BVAM model. In Section 3.6 we will compare the patterns obtained in the previous section with those of the *Pseudoplatystoma* fishes. Finally, in the last section we will present the relation of the reaction diffusion patterns with the phenotypic index.

2 Using a reaction diffusion model to quantify the phenotypic index

The first step towards the determination and quantification of a phenotypic index by using a mathematical model is the detailed evaluation of the capabilities of the latter in order to reproduce the traits of interest. These capabilities are related, in the case of reaction–diffusion models, with the value and spatio-temporal dependence of the coefficients entering the set of mathematical equations and, also, with initial and boundary conditions. Once one understands how the variations in the expression of the trait of interest can be reproduced by the model, then it is possible to infer which coefficient can be used as a phenotypic index, and which conditions (spatial dependence of the coefficients and initial and boundary conditions) may reflect possible developmental and growth variations that participate in the expression of the trait, that is, how they characterize the ontogenetic plasticity of the species.

Thus, before proceeding with the detailed analysis, it is convenient to stress that the following numerical study was not done with the exclusive aim to find new patterns (effects) by introducing complications to the mathematical model. On the contrary and although our determination of novel combinations of patterns that reproduce new skin-pattern traits of the *Pseudoplatystoma* fishes is a completely original contribution, our attention is on tracking down the aspects relying the species differentiation and its correlation with their geographical distribution.

In order to achieve our objective, it is convenient to introduce the basic model we will analyze, that is, the so-called the BVAM reaction–diffusion model. This type of RD model can be introduced, in general, by considering that the interactions among morphogens within living organisms may be conceptualized as coupled processes involving chemical reactions and unequal diffusion [37]. Therefore, RD models of the Turing-type seem to be the appropriate quantitative tools for reproducing the spatial distribution of these morphogens previous to their manifestation as a given pattern on the skin of organisms. Since the BVAM model has shown its utility in this context, we will use it as a reference in our analysis. Near the equilibrium concentration of both morphogens u and v , the BVAM model assumes that the interaction between them can be described as a third order reaction and that both morphogens have unequal diffusion coefficients. The resulting RD model has the following dimensionless form [19]:

$$\frac{\partial u}{\partial t} = D\nabla^2 u + \eta(u + \alpha v - \delta uv - uv^2), \quad (1a)$$

$$\frac{\partial v}{\partial t} = \nabla^2 v + \eta(\beta v + \gamma u + \delta uv + uv^2). \quad (1b)$$

In writing (1a) and (1b), we have normalized the spatial scale with the characteristic length, L , of the domain. Time was normalized with a combination of the diffusion coefficient of the morphogen v and the spatial scale, L^2/D_v , [19]. Thus, $D = D_u/D_v$ is the ratio of the diffusion coefficients associated with both morphogens, and η provides the characteristic spatio-temporal scale of the pattern formation process. The coefficients α , β , δ and γ are adjustable parameters which determine the appearance and form of the patterns. The idea of using a third-order reaction scheme is that it has three different fixed points and, as a consequence of this, it provides a large variety of patterns. These fixed points are the origin, $(u_0, v_0) = (0, 0)$, and $(u_0, v_0) = (-\zeta, 1)w_{\pm}$. Here, $w_{\pm}$ is given by

$$w_{\pm} = \frac{-\delta \pm \sqrt{\delta^2 + 4\epsilon}}{2}, \quad (2)$$

where, ϵ and ζ were defined by $\epsilon = \beta/\zeta - \gamma$ and $\zeta = (\alpha + \beta)/(1 + \gamma)$. A detailed study on the predictions of this model is given in Ref. [38]: The main conclusion is that the model produces different patterns, ranging from spots to strips, by changing the single parameter δ , see Fig. 1. If we take into account that the variability of the phenotypic expression in fishes reflects different trends in its evolutionary processes [39], then as we will see, it is possible to find a link between the value of this coefficient and the differentiation of species of catfishes [7, 40].

Several numerical studies have confirmed the great variety of stationary and transient patterns that can be obtained from the BVAM scheme when used with conventional conditions. This means the use of a closed non-growing domain with random initial concentrations near their equilibrium values [19, 24]. The broad use of these conditions in previous works aims to emphasize the fact that the RD mechanism can produce patterns from practically homogeneous systems, that is, it represents a mathematical test of the robustness of the predictions of RD models of the Turing-type. As previously mentioned and shown in Fig. 2, our analysis contributes to these studies by considering a wider range of the parameters D , η , and δ in the numerical solutions of (1a) and (1b), as well as other modifications that will be discussed later. As expected, we obtained dots, stripes, and reticulated patterns for the BVAM model. However, as we have corroborated by comparing Fig. 2 with Fig. 1, the alignment of stripes and the existence of multiple motifs appearing in the patterns of the *Pseudoplatystoma* fishes cannot be reproduced by only using conventional conditions. Other ingredients are necessary. The following section deals with possible changes that can explain these particular features.

3 Phenotypic versus ontogenetic plasticities: External factors producing complex patterns

The present section is devoted to analyzing the effect that a change on some external conditions may have on the motifs and patterns predicted by the BVAM model. The biological interpretation of the results will be given in following sections.

We start by considering the parameters leading to the basic patterns obtained previously and shown in Figs. 1 and 2. We then introduce the following variations to the conventional conditions already stated: (1) different initial conditions, (2) non-homogeneous kinetic coefficients, and (3) the introduction of advection. These variations correspond to different developmental and growth conditions and therefore may be related to the ontogenetic plasticity of each species.

Fig. 2 Patterns (not necessarily stationary) of the BVAM model in a square domain of size $L = 80$, after a time of $T = 750$. Initial conditions are given by both concentrations near the equilibrium value $(0, 0)$, with a random addition of maximum amplitude 0.05. Furthermore, we use zero flux boundary conditions at the four boundaries. The values of the parameters ϵ , ζ and γ are given in the caption of Fig. 1. The values taken for the set of parameters (D, δ, η) are given in the [Online Supplementary Material](#)

3.1 The effect of initial conditions

The influence of initial conditions on the patterns predicted by the BVAM model is shown in Fig. 3. Each row labeled with capital letters tracks the temporal evolution of the pattern after starting with different initial conditions (left) until the stationary state (right). All computations were done by maintaining constant the size of the domain, the boundary conditions (Neumann, zero flux), and the whole set of parameters.

The results shown in rows Fig. 3a and b were obtained by using conventional random initial conditions in the whole domain but with different intensity (case a has the lower intensity). The results show that the formation of dots and the shortening of stripes is a consequence of using a closed domain since the total initial concentration of both morphogens can affect the resulting pattern. Therefore, a pattern could depend strongly on the

Fig. 3 Different patterns obtained varying only the initial conditions. The *left column* shows the initial condition; the *middle columns* show three intermediate states, and on the *right* the stationary pattern obtained after a time T , given in each case by: **a)** 875 **b)** 875 **c)** 5000 **d)** 875 **e)** 5000, **f)** 4000, **g)** 500. The domain is also a square of side 80 and the reaction parameters were the same as Fig. 1b for all cases. The details of the simulations are given in the [Online Supplementary Material](#)

aleatory amount of morphogens present in the initial conditions. A biological perspective on this result suggests that the organization achieved by a Turing mechanism from practically homogeneous systems can require, in turn, a previous chemical mechanism which provides the precise concentration of both morphogens.

For the results shown in rows Fig. 3c and d, we set the initial condition with a stripe in the left side of the domain. The former has a constant concentration whereas the latter an stochastic distribution of intensities. In row c, the propagation wave is more organized than in row d. This result emphasizes the relation between the organization of a pattern in a closed and finite domain (such as the skin of any animal) with the initial disposition of morphogens. An initial condition can anticipate the organization of a pattern, which, in other case, would be a disordered pattern.

In rows Fig. 3e and f we have tested the relation between the amount of stripes in a pre-pattern (shown in the upper part of each figure) and the size of the domain. When the number of stripes in the initial condition coincides with an specific number of stripes (related to the size of the domain) as in row e, the resulting pattern becomes organized. In any other case, the vertical lines become disorganized, like in row f. These results suggest that the presence of aligned stripes in a system can be achieved in a more efficient way as the result of a specific coupling between a basically one-dimensional pre-pattern and a subsequent process of dispersion along the entire domain. As the former process can be attained in a robust way by a RD process [32, 41, 42], this result also suggests that the alignment of motifs can require a chemical pre-pattern along a one-dimensional domain, for example, of a process occurring at the neural crest, see Ref. [43] and Fig. 4.

Finally, in row Fig. 3g we show that an initial pre-pattern of morphogens helps the formation of an organized pattern of vertical stripes. We tested several initial conditions with different number of stripes (not shown). We have found that if the number of initial oscillations differs from an specific number (four, in our case), the way the stripes fade is very different, that is, the final pattern do not has any preferential orientation since it becomes very similar to that of Fig. 3d. Only for a given number of spatial oscillations the stripes remain vertical. This example confirms the idea that the occurrence of an aligned pattern, just as the occurrence of defects in the stripes, can result from a combination of a pre-pattern which anticipates a fixed number of initial spatial oscillations and a reaction–diffusion mechanism.

Fig. 4 Stages of larval development. It is up to the ninth day that the pigmentation starts to be noticed, mainly in the head [44]

The results of this section allow us to conclude that: (1) Neumann boundary conditions tend to align the patterns with the edges; (2) The initial forms of the pattern may propagate as a perturbation and stay or fade depending upon the total initial concentrations of the morphogens; finally, (3) for some closed systems as the fish skin, it seems that only specific initial conditions of the morphogens related to a robust one-dimensional chemical pre-pattern can yield specific orientations of the stripes, like those observed in *Pseudoplatystoma* fishes. The last two results suggest that a previous chemical mechanism may be necessary to establish the specific conditions for the RD mechanism operating in each species. In this form, the development of a complex organ, like the skin, would occur as a series of stages that involve different time scales and activation/deactivation sub-processes, that is, they are an ontogenetic drifted process.

It is convenient to mention that we have also studied the effect of non-conventional boundary conditions on the formation of different patterns. Our results (not shown) indicate that they have not important influence on the formation of the patterns.

3.2 The effect of space-dependent coefficients

As can be noticed in Fig. 1, the motifs in the skin of catfishes can (1) change its size as function of the position in the skin, and (2) have two types of motifs in different zones of the fish body. In view of these factors, our aim in the present section is to propose combinations of the basic patterns of the BVAM model, which are shown in the bottom panel of Fig. 1, in order to reproduce the complex patterns appearing in the *Pseudoplatystoma* fishes, shown in the top panel of Fig. 1. In order to make such changes, we use previous results that highlight the fact that variation of the coefficients η and δ yields to substantial changes in the motifs of the patterns predicted by the BVAM model. Hence, in order to achieve the complex patterns of the *Pseudoplatystoma*, in this section we will assume that these coefficients may have a spatial dependence. It is worth stressing that we are not considering the spatial dependence of the diffusion coefficients since it has been studied previously in Ref. [21, 45]. As can be expected, anisotropic diffusion can generate orientated patterns in any direction dictated by the diffusive matrix of coefficients [20, 21, 46, 47]. In the present work, we want to stress the role of the spatial dependence of parameters on the production of combinations of motifs because it is related with the grow and development of the individuals and, therefore, emphasizes how ontogenetic plasticity impacts on the phenotypic plasticity of the species.

3.3 The spatial variation of η

The dependence of η on position can be proposed after considering that it provides a spatio temporal scale proportional to L^2/t , in such a way that if the size of the domain L is fixed, increasing η represents a decrease in the size of the pattern shape and an increase in the reaction rate [48]. Therefore, spatial dependence in this parameter can be viewed as changes in the size of the domain.

The results of our numerical computations when δ is constant and η increases linearly according to

$$\eta(y) = 0.15 + (0.40 - 0.15)\frac{y}{L}, \quad (3)$$

are summarized in the first row of Fig. 5. This election for the linear variation of η between the values 0.15 and 0.40 was chosen by trial and failure. Here, Fig. 5a corresponds to the

case in which $\delta = 0.0$, Fig. 5b corresponds to $\delta = 0.6$ and Fig. 5c corresponds to $\delta = 0.72$. These results are therefore modifications of their corresponding Fig. 1a, b, and d.

As was expected, the increase of η decreases the size of the different motifs. Therefore, we can conclude that the decrease of the size of the spot and stripes near the fish tail in most of the *Pseudoplatystoma* fishes is probably related to the diminution of area available in that region, see Fig. 1.

3.4 The spatial variation of δ

The spatial variation of δ is proposed after considering the four different patterns that arise with the BVAM model when different constant values of this parameter are imposed [19]. Those patterns are: (1) reticulated, (2) stripes, (3) dots and stripes, and (4) disordered dots. These motifs are obtained for specific values of δ that we have labeled by: δ_1 , δ_2 , δ_3 , δ_4 in the caption of Fig. 1. Hence, the idea is to propose position-dependent functions that interpolate these four values within the domain under consideration in order to reproduce the existence of different motifs in the *Pseudoplatystoma*. The hypothesis behind these local changes is that the formation of the skin pattern can be related with other structures of the body of the fish and therefore it better manifests how the ontogenetic plasticity influences the phenotypic plasticity. The results presented below were obtained by considering $\eta = 0.15$. Figure 5 summarizes several combinations of functional dependencies in δ and only the most relevant results are shown.

It is worth mentioning that the functional dependencies used for δ , which are explained in detail in the [Online Supplementary Material](#), have the objective of mimicking the disposition of patterns in the skin of each species of *Pseudoplatystoma* fishes. However, as we will discuss later, this search does not constitute an ad hoc method for predicting *biological patterns*, but a method for finding biological correlations between the species. This means that our purpose is not to reveal the exact mechanism giving place to the patterns, since this can be achieved only when the respective morphogens are directly measured in experiments. Our purpose here is to use the RD model in order to describe a specific palette of patterns of the eight species that allow to visualize biological connections about the species differentiation within the genus Teleostei.

The results given in Fig. 5 show that the spatial variation of the kinetic parameters increases the palette of motifs that can be obtained in the same pattern. Two important conclusions can be obtained from these numerical experiments. First, the existence of a constant gradient of the parameter δ turns the spots into stripes, and reticulated patterns into a pattern of stripes (Fig. 5g-i). In contrast, abrupt changes of the value of δ in different regions of the domain has the general result of subdividing the pattern in each region (Fig. 4j-l). This is an important result because it suggests that the difference of the pattern motifs in ventral and dorsal areas of the fishes have to be related with other sub-processes which differentiate both areas, and not just with the different light adsorption of both regions. Secondly, our numerical experiments show that the patterns obtained by introducing spatial non-homogeneities of the parameter δ present a weak vertical and horizontal preferential orientations when compared, for instance, with the results obtained after varying the initial conditions, see Fig. 3. In the next section, we will consider another possibility for obtaining a more robust mechanism of preferential orientation in a pattern.

Fig. 5 Patterns with spatial dependence in the parameters η and δ . The other parameters are the same as in Fig. 1. The details of the simulations are given in the [Online Supplementary Material](#). See text for biological details

3.5 The effect of advection

It has been reported that the pigmentation in *Pseudoplatystoma* fishes begins around the head of the fish at the ninth day and then evolves until some pattern is clearly defined along the body at the tenth day [44], see Fig. 4. The initial peculiar pattern of post-larvae is kept for two and a half months until it takes its final form [40]. Those patterns serve to camouflage the fish in sites where the vegetation provides ideal sites for concealment [44]. The fact that the coloration appears first in the head and then is dispersed along the entire skin, forming almost aligned stripes in most of these fishes, suggests the possibility of an underlying transport process besides the reaction diffusion interaction [49].

In this section, we explore the possibility that this underlying mechanism can be modeled in terms of advection along the fish skin. We hypothesize that a traveling chemical wave (given by the RD mechanism) originates the disordered motifs of the pattern and then, the advection mechanism aligns the pattern in specific directions. From a biological point of view, the RD-advection mechanism has the advantage that it does not have to recourse to the regularity of the boundaries, regularity that is not observed in most living organisms [46]. A second advantage is that this mechanism can be related to other possible sub-processes in the skin of the fish, for example, growing and development, which is directed from the neural crest [36, 50, 51].

Consequently, we add to (1a) and (1b) an advective term proportional to the volumetric velocity $\mathbf{z}$, obtaining the following RD-advection equations [47, 52]

$$\frac{\partial u}{\partial t} + \mathbf{z} \cdot \nabla u = D \nabla^2 u + \eta(u + \alpha v - \delta uv - uv^2), \quad (4a)$$

$$\frac{\partial v}{\partial t} + \mathbf{z} \cdot \nabla v = \nabla^2 v + \eta(\beta v + \gamma u + \delta uv + uv^2). \quad (4b)$$

Since the patterns shown by the fishes have mostly a vertical orientation, we will assume that the advective flow is of the form $\mathbf{z} = z \hat{e}_y$, with z a constant volumetric velocity for both morphogens and $\hat{e}_y$ the unitary vector in the vertical direction.

In Fig. 6 we show the corresponding predictions of the advective BVAM model with constant parameters. Each row corresponds to the parameters of the BVAM model corresponding to the cases a, b, c, and d of Fig. 1. As is expected, the original patterns tend to align along the direction in which advection takes place. Finally, at the end of the lines, some dots are present (as long as they are present in the set of parameters chosen). From these experiments, it follows that advection along the vertical direction introduces the desired orientation of the patterns and also a set of combinations of dots and stripes that agree very well with those appearing in *Pseudoplatystoma* fishes.

3.6 Summary of results and comparison with patterns observed in *Pseudoplatystoma* fishes

Pseudoplatystoma fishes represent a monophyletic fishes group distributed in South American rivers. The eight recognized species exhibit about six geographic distributions, some of them sympatric [7]. The differences between species are manifested through the interplay between the ontogenetic drift and the phenotypical traits like its body shape, skeletal anatomy, vertebral numbers, and of course its color and pigmented patterns in their skin [40]. In this form, as we have previously mentioned the resemblance of the observed patterns by means of a RD model that allows us to infer the existence of a quantitative phenotypic index characterizing not only the differences of patterns among species but also the

Fig. 6 Results obtained with the same four set of parameters of Fig. 1, but with the effect of advection in the vertical direction. For these simulations, we used $\mathbf{z} = 0.02\hat{e}_y$ in (4a). At the beginning (left column), the pattern resembles the reaction diffusion pattern of Fig. 1, but as time goes, the advection aligns the forms (right column). The simulations use zero flux boundaries conditions at the top and bottom boundaries, and periodic boundary conditions at both vertical sides

close interrelation between the ontogenetic and phenotypic plasticities without avoiding the geographical distribution of the species.

The qualitative comparison of the patterns observed in *Pseudoplatystoma* fishes (indicated with capital letters) with the most similar patterns obtained from our numerical computations (indicated with lowercase letters) are shown in Fig. 7, which summarizes some possible causes in the heterogeneity of patterns between the various species of *Pseudoplatystoma*.

The patterns obtained from our the numerical simulations depend upon different combinations of the factors shown below:

- **Figure 7a; *P. metaense*.** Patterns consisting of stripes and dots are obtained assuming a spatial dependence on δ , see Fig. 5e. A similar pattern occurs for the *P. fasciatum* (not shown).
- **Figure 7b; *P. corruscans*.** The pattern shown by this fish presents semicircular spots horizontally staggered, with some elongated spots on the top. A similar pattern was obtained with a combination of the parameters of Fig. 1d, but with an horizontal dependence in the parameters to give regularity in the horizontal direction.

Fig. 7 Comparison between the pattern in the skin of the *Pseudoplatystomafishes* (capital letters) and some of the patterns derived from numerical simulation of the BVAM model (lowercase letters). See text for details. The order of the species is *P. metaense*, *corruscans*, *orinocoense*, *reticulatum*, *tigrinum* and *P. magdaleniatum*, respectively

- **Figure 7c; *P. orinocoense*.** The pattern consist of aligned stripes with disperse dots at the bottom is reproduced by the RD-advection model, see Fig. 6c and d. A similar pattern occurs for the *P. punctifer* but with a larger separation between stripes and dots (not shown).
- **Figure 7d; *P. reticulatum*.** The reticulated motif at the top that switches to vertical lines at the bottom can be reproduced in two ways. One by assuming a vertical dependence in parameter δ , see Fig. 5n, and with a combination of a spot pattern with advection, as in Fig. 6a.
- **Figure 7e; *P. tigrinum*.** In this case, the pattern includes interlaced vertical lines and dots, and can be reproduced using initial conditions as in Fig. 3e.
- **Figure 7f; *P. magdaleniatum*.** The vertical lines of this pattern can be achieved with a horizontal pre-pattern such as that of Fig. 3g.

Our numerical experiments provide remarkably new insights about some possible causes of the heterogeneity of complex patterns on fishes that permit us to draw the following hypotheses: (1) An aligned pattern on the skin could be achieved in a robust way by a two-stage process. The first stage involves the production of a one-dimensional pattern. The advantage of this separation is that the one-dimensional pattern is a robust mechanism, see Fig. 3e and f. (2) The appearance of a specific motif in a pattern depends not only in the initial distribution of morphogens but upon the specific amount of them at the beginning of the process. Therefore, it is possible that a previous mechanism could control the specific

amount of morphogens for a specie or an individual, see Fig. 3a and b. (3) Since the appearance of patterns in many fishes changes notably along the anteroposterior axis, it is possible to relate these changes with an abrupt spatial change in the kinetic parameters of the RD scheme. This change could be related with the different light adsorption in dorsal and ventral sides of the fish, see Fig. 5g–l. (4) Another possibility for the alignment of stripes in a pattern is the inclusion of advection. This mechanism align stripes and preserves some dots, see Fig. 6c and d, and can be related to grow and development.

All these mechanisms can be interpreted in terms of the ontogenetic plasticity we have mentioned before, and that it is associated with the growth and development of the individuals. However, they also show that the ontogenetic factors determining the expression of some traits may be externally regulated by the presence of chemical and even photonic interactions depending on the environment in which the eight species of *Pseudoplatystoma* fishes live. Therefore, our results provide good quantitative evidence that the degree of interplay between the ontogenetic and phenotypical plasticities depends on the biological and physicochemical conditions of the environment, and that this degree of coupling is responsible for the trait differences (the phenotypic expression) observed.

4 Discussion and conclusions: Phenotypic index and geographic distribution

Notwithstanding the simplicity of reaction diffusion models, when they are applied to elucidate certain characteristics of particular species, it is possible to outline some deeper conclusions related with the variability of the phenotypic expression. In addition, this information allows one to correlate different trends in the evolutionary processes of the studied species with the respective environmental conditions where the species live. In the case of *Pseudoplatystoma* fishes, this information, closely linked to geographic differences, offers a *global* view of the species development and distribution throughout South America's rivers.

In our simulations, we have exploited the fact that the BVAM has a well-differentiated and robust palette of pattern motifs, which are represented in Fig. 1, and that it contains the main motifs of the patterns found in the eight different species of the *Pseudoplatystoma* fishes, see Fig. 8.

As we have already noted, all the patterns of Fig. 8 can be obtained by simply changing the parameter δ that enters in (1a) and (1b) and considering some specific peculiarities of the geographic conditions, environment, and of the growth development reflected in the spatial dependence of the parameter, initial conditions, or through the effect of advection. In this way, we have obtained that the formation of the patterns reproducing the traits of the eight species can all be obtained from the BVAM reaction–diffusion model by using the following characteristic values of the parameter $\delta = 0.72, 0.71, 0.60$, and 0.0 . Using these characteristic values of δ , we have reproduced, respectively, the dotted pattern of the *P. corruscans*; the pattern composed by dots and stripes like those of the *P. metaense*, *orinocoense*, *fasciatum*, *punctifer*, and *tigrinum*; the pattern of the *P. magdaleniatum* composed by stripes; and even a reticulate pattern resembling that of the *P. reticulatum*.

Hence, we propose that the parameter δ can be used as a *phenotypic expression index* (PEI), indicating the differentiation of the species of the genus *Pseudoplatystoma*, that is, the PEI allows, in turn, to classify the species with similar patterns under a single criterion, for instance, $\delta = 0.71$, corresponding to *P. metaense*, *orinocoense*, *fasciatum* and *tigrinum*.

In addition, this PEI also reveals a geographic distribution pattern of the eight species. This important and very interesting statement is corroborated in Fig. 8, which shows how the

Fig. 8 Geographic distribution and sympatric relations among different *Pseudoplatystoma* species and its characterization with the *phenotypic expression index* (PEI), indicated by the numbers. Crossed out circles correspond to type localities for each species. This map was constructed using information of Ref. [7]

index characterizes well the sympatric relations between the *P. tigrinum* and the *P. punctifer* in the Amazon River, and between the *P. metaense* and the *P. orinocoense* in the Orinoco River in the northern region of South America. The strong similarity of the patterns shown by these species opens the possibility of an original evolutionary connection between them along the basin's of these two rivers that was geo-morphologically disrupted with time [7]. Beside this evolutionary hypothesis, the concentration of the five species mentioned in the north of South America suggests that their very similar traits (stripes and dots patterns) can be a consequence of the selective pressure related with the environmental characteristics of each region.

Another aspect that should be considered under the view of this study is that the differences among the patterns of these five species could be associated with morpho-taxonomical studies based on principal component analyses (PCA), see for instance Ref. [7]. This means that the differences in some details of the patterns of these species, associated with the same characteristic value of the parameter δ , can be related as additional phenotypical changes that affect other structures of the fishes. In the case of the *Pseudoplatystoma* fishes, those structures are closely related with the length of the dorsal and anal fins, as well as the lengths of the maxilla and rear whiskers [7]. Thus, the factors considered in our analysis (initial conditions, spatial dependence of the parameters, and advection) offer a clue on the possible environmental factors modifying the differentiation of this subgroup of species, and therefore, of the factors affecting the morphogenesis of the fishes' skin traits.

To conclude, we suggest that the importance of our study in Biology is that it provides a theoretical framework indicating how mathematical and computational modeling can be used to infer *phenotypic expression indexes* which could represent, in a future, a predictive tool able to enhance the comprehension of ontogenetic and even evolutive trends. It could be applied as an ontogenetic and taxonomic tool with the aim of having a more comprehensive understanding of the evolutionary lineages of the *Pseudoplatystoma* fishes, and their geographic distribution [7].

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Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflicts of interest.

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