Evolutionary Ecology Research, 2008, **10**: 1037–1050

Emergent phenotypes: association between morphology and coloration in fish

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ABSTRACT

Hypothesis: Although the morphological and colour traits of an organism are adapted to the environment, they generally do not share common functional roles and are not subjected to the same selective pathways. We hypothesize that an integration of these traits in individuals sampled across a broad gradient of habitats and taxa should be indicative of the existence of emergent phenotypic patterns.

Organisms: 501 standardized photographs of fish species, each belonging to an exclusive genus, were downloaded from *FishBase*.

Field site: 77 geographical locations around the world.

Methods: Morphology and coloration traits were described respectively using nine and seven variables coded with a discrete semi-quantitative scale. Relationships were explored between these two sets of traits to highlight phenotypic patterns. Furthermore, a validation experiment was conducted on two phylogenically independent samples because some phylogenic inertia may drive the association among fish traits.

Results: A multivariate correlation between morphology and coloration of fishes supports the hypothesis of emergent phenotypic patterns characteristic of different habitats. We describe four main phenotypic patterns that correspond to fish species found in the offshore or inshore zones, and in deep or shallow water.

Conclusion: Integration between morphology and coloration can be seen as the consequence of a habitat-mediated convergence of phenotypic traits, at the individual level, and in response to both the physical habitat and the biological community.

Keywords: functional ecology, macroecology, species diversity, trait integration.

INTRODUCTION

It is generally agreed that selection mechanisms act upon the traits of an individual in interaction with its physical environment and biological community. In this context, functional ecology aims to establish links between phenotypic traits and their relative

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function in the environment for which they appear to be adapted (Keddy, 1992; Wainwright and Reilly, 1994), where phenotypic traits are defined as the whole set of variables that one could measure from an individual. Links between phenotypes and their function are generally sought through the use of deductive methods that address the following objectives: (1) to evaluate inter-individual relationships through the analysis of phenotypic distances, (2) to measure the correlation between the hypothetical and the realized niche of different phenotypes, (3) to investigate the adaptive value of functional phenotypes (and indirectly their potential for divergent selection) through the comparison of their reaction norms, and (4) to assess the generality of causal models from an evolutionary perspective. The complex dynamics giving rise to phenotypic integration at the level of the individual organism make these objectives extremely difficult to achieve using a mechanistic approach (Pigliucci, 2003).

For many taxonomic groups, progress in the achievement of these objectives may now require a reversal of the deductive chain, permitting the study of more holistic questions (Naeem, 2002), such as: Are an individual's phenotypic traits well integrated across a broad gradient of habitats and taxonomic levels? Similarly, Goodwin (1994) has argued for a rejection of approaches searching for mechanistic, causal explanations for the presence of single traits. Goodwin views the organism as an 'integrated system that is itself integrated into a greater system, which is habitat' (p. 179). He proposed that both environmental and inherited particulars create the generative field in which an organism develops.

Here we propose that rather than seeking causal or historical explanations for particular phenotypes, seeking to identify phenotypic patterns (i.e. collections of integrated traits) that are characteristic of a particular habitat may be of interest. If such patterns exist, it could be argued that the associated traits have emerged together as a result of a coupling between the developmental and selective forces specific to a given habitat. This coupling serves to restrict the number of patterns that can be realized from a wide range of possibilities to a limited subset of emergent phenotypes (Goodwin *et al.*, 1993; Goodwin, 1994). According to Goodwin's (1994) view, an 'emergent phenotype' can be defined as a stable attractor shaped by both present (e.g. energetic requirements) and past (e.g. phylogenic constraints) life strategies experienced by the organism. This 'emergent phenotype' is the entire collection of traits, which together provide the most robust and stable configuration for the species in a given habitat.

Placing particular traits in the broader context of an emergent phenotypic pattern that is the product of a feedback process between an individual and its past and present environment may be more informative than viewing each trait as being strictly adapted for one specific environment (Proulx, 2007). The emergent phenotype approach may be an alternative when it is difficult to formulate testable hypotheses about phenotypic integration at the individual level under the restrictive view of strict causality between phenotypic traits and their particular function in the environment (Fig. 1). To provide such an estimate of phenotypic integration across a broad gradient of habitats and taxa is what motivated the present study.

Morphological and colour traits are among the most studied variables in fish (Moyle and Cech, 2000). Morphological traits provide insights on feeding and foraging activity, antagonistic and sexual behaviours, trophic position, habitat structure, ecological integrity of a population, and on several other aspects of fish ecology (Wainwright and Reilly, 1994; see also Luczhovitch *et al.*, 2001, in a special issue devoted to fish ecomorphology). Similarly, systems such as Hawaiian

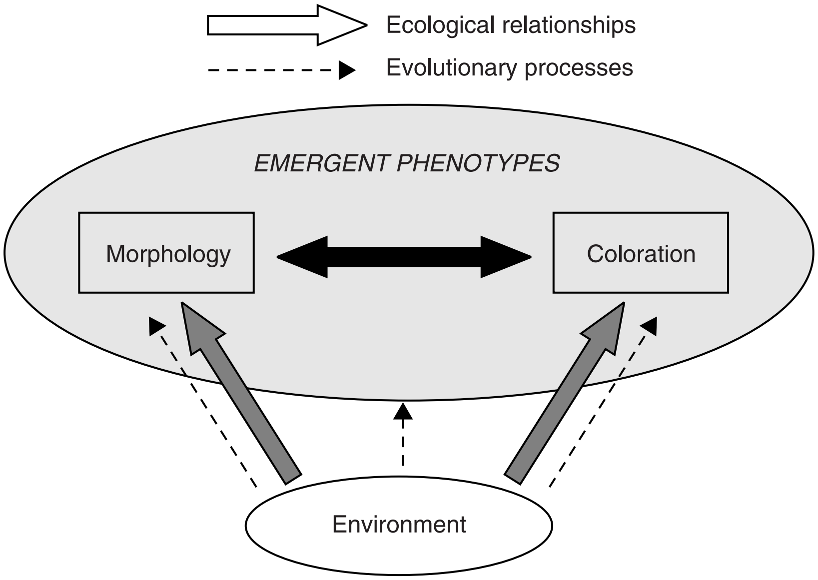


Fig. 1. Conceptual model of the phenotypic integration of morphological and colour traits at the individual level. The classical view in functional ecology is illustrated by a deductive, process-oriented approach that aims to establish direct relationships between phenotypic traits and their relative function in the environment for which they are adapted (grey arrows). Alternatively, the emergent phenotype hypothesis is represented by a holistic approach that aims to identify patterns of integrated traits that are characteristic of a particular environment (black arrow), with no emphasis on the causal relationships *per se*. The emergent phenotype hypothesis claims it may be too hard to test for the relative contribution of all ecological processes that occur between the environment and an individual phenotype (as summarized here by the short dashed arrow). Instead, testing for the multivariate relationship between two sets of phenotypic traits should provide an indirect confirmation that such habitat-mediated integration occurs at the individual level.

coral species (Marshall *et al.*, 2003a, 2003b) and African cichlids (Seehausen *et al.*, 1999) have exemplified the ecological relationships between colour and function in fish communities. Colour patterns are important to fish ecology, notably in sexual selection (Endler, 1983; Kodric-Brown, 1998) and shoaling behaviour (McRobert and Bradner, 1998), but also in thermoregulation, predator avoidance, and inter-individual communications (Fujii, 1993).

While both morphological and colour traits are linked to the environment of an individual (Fig. 1: grey arrows), they generally do not share common functional roles and should not be subjected to the same selective processes in a specific system (Fig. 1: dotted arrows). For example, predation risk might select predominantly for the morphology of a fish while sexual selection might select for its colour traits. We hypothesize that an integration of these traits at the individual level in fish should be indicative of the existence of habitat-mediated emergent phenotypic patterns. More precisely, we predict a direct correlation between morphological traits and colour patterns (Fig. 1: double-headed black arrow). Using semi-quantitative variables, the relationship between morphology and coloration of individuals representing 501 fish species worldwide is investigated.

METHODS

Data acquisition

The study was conducted in an Ichthyology class at the Université du Québec à Rimouski. Twenty-three biology students performed a semi-quantitative characterization of morphological and colour variables from digitized photographs following a short period of training to ensure uniformity in data collection. Images were downloaded freely from www.fishbase.org [an online global information system (Froese and Pauly, 2004)]. Each image was displayed on a computer screen and the investigators identified and recorded values of morphological and colour variables as well as the taxonomic description of each fish (i.e. species, genera, family, and order) and its habitat preference ('environment' in *FishBase* terminology). Based on the adult life stage, the habitat preference of fish was classified as: reef-associated, pelagic or deep-water. To ensure more uniformity, only images from J.E. Randall's collection were considered in further statistical analyses. All fish were adults and were photographed from a lateral view. To maximize the phenotypic gradient, we examined a total of 501 fish, belonging to 501 different species (Table 1). Hereafter, the term 'species' will be used in the text when referring to an individual fish. For a given species, the choice of a particular image was constrained by resolution, contrast, and luminance prerequisites.

Endler (1990) reported that the assessment of colours by different observers can lead to erroneous conclusions because of: (1) the observer's subjectivity in the discrimination of colour categories, (2) the interference of adjacent colours on the target one, (3) variations in

Table 1. Distribution of the 11 orders and 501 species photographed by J.E. Randall

Perciformes (Family)	No. of species[a]	Non-Perciformes (Order)	No. of species[a]
Apogonidae	18	Anguiliforme	20
Blenniidae	31	Beloniforme	9
Carangidae	19	Beryciforme	15
Chaetodontidae	11	Clupeiforme	11
Cirrhitidae	10	Lophiiforme	8
Gobiidae	44	Ophidiiforme	7
Kyphosidae	8	Pleuronectiforme	16
Labridae	41	Scorpaeniforme	35
Lutjanidae	14	Syngnathiforme	19
Mugilidae	9	Tetraodontiforme	45
Pleisiopidae	7	**Total**	**185**
Pomacanthidae	7		
Pomacentridae	21		
Scarridae	9		
Scianidae	10		
Scombridae	8		
Serranidae	36		
Sparidae	13		
Total	**316**		

Note: Photographs were taken between 1966 and 2000 in 77 geographical locations around the world.

[a] Each of the 501 species belongs to a different genus.

luminance conditions among images, and (4) variations in colour perception among the observers. In the present study, precautions were taken to account for the above considerations. Categories were chosen so as to limit the ambiguity of colour assignments (see next section for details). In addition, the final selection was restricted to images with a neutral background (i.e. black or dark grey) and which were obtained from the specifically designed 'Randall's tank' (J.E. Randall, unpublished). While these data may contain unknown variability due to the methodological impediments, we argue that it should only reinforce our conclusions by assuming here the error associated to observers was randomly distributed.

Morphological and colour variables

To describe phenotypic traits, a discrete semi-quantitative scale was used (i.e. a coded narrative scale ranging from zero to three, where zero refers to the absence of the trait). Morphology was described by nine semi-quantitative variables. Coloration was described by six semi-quantitative variables that referred to the prevalence of specific categories of colour on an individual, plus an additional 'colour design' variable that referred to the pattern of coloration (Table 2). Except for the caudal fin aspect and the fusiform shape, the dominance of each morphological variable was estimated relative to the overall fish size as seen on the computer screen. The maximal length of each species was extracted from *FishBase* and used as a proxy for fish size. Except for the assignment of a colour design, the prevalence of each colour variable was estimated relative to the overall colour mosaic of the individual (Table 2). The use of a relatively limited, discrete scale coded from zero to three for each of these variables was intended to reduce the ambiguity of observers' decisions.

Reference values for the colour categories were obtained by taking the median of the non-overlapping wavelength ranges and subsequently converting this value into a hexanumeric web-safe notation: respectively for BLUE (480 nm, #0000FF HEX standard), GREEN (530 nm, #00FF00 HEX standard), YELLOW-ORANGE (580 nm, #FF9900 HEX standard), and RED (630 nm, #FF0000 HEX standard). To any web-safe notation is related a web-safe colour that is linearly dependent on computer screen settings, thus independent of the variation among them. On each computer screen, a web-safe sample of the target colours was permanently visible so as to provide a standardized reference. Before data acquisition, the 23 observers were given an overview of the 16 variables over a diversified set of morphological and colour patterns. The coding scale was designed such that the sum of code values conveys information on the species' complexity in morphology and coloration (e.g. a fish with code values of 3 for all variables has a more complex morphology and coloration design than a fish having code values of 1).

Data transformation and analysis

When data contain several null values, statistical techniques preserving the Euclidian distance between objects are inadequate (Legendre and Legendre, 1998). Nevertheless, it is possible to use Euclidean mathematical techniques such as principal component analysis (PCA) if the raw data are transformed beforehand. One measure recommended for partitioning and ordination analyses of non-Gaussian distributions is the Hellinger distance (Rao, 1995). The first step is to transform the table of raw data using the following operation:

$$y_{ij}^{*} = \sqrt{y_{ij} / y_{i+}} \qquad (1)$$

Table 2. List of morphological and colour semi-quantitative variables estimated from the images of 501 fish species

	Semi-quantitative measures			
Phenotypic traits	0	1	2	3
Morphological variables				
Body length	Continuous quantitative variable (mm)			
Head size	None	Small	Intermediate	Large
Mouth size	None	Small	Intermediate	Large
Eye size	None	Small	Intermediate	Large
Dorsal fin	None	Small	Intermediate	Large
Pectoral fin	None	Small	Intermediate	Large
Pelvic fin	None	Small	Intermediate	Large
Caudal fin	None	Round	Emarginated	Forked
Fusiform shape	*[a]	Round	Ovoid	Fusiform
Colour variables				
White	None	Subtle	Intermediate	Dominant
Black	None	Subtle	Intermediate	Dominant
Blue	None	Subtle	Intermediate	Dominant
Green	None	Subtle	Intermediate	Dominant
Yellow-Orange	None	Subtle	Intermediate	Dominant
Red	None	Subtle	Intermediate	Dominant
Colour design	*[a]	Uniform	Regular	Complex

Note: The size of morphological traits was scored relative to the size aspect of the fish, whereas prevalence of colour traits was scored relative to the number of colours in the overall mosaic. Measures of the caudal fin were estimated according to its level of roundness, while the fusiform shape followed a gradient of slenderness. The colour design followed a gradient of complexity. All variables were standardized before performing the Hellinger transformation.

[a] A score of zero makes no sense for these variables.

where y_{ij} is the value of the phenotypic trait in column j for the species in row i, and y_{i+} is the sum of the j values for the species i. The Hellinger distance is obtained by calculating the Euclidean distance on the transformed values y^*_{ij} (Legendre and Gallagher, 2001). Although this transformation commonly applies to the analysis of frequencies in a community matrix (i.e. sites in rows and species in columns), the method is appropriate for our data. In our case, the sum of the semi-quantitative scores (y_{i+}) provides an indication of the overall species' complexity in morphological and colour traits.

A potential pitfall to our experimental design is that phylogenic dependence may drive the correlation between morphology and coloration. In an attempt to generalize the results and control for phylogenic dependence, we conducted the statistical analyses on two independent samples: the Perciformes and Non-Perciformes species (Table 1). If similar morphology–coloration correlations and phenotypic patterns are found independently in both samples, this would provide additional support to the emergent phenotype hypothesis. While testing for a multivariate correlation between morphology and coloration, phylogenic dependence was controlled by restricting permutations to occur within taxonomic groups – that is, within family and order group for Perciformes and

Non-Perciformes species respectively. Similarly, to determine if the multivariate correlation between morphology and coloration is habitat-mediated, permutations were restricted to occur within combinations of taxonomy and habitat preference – that is, within each taxonomic group in each reef, pelagic, and deep-water *FishBase* category. The presence of a significant correlation when controlling for phylogeny, which vanishes when further controlling for habitat preference, would suggest that phenotypic integration among fish traits is habitat-mediated.

We performed PCAs on Hellinger's transformed data of morphology and coloration separately to extract the phenotypic patterns. We then determined the correlation between morphology (the reference matrix M) and coloration (the transform matrix C) using a Procrustean superimposition approach (Peres-Neto and Jackson, 2001) on the scores of the first three PC axes. This method attempts to find an optimal solution that maximizes the fit between the two matrices through translation, scaling, and rotation transformations of the following form: $C_{\mathbf{optimal}} = \text{scaling}*C*\text{rotation}*\text{translation}$. The multivariate correlation between M and C in their optimal superimposition is tested using sum of square residuals (SSR) and a specific permutation procedure (see Peres-Neto and Jackson, 2001). The pivotal statistic of the test is interpreted similarly to the Pearson's r in a bivariate correlation. Instead of searching for the optimal linear combination of traits in the multivariate space, the Procrustes analysis searches the optimal alignment between two data sets, which minimizes the SSR between morphology and coloration signatures of each species. The approach has been shown to be superior to the Mantel test in assessing the fit between two multivariate data sets (Peres-Neto and Jackson, 2001).

We investigated the relationship among the PCA's loading coefficients (i.e. eigenvectors from the correlation matrix) to distinguish emergent phenotypes among the multiplicity of possible phenotypic patterns. Because loading coefficients obtained separately for morphology and coloration may be arbitrarily rotated in relation to one another, the Procrustes matrices were used to align loading coefficients in the same ordination plane. The alignment was realized by multiplying the rotation matrix with the loading coefficients of the coloration matrix (i.e. loading coefficients of the transform matrix). To distinguish phenotypic patterns that relate to all fish species, we combined the loading coefficients for Perciformes and Non-Perciformes species into one matrix of 16 morphology/colour traits (in rows) and 6 axes of aligned loading coefficients (in columns). Finally, we distinguished the emergent phenotypes by clustering traits in the above matrix through a hierarchical algorithm, using Ward's distance as the fusion criterion. All analyses were conducted under Matlab version 7.0.1 (MathWorks, Natick, USA). The PCA and Procrustes analyses were performed using the FATHOM toolbox (Jones, 2002). All four statistical analyses are summarized in Fig. 2.

RESULTS

The percent variation among morphological traits explained by the first three PC axes was respectively 21, 17, and 13% for Perciformes, and 26, 17, and 13% for Non-Perciformes species. The total percent variation explained by the first three PC axes reached 50% for morphology variables and 60% for coloration traits. The multivariate correlation between morphology and coloration was $r = 0.21$ for Perciformes and $r = 0.23$ for Non-Perciformes species. The two correlations differed significantly from zero at the probability cut-off $\alpha < 0.01$ (using 10,000 restricted permutations based on taxonomy), suggesting that fish

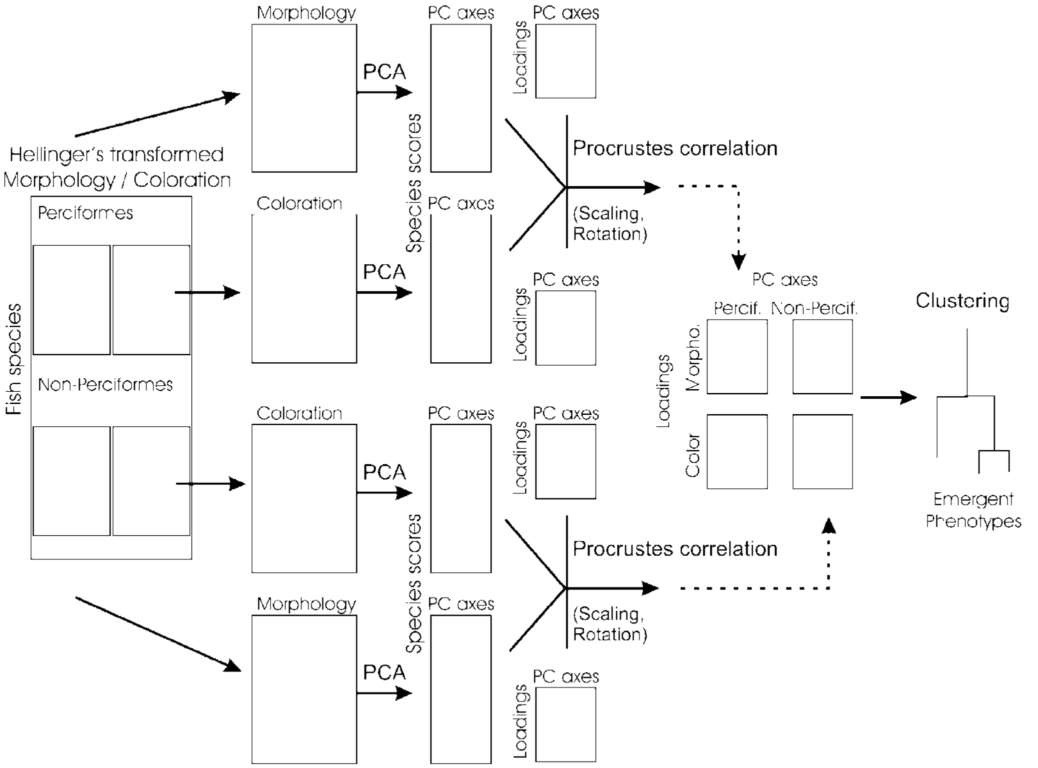
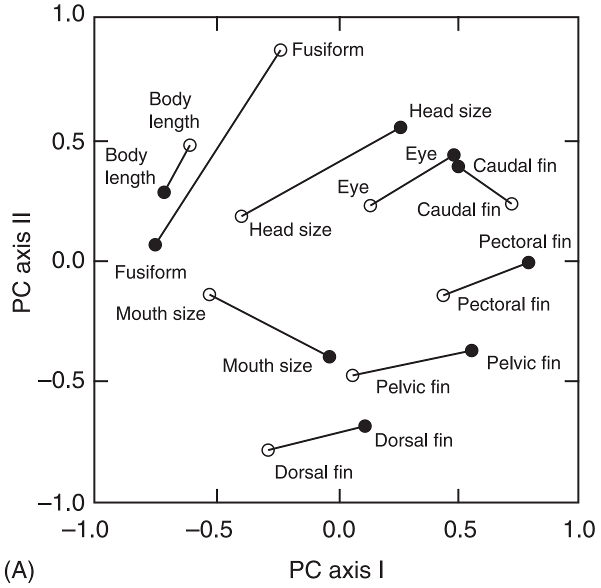


Fig. 2. Schema summarizing the statistical analyses performed to evaluate the correlation between morphology and coloration and to distinguish phenotypic patterns in fishes. (1) Hellinger's transformed morphological and colour traits; (2) the data set is split into two independent samples, Perciformes and Non-Perciformes species; (3) morphology–coloration trait combinations are revealed through PCA ordinations; (4) Procrustes translation, scaling, rotation, and restricted permutation procedures are used to evaluate and test the correlation between morphology and coloration; (5) aligned PC loading coefficients for Perciformes and Non-Perciformes species are merged to distinguish phenotypic patterns that relate to all fish; (6) emergent phenotypes are distinguished by grouping traits in the loading coefficients matrix through a hierarchical cluster algorithm.

phylogeny is not driving the relationship. In contrast, the null hypothesis was retained (i.e. the correlation was not significant) when permutations were restricted to occur within taxonomy–habitat group combinations in Non-Perciformes species ($P = 0.562$), suggesting a habitat-mediated phenotypic integration among fish traits. The correlation remained significant in Perciformes ($P = 0.005$) after controlling for both taxonomy and habitat. The 18 Perciformes families formed 28 taxonomy–habitat categories (each including at least 10 species) when combined with *Fishbase* habitat preference index. The 10 Non-Perciformes orders formed 17 taxonomy–habitat categories (each including at least five species) when combined with the habitat preference index.

The emergent behaviour of the phenotypic patterns revealed through PCA ordination and Procrustes superimposition methods is illustrated in Fig. 3. It reports the original loading coefficients of morphological traits and the rotated loading coefficients of colour traits for both Perciformes and Non-Perciformes species in the same ordination plane



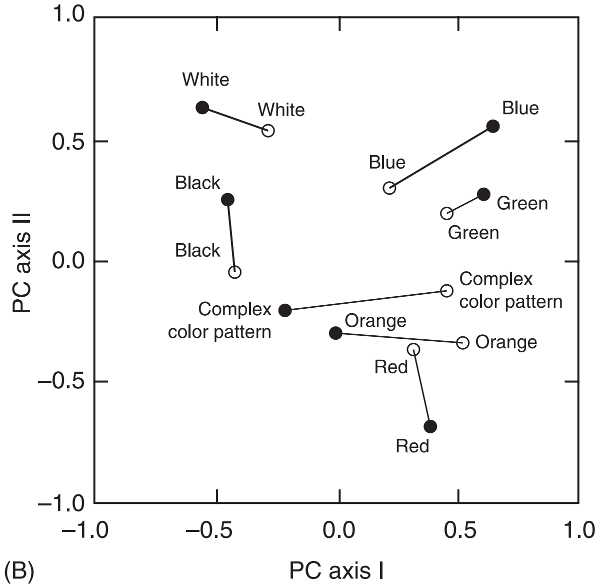


Fig. 3. Congruence between the original loading coefficients of (A) morphological traits and the rotated loading coefficients of (B) colour traits for both Perciformes (solid dots) and Non-Perciformes (open dots) species in the same ordination plane. The loading coefficients for Perciformes and Non-Perciformes species were produced independently and are connected to assist the interpretation.

(PC axes I and II). Although PCA and Procrustes analyses were performed separately and independently on the two species samples, morphological (Fig. 3A) and colour traits (Fig. 3B) cluster in the same regions of the ordination biplot. We note that species-specific

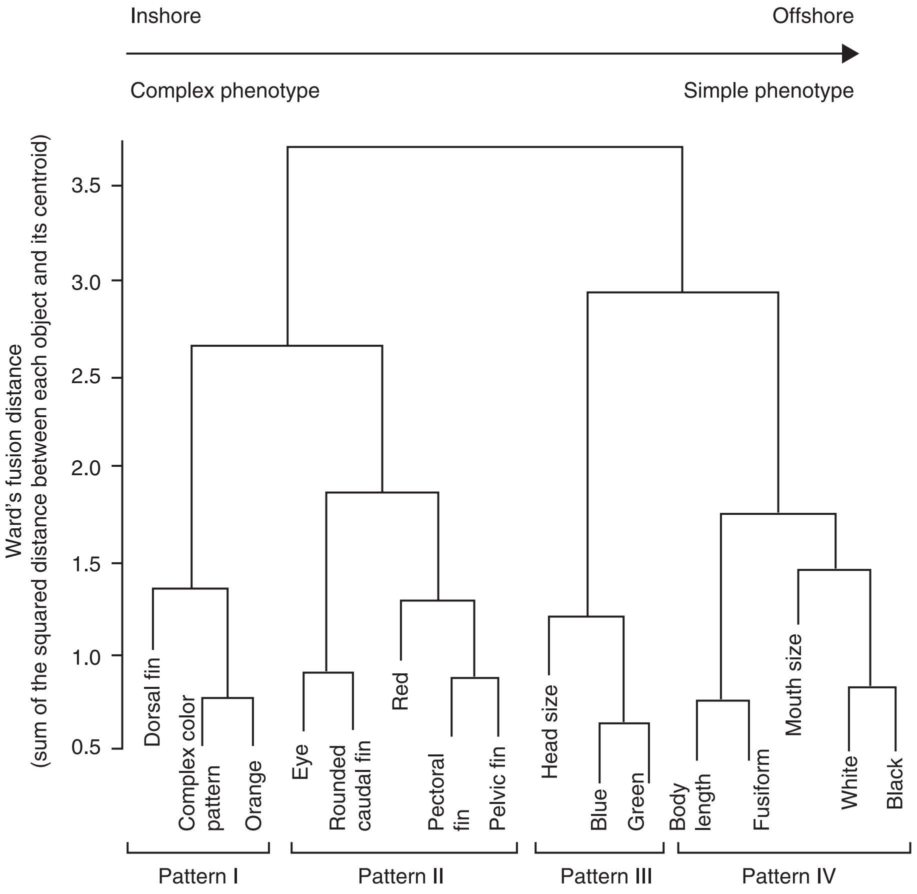


Fig. 4. Four main phenotypic patterns revealed by clustering the loading coefficients of morphology and coloration traits (see Fig. 2). Emergent phenotypic patterns in morphology and coloration describe a horizontal gradient corresponding to species found in the offshore zone and in the inshore zone (I vs. III and II vs. IV). The phenotypic patterns further illustrate a vertical gradient related to species living in deep and in shallow water (I vs. II and III vs. IV). As a general trend, morphology and coloration designs are less complex as we move from Pattern I towards Pattern IV.

scores used to assess the correlation between morphology and coloration can be projected on that plane as well, but are not shown for aesthetic reasons.

Four main phenotypic patterns were highlighted by clustering the loading coefficients of morphology and coloration traits (Fig. 4):

- *Pattern I*: Round-shaped species with a larger dorsal fin. Colour designs are complex and dominated by yellow-orange hues.
- *Pattern II*: Smaller species with longer pelvic or pectoral fins and bigger eyes. Coloration dominated by reddish colours.
- *Pattern III*: Slender species exhibiting smaller pectoral and pelvic fins. Coloration dominated by uniform blue-green colour designs.

- *Pattern IV*: Large species with a forked caudal fin and a larger mouth for their size. Coloration dominated by neutral colours of black and white.

To summarize, the phenotypic patterns in morphology and coloration describe a horizontal gradient corresponding to species found in the offshore zone and in the inshore zone (e.g. Pattern I and IV; Fig. 4). The phenotypic patterns also illustrate a vertical gradient related to species living in deep and in shallow water (e.g. Pattern I and II; Fig. 4). Despite the low information content of species observations due to the simplified data transformation of variables into semi-quantitative codes, the presence of morphology–coloration correlations associated with functional phenotypic patterns suggests that fish traits are somehow tuned to their local habitat along a gradient of complexity.

DISCUSSION

The multivariate correlation among fish traits revealed phenotypic patterns across a broad gradient of species and localities, supporting the hypothesis of emergent phenotypes characteristic of different habitats. More specifically, the analyses distinguished four main phenotypic patterns and the presence of morphology–coloration correlations in two independent samples (i.e. Perciformes and Non-Perciformes species). Fish from different taxonomic categories in the same habitat converge to the same phenotypic patterns. Akin to functional ecology theory, the emergent phenotype hypothesis posits that phenotypic traits are selected under habitat-mediated evolutionary processes. However, rather than interpreting each individual's trait as being strictly adapted to perform a given function, the emergent phenotype hypothesis interprets the whole combination of traits as a natural attractor, or phenotypic manifold. The habitat acts here by restricting the multiplicity of possible phenotypic patterns to a limited set. It is therefore possible under the emergent phenotype hypothesis to predict a correlation between two multivariate sets of traits, such as morphology and correlation. A similar prediction is hard to make when dealing with confounded cause-to-effect functions, which are typically used to link phenotypic traits to habitat descriptors.

Under Goodwin's view of the emergent phenotype, evolutionary processes do not operate on different traits through different selection pathways, but operate on each individual as an integrated whole (Goodwin *et al.*, 1993; Goodwin, 1994). For instance, it is relatively straightforward to correlate a list of phenotypic traits to habitat descriptors, and then to some fitness responses. In most of these cases, the observed phenotypic patterns maximizing the fitness are interpreted retrospectively to identify the mechanisms. By modifying the list of phenotypic traits or habitat descriptors, we also modify our interpretation of the mechanisms. In contrast, by reversing the cause-to-effect deductive chain, assuming right from the start that the fitness in a given habitat is intimately tied up with the phenotype, the integrated combination of traits we observe most frequently is the emergent phenotype. Across a broad gradient of taxonomic groups and habitat types, a correlation is predicted between sets of traits that do not necessarily share common functional roles and thus should not be subjected to the same selection pathways according to functional ecology theory.

Because the emergent phenotype hypothesis forms a complementary top-down approach to the bottom-up approach of functional ecology, it does not aim to identify the mechanisms that generate phenotypic variation (e.g. phylogenetic, phenotypic plasticity). Instead, if a more inclusive framework such as the one defined by the emergent phenotype is confirmed by functional ecology theory, the two views may provide complementary insights on the same evolutionary processes (see Fig. 1).

Linking emergent and functional phenotypes

Pattern I: The morphology of these fish is typical of species adapted to swimming in complex habitats (Webb, 1984). A compact shape, a more developed dorsal fin, and a rounded caudal fin allow rapid and intricate manoeuvres such as turning at severe angles. Anterior structures are often smaller and typical of prey species found in shallow water (e.g. Tetraodontiformes, Perciformes families such as Cheatodontidae and Pomacanthidae). These species also share a complex colour design dominated by yellow-orange, a representative combination of coral reef associates (Marshall *et al.*, 2003a) and cichlids from lentic water (Allender *et al.*, 2003). Complex designs generally fell into two categories described by Moyle and Cech (2000): 'poster colour' and 'disruptive colour' (see also Fujii, 1993). Such colour designs are known to play an important ecological role in predator avoidance and intra- or inter-specific communication.

Pattern II: Deep-water species belonging to this category include very diverse morphotypes adapted to living in poor habitats [low light, oxygen, and energy (Moyle and Cech, 2000)]. Among Beryciformes, for instance, the lantern fishes (Myctophidae) exhibit frontal appendices to delude their prey. Other families pertaining to this group include the Scopaenidae and Platycephalidae (Scorpaeniformes), the Bleniidae and Gobiidae (Perciformes). Common morphological adaptations in these species are the long pectoral and pelvic fins that suggest an affiliation to the marine substrate. The exaggerated eye size is typical of demersal-diurnal and deep benthic-noctural feeders (Pankhurst, 1989). The red prevalence may either serve as a cryptic or camouflage design. Red colours are the only wavelengths to reach great depths (> 630 nm), as the short wavelengths are scattered and absorbed by the chlorophyll contained in algae and coral (Marshall *et al.*, 2003b).

Pattern III: Pelagic species that are not necessarily apex predators are found in this cluster, which represents well-known species, including the needle fish (*Belone* spp.; Beloniformes), shads (*Alose* spp.; Clupeidae), and tunas (*Thunnus* spp.; Perciformes). This group exhibits a common morphology adapted to pelagic swimming and foraging: a slender body shape, smaller dorsal and pectoral fins relative to body size. Marshall *et al.* (2003b) have determined that uniform and bluish colours allow fish to camouflage themselves in the photic zone of the pelagic environment. Uniform colour designs in this group of fish can be characterized according to two categories used by Moyle and Cech (2000): 'countershading' and 'chromatism'. Fish exhibiting a countershading colour design appear darker on the back and lighter on the ventral face to dissimulate it when facing a prey or a predator. Chromatism refers to the shiny, often silvery, coloration common to pelagic fishes. Uniform designs associated with colour reflectance in the short wavelengths give pelagic species a vertical and horizontal camouflage in the water column.

Pattern IV: The morphology of these species is typical of large pelagic predators hunting over large territories. For evident reasons, piscivores attain greater body lengths than their subordinates (Moyle and Cech, 2000). Body length also impacts the scaling of several activities, such as swimming speed, home range size, and energetic requirements (Schmidt-Nielsen, 1997). The absence of colours (or the prevalence of neutral colours such as black and white) suggests an open water life, as colours might not play an essential role in the ecology of these species (e.g. Anguiliformes, Perciformes families such as Carangidae and Lutjanidae).

The emergent phenotype hypothesis proposes a conceptual framework for linking functional and macroecological patterns of phenotypic variation through habitat-mediated processes. The Perciformes species, for instance, which number more than 9200, exhibit well-known examples of morphological and colour polymorphisms (Seehausen *et al.*, 1999). In this study, the 316 Perciformes species alone would support the hypothesis of an integration of phenotypic patterns at the individual level across a broad range of habitats. Correlation between functionally distinct trait combinations reinforces the possibility that phenotypic integration operates at the individual level in nature. It further suggests that different emergent phenotypes can possibly be distinguished for different regions. Such a phenotypic manifold may be used for determining the phenotypic distance between a given species and its local optimum (the emergent phenotype) without relying on causal mechanisms or habitat descriptors in the first place. Specific traits causing species to be 'phenotypically distanced' could be identified, while the functional value of these traits could be interpreted retrospectively to isolate the mechanisms. Understanding these key mechanisms would become especially important in the context of species conservation programmes.

CONCLUSION

In spite of important disparities in phenotypic plasticity between morphology and coloration (both in divergence rate and signal intensity in response to environmental changes), these two sets of traits appear to be correlated. To define each individual as an emergent phenotype attractor is appealing and opens the way to complementary approaches in functional ecology. The success of alternative, more holistic, evolutionary theories to find macroecological patterns may yield better narratives to characterize the interrelations between processes happening in ecosystems at multiple scales. We hypothesize that emergent phenotypes are likely to be present in other taxonomic groups (e.g. birds, arthropods) and that these patterns may be found directly from the correlation of morphology and colour traits, but also from other phenotypic sets such as physiological and behavioural descriptors.

ACKNOWLEDGEMENTS

We thank P. Legendre and K. Arii for helpful comments on an earlier draft of this manuscript. We also wish to thank Y. Lemay, teaching assistant at the Université du Québec à Rimouski (UQAR), for his contribution to data acquisition. We acknowledge the biology students at UQAR who participated in this project: A.-C. Angers, M. Bellemare, M. Belley, C. Bouchard, M. Chabot, L. Chavarie, M. Coutu, E. Dufour, S. Houle, M. Leblond, É. Marquis, M.-J. Martel, V. Nadeau, A. Neveu, Y. Ognibo, J. Pilote, C. Richard, J. St-Laurent, D. St-Pierre, S. Tremblay, and K. Tseng-Valiquette.

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