

Journal of Applied Biological Sciences 9 (1): 36-42, 2015 ISSN: 1307-1130, E-ISSN: 2146-0108, www.nobel.gen.tr

Patterns of Body Shape Variation in *Capoeta gracilis* (Pisces: Cyprinidae) in Relation to Environmental Variables in Sefidrud River Basin, Iran

Mazaher ZAMANI FARADONBE¹ Soheil EAGDERI¹* Mohammad MORADI² ¹ Department of Fisheries, Faculty of Natural Resources, University of Tehran, Karaj, Iran. ² Department of Biology, Faculty of Science, University of Zanjan, Zanjan, Iran.

*Corresponding author:	Received: December 16, 2014
Email: soheil.eagderi@ut.ac.ir	Accepted: January 29, 2015

Abstract

This study investigates the morphological variation of *Capoeta gracilis* (Cyprinidae) in relation to the environmental conditions across its distribution range in the Sefidrud River basin. The correlations between environmental variables and body shape of 487 specimens of *C. gracilis* was studied using a combination of geometric morphometric technique and multivariate statistical analysis i.e. Two-Block Partial Least-Squares (2B-PLS). The studied environmental variables were including depth (cm), width (m), slope (m/km), current velocity (cm/s), number of large stone (>25 cm), average stone diameter (cm), substrate index (%), Potamal Cover Index, Periphyton Cover Index. The body shape of fishes living in habitats with fast flow water and lower depth, substrate index, PeCI and PoCI as seen in specimens of downstream of Taleghan and Totkabon Rivers, are fusiform including smaller head, longer caudal peduncle and relatively deeper body. The results also showed that increasing depth and width of river along with increasing PeCI. PoCI and larger bed stones induce larger head and shorter and deeper caudal peduncle forming relatively deeper body shape. The most of observed differences were in head and tail regions, but in lower degree suggesting *C. gracilis* as a generalist species. Based on the results, ecomorphological analyses is a valid tool to predict habitat preferences in the genus *Capoeta* in riverine ecosystems.

Keywords: Ecomorphology, Geometric morphometric, 2B-PLS, Phenotypes, Environmental variation.

INTRODUCTION

The environmental parameters can affect fish performance and survival via environmentally induced phenotypic variation. Therefore, body shapes of fish are related to biotic and abiotic factors of habitats e.g. feeding regime, habitat and predation risk [11, 13]. Effect of environmental factors on fish morphology is well-documented [17, 20, 33] and the body shape–environment associations across space and between species suggest that patterns are adaptive [28, 42].

Morphological plasticity has been reported in many fish species, especially in freshwater fish species. Phenotypic plasticity is defined the ability of an organism to respond to environmental alteration by changing its form and movement or rate of activity [47]. Therefore, the change of body shape can reflect behavioral and ecological differences. Because morphological variation can enhance ecological partitioning or sharing between competitors and facilitate co-occurrence of closely-related fishes [5, 43].

Phenotypic variability of fish is considered to be an important adaptive strategy for populations experiencing inconsistent environments such as rivers [41]. Phenotypic plasticity is evolved under temporal environmental variation when the range of environmental change is coarse, allowing organisms to perceive variation and display appropriate phenotypes [7, 47]. Most of the environmental factors in an aquatic environments are determined by geographic location where the species inhabit. Therefore, geographical variations could directly or indirectly to be correlated with morphology of a species including the body size and shape [3, 21], head form and appendix of body [3].

The genus *Capoeta* is a potamodromous cyprinid fishes, with about seven species reported from interior water of Iran, occurring in both lotic and lentic water bodies [39]. *Capoeta gracilis* [Keyserling, 1861], is a predominant fish species of the Caspian Sea basin including Sefidrud River. In addition to its ecological significance, C. *gracilis* is an important species for sport and inland water fishing. There is no sexual dimorphism in this species and both sexes have similar morphometric characteristics [2].

The wide dispersal range of *C. gracilis* occurring in diverse ecological niches an variation of its body shape in its habitats [2, 19, 40], provide a case to study the effect of environmental factor on the body shape of this riverine species. Hence, this study was conducted to investigate the effect of environmental characters on the body shape of *C. gracilis* in the Sefidrud River basin.

MATERIALS AND METHODS

Sampling

For this study three station, along the Sefidrud River including up- and downstream of Taleghan River (as main river) and Totkabon River (a tributary stream of the Sefidrud River) were selected (Figure 1). Number of sampling sites in up- and downstream of Taleghan River and Totkabon River was 11, 18 and 9, respectively and sampling area were selected based on Lotfi (2012) [29].Sampling were carried out in autumn 2014, by backpack electrofishing (Samus Mp750,with aluminum ring anode,45 cm diameter) and using upstream and downstream stop-nets of 1.2 cm mesh. For sampling, oneremoval method with similar catch-per-unit effort sampling strategy was employed [24]. In total 487 specimens of *Capoeta gracilis* were collected from upstream (103 specimens), downstream (286 specimens) of Taleghan river and Tonkabon River (98 specimens) (Figure 1). All collected specimens were anaesthetized in 1% clove oil solution and returned to the river after photographing.

Obtaining Morphological Characters

For extracting shape data, geometric morphometric method was applied. In this method, the left side of live specimens were photographed using a digital Kodak camera mounted to a Copy-stand (Kodak, 6 MP). To avoid the impact of allometric growth pattern only specimens longer than 11 cm (Age 2^+ or more) were selected [32, 35].Then, fourteen landmark-points were defined and digitized on 2D images using tpsDig2 software version 2.16 [37] (Figure 2) and a tps file containing coordinate of landmark-point were obtained for further analysis.

Habitat Data

The habitat variables in all sampling sites were measured immediately after fishing. The measured habitat variables were including depth (cm), width (m), slope (m/km), current velocity (cm/s), number of large stone (>25 cm), average stone diameter (cm), substrate index (%), level of potamal cover and level of periphyton cover.



Figure 1. Map showing area of fish sampling and data collection of environmental variables in Sefidrud River basin (northern Ira).



Figure 2. Defined landmark-points on the left side of specimens to extract body shape data: (1) the anterior-most point on the head; (2) the center of eye; (3) the dorsal margin of head vertical to the center of eye; (4) the junction of the head and trunk; (5) the anterior edge of dorsal fin base; (6) the posterior edge of dorsal fin base; (7) the upper edge of caudal fin base: (8) the lower edge of caudal fin base: (9) the posterior edge of anal fin base; (10) the anterior edge of anal fin base; (11) the anterior edge of pectoral fin base; (12) the posterior end of head; (13) the ventral corner of opercular slit; (14) the ventral of margin of head vertical to the center of eye.

Depth in each sampling station was measured using a measuring bar with 20 replicates and its average was considered as depth of station. Width of river was measured by a tapeline by measuring anterior, middle and end of each station and its average was regarded as width of station. River slope was measured using sonto device, velocity with a floating material based on Hasanli (1999)[18], number of large stone (>25 cm) with counting large stone in 20 selected quadrates (50×50) in each station based on [29], average stone diameter with a measuring diameter of bed stones in 20 selected quadrated (50×50) based on Lotfi (2012)[29] and substrate index (SI) using following formula: (Substrate Index) SI $(0.08 \times bedrock\%) + (0.07 \times boulder\%) + (0.06 \times cobble\%) +$ $(0.05 \times \text{gravel}\%) + (0.035 \times \text{fines}\%)$ [22]. The Potamal Cover Index (PoCI) and Periphyton Cover Index (PeCI) was determined visually in site as percent of surface according to Platts et al. (1983) [34].

The variables were standardized to remove the effects those variables with large variances [25, 36]. For this purpose, we used following formula: $Z=(n-x)/\sigma$, Where N is a variable score, x is the mean of the variable, σ is the standard deviation of the variable.

Data Analysis

A Two-Block Partial Least-Square (2B-PLS) analysis [38] was used to analysis the relationships between body shape patterns and habitat variables. This method permits us to analysis the relation between two sets of variables/Block (habitat variables as first block and body shape as second block). 2B-PLS extracts several groups of vectors (PLSs) that show covariation between the body shape and habitat variables blocks that each has a related singular value, correlation coefficient and vector coefficients. As an overall measure of covariation between the two set of variables (shape and environmental variables), we used the RV coefficient [14]. The significance of the RV coefficient was tested with 10000 permutations using MorphoJ software. To remove nonshape data including orientation, direction and size, the landmark-points data were superimposed based on Generalized Procrustes Analysis (GPA). Relative warp scores were applied as shape descriptive in 2B-PLS analysis. Thin-plate spline transformation grids with respect to the consensus configuration along the PLS axis were visualized using MorphoJ software. The variable gradient plots for the habitat variables related to first two PLS vectors were depicted using MorphoJ 1.05f [25] and PAST 2.17c software.

RESULTS

The results of 2B-PLS analysis showed that the body shape changes in relation to the environmental variables (Figures 3-6). The results also showed an RV coefficient of 0.0907 (p<0.0001) indicating a significant and higher pattern of covariation between the body shape and environmental variables. The first vector of PLS explains 67.956% and second one 20.897% of the covariance among the data sets.

The body shape changes along the PLS1 revealed a higher positive covariation with slope and velocity and higher negative covariation with depth, substrate index, PeCI and PoCI (Table 1 and Figures 3, 4) that effect the head, trunk and tail shapes and dorsal fin position. The specimens with positive PLS1 scores possess longer and deeper head, anterior position of dorsal fin and higher body depth in posterior part of trunk and longer caudal peduncle forming a fusiform body shape (Figure 3).

The body shape changes explained by PLS2 vector showed a higher positive covariation with PoCI and stone diameter and higher negative covariation with depth and width (Table 1 and Figures 5, 6) that effect head and caudal peduncle shapes, dorsal fin base length and anal fin position. The specimens with positive PLS2 scores have smaller head, longer dorsal fin base, higher caudal peduncle length and depth and posterior position of anal fin (Figure 5).

Table 1. Partial least squares (PLS) results. The weighting of each variable on the vector (1-4) is reported with the singular value and percent covariation explained by each vector and the correlation between body shape and other variables on that vector (*p<0.05).

	PLS			
Variable	1	2	3	4
Height	0.01929400	-0.10659775	0.02562975	-0.02748107
Depth(cm)	-0.37279918	-0.47746694	0.42100929	-0.11314577
Width(cm)	-0.23122091	-0.62207385	-0.12875105	0.10938407
Slope (m/km)	0.39112477	-0.00054422	-0.35788272	-0.48422077
Velocity(m/s)	0.06117617	-0.07568317	-0.23333674	-0.00094742
Stone Diameter (cm)	-0.08903872	0.22075981	0.50452626	-0.55556584
Large Stone>25	-0.14914493	-0.01466168	0.11231124	-0.43748463
%Substrate Index	-0.31449761	0.07664558	-0.37076364	-0.37679560
Periphyton cover Index	-0.45377439	-0.08262643	-0.46660392	-0.18238863
Potamal Cover Index	-0.56166917	0.55344973	-0.02541491	0.25440233
Singular Values	0.00967602	0.00536343	0.00253752	0.00201259
% Total Cover	67.956	20.879	4.674	2.940
Correlations	0.46071	0.34496	0.25578	0.23119



Figure 3. Plots representation of 2B-PLS results based on the first paired vectors of body shape and environmental variables; scatter plot shows the projections of the *C. gracilis* specimens onto the first shape and environmental variables vectors (Deformations grids show the body shape changes in negative (bellow) and positive directions (above) respect to the consensus configuration.



Figure 4. Variables gradient plot for the first vector of environmental variables data.

The specimens of downstream of Taleghan and Totkabon Rivers were interrelated with the positive PLS1

scores (Figure 3, upper grid) presenting a relatively smaller head (in terms of depth and length), anterior position of dorsal fin, lower body depth, lower caudal peduncle depth and longer tail. The specimens of upstream of Taleghan River, inhabiting in fast flow water were interrelated with the negative PLS1 scores (Figure 3, bottom grid) having smaller head (in terms of depth and length), posterior position of dorsal fin, smaller caudal peduncle length. Some specimens of Totkabon and downstream of Taleghan Rivers show an average body shape in relation two extreme end body shape changes.

The specimens of upstream of Taleghan River and most part of its downstream population were interrelated with the positive PLS2 scores (Figure 5, upper grid) showing a deeper head, longer dorsal fin base, posterior position of anal fin and short caudal peduncle. Some downstream specimens of Taleghan river and Totkabon population were interrelated with the negative PLS2 scores (Figure 5, bottom grid) having pointed head, short dorsal fin base and longer caudal peduncle with less depth showing a fusiform body shape.



Figure 5. Plots representation of 2B-PLS results based on the second paired vectors of body shape and environmental variables, scatter plot shows the projections of the *C. gracilis* specimens onto the second shape and environmental variables vectors; (Deformations grids show the body shape changes in negative (bellow) and positive directions (above) respect to the consensus configuration.



Figure 6. Variables gradient plot for the second vector of environmental variables data.

DISCUSSION

The results revealed that morphometric variations in different populations of C. gracilis can be explained by an adaptation to local habitat conditions supporting the hypothesis that morphological characters of fish populations exist across environmental gradients tend to alter based on environment characteristics [8, 27, 31, 48]. In other word, the results confirm that the morphological traits of C. gracilis are related to its habitat preference [48, 8, 27]. These findings also showed that body shape particularly head and caudal regions and fin size and position are important morphological traits in C. gracilis that respond to the alternation of environmental factors [12, 15]. In addition, our finding can suggest that ecomorphological analyses is a valid tool to predict habitat preferences of the member of genus Capoeta in riverine ecosystems.

We found a strong correlations between environmental and morphological variables suggesting that certain morphological features may be adapted to specific habitat characteristic. Based on the results of PLS1, the specimens of downstream of Taleghan and Totkabon Rivers have smaller head, anterior position of dorsal fin, relatively deep body and longer caudal peduncle forming a fusiform or almost streamlined body shape. These features have positive relationship with water velocity and negative relationship with water depth, substrate index, PeCI and PoCI, i.e. in habitats with higher velocity and lower depth, substrate index, PeCI and PoCI, fish have a fusiform body shape including smaller head, longer caudal peduncle and relatively deeper body. Fishes with fusiform or streamlined morphologies are better able to overcome hydrodynamic drag in high flow environments [4] and can cause foraging success [26] in such a condition. Based on the results of PLS2, the smaller head, longer dorsal fin base, deep caudal peduncle and posterior position of anal fin are interrelated with PoCI and stone diameter positively and periphyton index, depth and width of river negatively showing similar situation as PLS1. This results revealed that increasing depth and width of river along with increasing PeCI, PoCI and larger bed stones induce larger head and shorter and deeper caudal peduncle forming relatively deeper body shape. Deep-bodied fishes can perform sustained swimming more efficiently in low flow environments [4]. Other studies have found similar associations between body shape, fin size and different habitat features [12, 15]. In this assumption, a more cylindrical body shape may enable individuals to better negotiate rapid flowing habitats with high substrate heterogeneity [9].

In addition, the specimens living in middle values of environmental variables, have approximately an average shape, i.e. the individuals that exhibit this general pattern of body shape are generalist in selection of area as habitat. Although most of observed differences were in head and tail regions, but the degree of these differences were low, therefore the results can suggest *C. gracilis* as a generalist species. Generalist species live in coarse habitats and have similar phenotypic adaptation as specialist but with less degree [23].

As conclusion, the body shape and fin morphology of *C. gracilis* is influenced by the environmental conditions where they live. Hence, the observed morphological variations in *C. gracilis* could be considered as an adaptive response to the factors of inhabiting environments. Therefore, similarities in morphology can reflected similarities in habitat use and/or feeding tactics [16]. Based on the results, the specimens from different locations display body shape patterns in relation to environmental factors, but the level of these differences need to be tested more carefully.

REFERENCES

[1] Abdoli A, Rasooli P, Mostafavi H. 2008. Lengthweight relationships of *Capoeta capoeta capoeta* (Gueldenstaedt, 1772) in the Gorganrud River, south Caspian Basin. Journal of Applied Ichthyology. 24:96-98.

[2] Anvarifar H, Khyabani A, Farahmand H, Vatandoust S, Anvarifar H, Jahageerdar S. 2011. Detection of morphometric differentiation between isolated up- and downstream populations of Siah Mahi (*Capoeta capoeta gracilis*) (Pisces: Cyprinidae) in the Tajan River (Iran). Hydrobiologia. 673:41-52.

[3] Atkinson D, Sibly RM. 1997. Why are organisms usually bigger in colder environments? Making sense of life history puzzle. Trends in Ecology and Evolution.12:235-239.

[4] Blake, RW. 1983. Fish locomotion. Cambridge,

UK: Cambridge University Press.

[5] Bolnick, DI. 2004. Can intraspecific competition drive disruptive selection? An experimental test in natural populations of sticklebacks. Evolution. 58:608-618.

[6] Bookstein, FL. 1991. Morphometric Tools for Landmark Data: Geometry and Biology. Cambridge Press, United Kingdom.

[7] Bradshaw, AD. 1965. Evolutionary significance of phenotypic plasticity in plants. Advances in Genetics. 13:115-155.

[8] Chan, MD. 2001. Fish ecomorphology: predicting habitat preferences of stream fishes from their body shape. PhD dissertation, Virginia Polytechnic Institute and State Univ., Blacksburg, VA.

[9] Chuang LC, Lin YS, Liang SH. 2006. Ecomorphological Comparison and Habitat Preference of 2 Cyprinid Fishes, *Varicorhinus barbatulus* and *Candidia barbatus*, in Hapen Creek of Northern Taiwan. Zoological Studies. 45 (1):114-123.

[10] Coad, BW. 2014. Freshwater fishes of Iran. Available at: http://www.briancoad.com (accessed on 17 May 2014).

[11] Costa C, Cataudella S. 2007. Relationship between shape and trophic ecology of selected species of Sparids of the Caprolace coastal lagoon (Central Tyrrhenian Sea). Environmental Biology of Fishes. 78:115-123.

[12] Douglas ME, Matthews WJ. 1992. Does morphology predict ecology? Hypothesis testing within a freshwater stream fish assemblage. Oikos. 65:213-224.

[13] Eklov P, Svanback R. 2006. Predation risk influences adaptive morphological variation in fish populations. American Naturalist1. 67:440-452.

[14] Escoufier, Y. 1973. Le traitement des variables vectorielles. Biometrics. 29:751-760.

[15] Gatz Jr. AJ. 1979. Ecological morphology of freshwater stream fishes. Tulane Studies of Zoology and Botany. 21:91-124.

[16] Gibran, FZ. 2010. Habitat partitioning, habits and convergence among coastal nektonic fish species from the São Sebastião Channel, southeastern Brazil. Neotropical Ichthyology. 8 (2):299-310.

[17] Grunbaum T, Cloutier R, Mabee PM, Francois NR, LeF. 2007. Early developmental plasticity and integrative responses in Arctic Charr (*Salvinus alpinus*): Effects of water velocity on body size and shape. Journal of Experimental Zoology, Part B, Molecular and developmental evolution. 308B:396-408.

[18] Hasanli, AM. 1999. Diverse methods to water measurement (Hydrometry). Shiraz University publication. 265pp.

[19] Heidari A, Mousavi-Sabet H, Khoshkholgh M, Esmaeili HR, Eagderi S. 2013. The impact of Manjil and Tarik dams (Sefidroud River, southern Caspian Sea basin) on morphological traits of Siah Mahi *Capoeta gracilis* (Pisces: Cyprinidae). International Journal of Aquatic Biology. 1(4):195-201.

[20] Hinder I, Jonsson B. 1993. Ecological polymorphism in Arctic Charr. Biological Journal of Linnean Society. 48:63-74.

[21] Jin Y, Liu N, Li J. 2007. Elevational variation in body size of *Phrynocephalus vlangalii* in the North-Xizang (Tibetan) plateau. Belgian Journal of Zoology. 137 (2):197-202.

[22] Jowett IG, Richardson J. 1990. Microhabitat preferences of benthic invertebrates in a New Zealand river and the development of in-stream flow-habitat models for *Deleatidium* spp. New Zealand Journal of Marine and Freshwater Research. 24:19-30.

[23] Kassen B, Bell G. 1998. Experimental evolution in *Chlamydomonas*. IV. Selection in Environments that vary through time at different scales. Heredity. 80:732-741.

[24] Klaar M, Copp GH, Horsfield R. 2004. Autumnal habitat use of non-native pumpkinseed *Lepomis gibbosus* and associations with native fish species in small English streams. Folia Zoologica-Praha. 53(2):189-202.

[25] Klingenberg, C P. 2011. MorphoJ: an integrated software package for geometric morphometrics. Molecular Ecology Resources. 11(2):353-357.

[26] Langerhans RB, Reznick DN. 2010. Ecology and evolution of swimming performance in fishes: predicting evolution with biomechanics. In Fish locomotion: an coethological perspective (eds P. Domenici & B. G. Kapoor), pp. 200-248. Enfield, NH: Science Publishers.

[27] Langerhans RB, Layman CA, Langerhans AK, Dewitt TJ. 2003. Habitat-associated morphological divergence in two Neotropical fish species. Biological Journal of the Linnean Society. 80:689-698.

[28] Losos JB, Jackman TR, Larson A, de Queiroz K, Rodriguez-Schettino L. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. Science. 279:2115-2118.

[29] Lotfi, A. 2012. Guideline on rapid assessment of environmental features of rivers. Environment Protection Department of Iran Publication. 120 p. (In Persian)

[30] Murta, A. G. 2000. Morphological variation of horse mackerel (*Trachurus trachurus*) in the Iberian and North African Atlantic: implications for stock identification. ICES Journal of Marine Science. 57:1240-1248.

[31] Motta PJ, Clifton KB, Hernandez P, Eggold BT. 1995. Ecomorphological correlates in ten species of subtropical seagrass fishes- diet and microhabitat utilization. Environmental Biology of Fishes. 44:37-60.

[32] Patimar R, Ownagh E, Jafari N, Hosseini M. 2009. Intrabasin variation in allometry coefficients of Lenkoran *Capoeta capoeta gracilis* (Keyserling, 1861) in the Gorganroud basin, southeast Caspian Sea, Iran. Journal of Applied Ichthyology. 25:776-778.

[33] Peres-Neto PR, Magnan P. 2004. The influence of swimming demand on phenotypic plasticity and morphological integration: a comparison of two polymorphic Char species. Oecologica. 140:36–45.

[34] Platts WS, Megahan WF, Minshall GW. 1983. Methods for evaluating stream, riparian, and biotic conditions. Gen. Tech. Rep. INT-138. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, 70 p.

[35] Ranjbar KS, Patimar R, Ghorbani R, Azimi A. 2012. Investigation of Fecundity and its Relationship with Some Growth Indices of *Capoeta capoeta gracilis* (Keyserling, 1861) in the Two Streams (Dough and Zarrin-Gol) of Gorganroud River Basin, Golestan Province, Northern Iran. World Journal of Fish and Marine Sciences. 4 (1):111-114.

[36] Rohlf, FJ. 2006. TpsPLS: Partial Least Squares, Version 1>18. Department of Ecology and Evolution, State University of New York at Stony Brook. (http://life.bio.sunysb.edu/ morph/).

[37] Rohlf, FJ. 2010. tpsDig, digitize landmarks and outlines, version 2.16.Department of Ecology and Evolution, State University of New York at Stony Brook.

[38] Rohlf FJ, Corti M. 2000. Use of two-block partial least-squares to study covariation in shape. Systematic Biology. 49(4):740-753.

[39] Samaee SM, Mojazi-Amiri B, Hosseini-Mazinani SM. 2006. Comparison of *Capoeta capoeta gracilis* (Cyprinidae, Teleostei) populations in the south Caspian Sea River basin, using morphometric ratios and genetic markers. Folia Zoologica. 55:323-335.

[40] Samaee SM, Patzner RA, Mansour N. 2009. Morphological differentiation within the population of Siah Mahi, *Capoeta capoeta gracilis*, (Cyprinidae, Teleostei) in a river of the south Caspian Sea basin: a pilot study. Journal of Applied Ichthyology. 25:583-590.

[41] Scheimer, SM. 1993. Genetics and Evolution of Phenotypic Plasticity. Annual Review of Ecology and Systematics. 24:35-68.

[42] Schluter, D. 1996. Ecological causes of adaptive radiation. American Naturalist1. 48:S40–S64.

[43] Svanbäck R, Eklöv P, Fransson R, Holmgren K. 2008. Intraspecific competition drives multiple species resource polymorphism in fish communities. Oikos. 117:114-124.

[44] Tudela, S. 1999. Morphological variability in a Mediterranean, genetically homogeneous population of European anchovy, *Engraulis encrasicolus*. Fisheries Research, 42: 229-243.

[45] Via, S., Gomulkiewicz, R., Scheiner, S. M., Schlichting, C. D., and Van Tienderen, P. H. 1995. Adaptive phenotypic plasticity: consensus and controversy. Trends in Ecology & Evolution. 10:212-217.

[46] Webb, PW. 1984. Body form, locomotion and foraging in aquatic vertebrates. American Zoologist. 24:107–120.

[47] West-Eberhard, MJ. 2003. Developmental Plasticity and Evolution. New York: Oxford University Press.

[48] Wood BM, Bain MB. 1995. Morphology and microhabitat use in stream fish. Canadian Journal of Fisheries and Aquatic Sciences. 52:1487-1498.