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Habitat-associated morphological divergence in four Shemaya, *Alburnus chalcoides* (Actinopterygii: Cyprinidae) populations in the southern Caspian Sea using geometric morphometrics analysis

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Abstract: In this study, Geometric morphometrics approach was used to explore body shape variations and growth trajectory among four population of Shemaya (*Alburnus chalcoides*). The shape of 114 individuals from three rivers (Lisar, Shiroud and Babolroud) and one lagoon (Anzali) from the south of Caspian Sea was extracted by recording the 2-D coordinates of 16 landmark points. We applied a GPA analysis to eliminate non-shape variations. PCA, CVA, MANOVA and DFA analysis were used to examine shape differences among populations. The significant differences found among the shape of populations. Since Shemaya is an anaderemus fish and all their populations have a common origin, we concluded that differences between habitat features might create selective pressures resulting morphological divergence among conspecific populations. We suggest that high level of plasticity, particularly in the depth of body, head and caudal peduncle shape may reflect low costs of maintaining the plastic response even in relatively isolated populations.

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Introduction

Study of phenotypic diversity between populations can help to better understanding of diversification of species within ecosystems and intraspecific diversification in fishes is well documented (reviewed in Robinson and Wilson, 1994; Smith and Skulason, 1996; Taylor, 1999; Jonsson and Jonsson, 2001). The body shape differences of populations is considered as essential steps in process of speciation (Balon, 1993; Margurran, 1998). Fish body shape can be the results of evolutionary adaptations to environmental pressures (Gatz, 1979; Watson and Balon, 1984; Winemiller, 1991), particularly, food collection and hydrodynamic conditions (Matthews, 1998) making feasible more efficient utilization of available resources and improving fitness and performance (Pianka, 1994). Hence, morphological characters can provide information about the ecological niches of fishes (Winemiller, 1991) allowing inferences about its distribution (Watson and Balon 1984), trophic patterns (Hugueny and Pouilly, 1999) and predicting its life habitats (Keast and Webb, 1966; Karr and James, 1975).

Understanding general patterns and causes of diversification requires an examination of divergence in multiple species (Endler, 1982; Johnson and Belk, 2001; Jennions and Telford, 2002; Van Buskirk, 2002) and an evaluation of potential constraints on divergence (Endler, 1977; Slatkin, 1987; Losos, 1996; Hendry et al., 2000). Divergent selection can be led to phenotypic differences through either genetic differences or phenotypic plasticity (Levins, 1968; West-Eberhard, 1989; Robinson and Wilson, 1994; Orr and Smith, 1998; Schluter, 2000). Both sources of divergence can drive microevolutionary change within species

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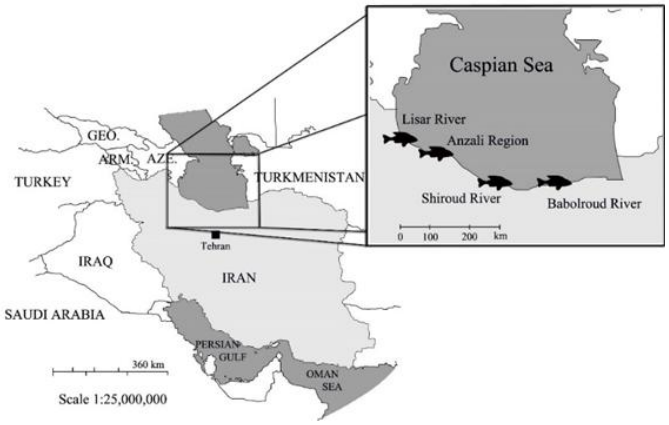

Figure 1. Sampling stations in the south Caspian Sea.

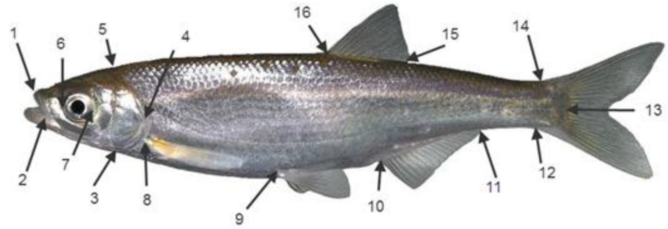

Figure 2. Used landmark points to extract shape of *A. chalcoides*. 1. Tip of the premaxilla; 2. End of the mouth; 3. The lower beginning of operculum; 4. End of operculum; 5. Beginning of the scales at the dorsal side; 6. Front of the eye; 7. End of the eye; 8. Base of the pectoral fin; 9. Base of the pelvic fin; 10, 11. Anterior and posterior insertion of the anal fin; 12. Lower margin of caudal peduncle. 13. End of the medial region of caudal peduncle; 14. Upper margin of caudal peduncle. 15, 16. Anterior and posterior insertion of the dorsal fin.

leading to speciation (West-Eberhard, 1989; Rice and Hostert, 1993; Losos et al., 2000; Schluter, 2000; Agrawal, 2001; Kaneko, 2002).

Geometric morphometrics is defined as a statistical study of biological shapes and shape variations among different populations (Bookstein, 1991) and it allows the characterization of growth trajectory and the visualization of allometric growth (Alberch et al., 1979; Klingenberg, 1996; Loy et al., 1998). Many reports on applications of geometric morphometrics method in different biological fields including fisheries are available (Marcus et al., 1996). These method, which allow the study of shape and size, offering powerful analytical and graphical tools for the quantification and visualization of morphological variation within and among organisms.

The Shemaya (*Alburnus chalcoides*) is widely distributed in the river systems of the Black, Caspian and Aral Seas (Bogutskala, 1997). This benthoplagic and anadromous species lives in fresh and brackish water. The populations that live in lakes migrate upstream for spawning from the early May till late July (Slastenenko, 1959). Little information is available about the environmental biology of Shemaya. Since, the Shemaya populations have a common genealogy population, therefore, its morphological variation may be considered a results of environmental expression. Hence, this study conducted to compare the morphological space occupied by Shemaya assemblages in three rivers (Lisar, Shiroud and Babolroud) and one lagoon (Anzali) along the southern Caspian Sea, for analyzing the hypothesis that morphological space changes among mentioned regions. For this purpose, a homologous landmark-based geometric morphometric technique was applied (coordinating of points located unambiguously on each specimen's profile or structure) (Bookstein, 1991; Rohlf and Marcus, 1993; Marcus et al., 1996). This study tries to obtain the relationship between morphological characters and environmental conditions in the Shemaya.

Materials and Methods

Sampling: In total 114 specimens of the Shemaya were collected from four regions of the south Caspian Sea (rivers of the Lisar: N: 37"58, E: 48"56, Shiroud: N: 36"49, E: 50"52, Babolroud: N: 36"42, E: 52"39 and Anzali Lagoon: N: 37"28, E: 49"27) (Fig. 1) using hand net, cast net, and electrofishing. After anaesthetizing in clove solution, they were fixed into 10% formalin solution and transformed to 70% ethanol for further examinations. All collected specimens were deposited in the Zoological museum Collection of Guilan University.

Geometric morphometrics analysis of Shape variations: The specimens were photographed using a digital camera (Canon G12, 10 MP) and sixteen homologous landmark-points were digitized using tpsDig2 software version 2.16 (Rohlf, 2004) on their

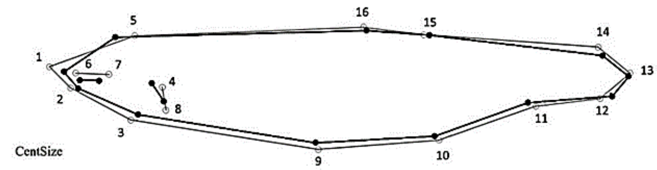

Figure 3. Deformation wireframe related to centroid size of *A. chalcoides*. Darker wireframe represent smallest specimen and lightness wireframe shows largest one.

left side (Fig. 2). The landmark-points were chosen at the specific points, in which a proper model of fish body shape was extracted (Bookstein, 1991). The digitization error was estimated according to Adriaens (2013). The obtained error based on a sub-sample was about 12% that is low enough to be ignored. Correlations between the procrustes and tangent shape distances were calculated using tpsSmall software version 1.2 (Rohlf, 2003) to certify that the amount of shape variation in the original data set is small adequate to allow statistical analyses to be performed in the linear tangent space, approximating the non-linear Kendall shape space (Rohlf, 1998a).

As a measure of size variation of the shapes, the centroid Size (Bookstein, 1991) were calculated for each shape in studied populations using tpsRelw (Rohlf, 2008) and tested for normality using the Shapiro-Wilk test. One-way ANOVA analysis were performed to compare the population's CS using their mean size. To explore allometry (how shapes vary with size; Klingenberg, 1998), multivariate regression of partial warps and uniform component on centroid size was performed with tpsRegr (Rohlf, 1998b). Within-species changes were investigated as linked with centroid size of the species and illustrated deformation in shape of the anatomical aspects related to centroid size in the smallest and the largest specimen. The landmarks were submitted to a generalized procrustes analysis (GPA). Partial warp (shape variables) and relative warp scores (with $\alpha=0$ which is a PCA of shape variables) (Rohlf 1993) were calculated using the software tpsRelw version 1.46 (Rohlf, 2008).

Principal component analysis (PCA) was performed to summarize the variation among the specimens as few dimensions as possible. Canonical variant analysis (CVA)/MANOVA was accomplished to investigate power of distinction among the populations. For discrimination of the individuals of four populations using shape variety, laniary discriminate analysis (LDA) by a cross-validation was performed for pair-wise of the populations. Partial warp scores have been used in CVA and discriminate analysis. To display the shape variation linked with the DAs in four body part aspects, thin-plate spline interpolation was used to produce transformation grids that show the transformation from a grid which superimposed onto the average configuration i.e. consensus shape.

The relationship between shape variables and centroid size (CS) was evaluated to compute the allometric growth patterns. Therefore, a principal component analysis (PCA) was performed for each new set of variables. The correlation test was used between CS and PCA scores (Rohlf, 1993). When significant correlation was found, the PC with the highest correlation plotted against CS representing the growth trajectory. The use of the thin-plate spline function allows the visualization of the shape change in the deformation grids (splines). Size related shape changes were then visualized as splines relative to the extreme values of the relative warp axis.

As a complement to discriminant analysis, morphometric distances between the individuals of two groups were inferred to Cluster analysis (Veasey et al., 2001) by adopting the Euclidean square distance as a measure of dissimilarity and the UPGMA (Unweighted Pair Group Method with Arithmetical average) method as the clustering algorithm (Sneath and Sokal, 1973).

Results

The variety of the specimens in shape spaces were perfectly correlated (for all the shapes r=1), therefore, they allow the use of the tangent plane approximation in further statistical analyses and interpretation of the results. Comparison of centroid size (CS) of studied populations showed that variations among populations were completely

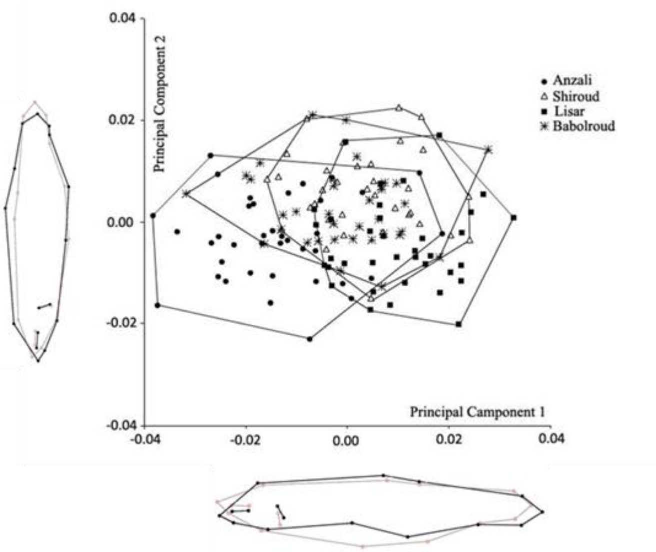

Figure 4. Scatter plot of individual scores from the first two principal components of *A. chalcoides*. Deformation wireframes show the most extreme positive (light wireframe) and negative (black wireframe).

significant (F=6.10E04, *P*=0.0001). Deformations in coordinate configurations related to CS have been showed in figure 3 and figure 7 representing the variation in CS of four populations (Table 1).

PCA analysis for all specimens explained 44.4% of shape variations by the first two PC axes extracted from the variance-covariance matrix (PC1=33.3% and PC2=13.1%). For covering more than 90% of the shape variation, 11 axes were needed. Anzali and Lisar populations showed more separation than the other populations along the first and second axis, respectively (Fig. 4).

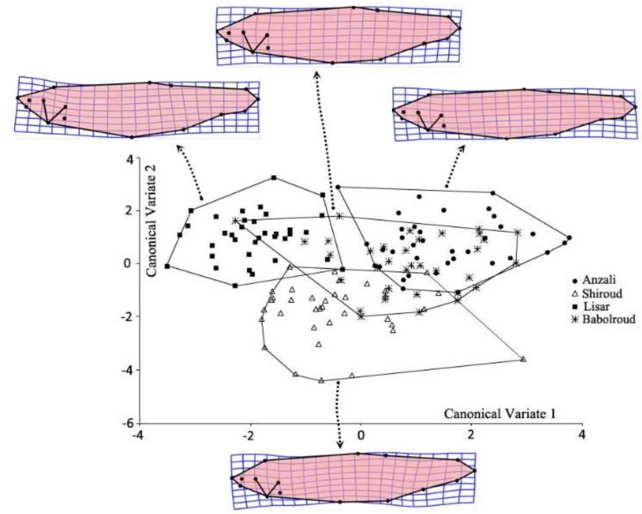

Figure 5. Scatter plot of individual scores from the first two canonical variant functions of *A. chalcoides*. Deformation grids show the mean shape of each population in relation to consensus shape.

The MANOVA/CVA analysis showed that geographically separated populations significantly differ in body shape (Table 2 and Fig. 5). The population of Lisar is separated from other groups, whereas Babolroud population showed an overlap with others. According to the table 2, shape variation among all populations is highly significant (Wilks' lamba= 0.0276, F=9.197, P=1.055E-45). Hotelling's pair-wise comparison showed that all populations are significantly different (*P*<0.01). The results of Mahalanobis distance confirmed the results of Hotelling's pair-wise comparisons (Table 2).

Discriminant analysis (DA) on relative warps classified 87.4% in origin data and 69.2 in cross-validation of specimen into the correct groups (Table

Table 1. On-way ANOVA test for Centroid Size of *A. chalcoides*.

	Sum of squares	Df	Mean Square	F	Sig
Between	3.88229	15	0.258819	6.10E04	2.337E-97
Within Groups	.203485E-3	48	4.24E-06		
Total	3.88249	63			

Table 2. Hotelling's pair-wise comparisons and Mahalanobis distance analysis for 4 populations of *A. chalcoides*.

	Lisar	Anzali	Shiroud	Babolroud
Lisar	0	8.68953E-10	1.28294E-06	0.000351966
Anzali	5.21372E-09	0	5.61428E-07	9.0279E-07
Shiroud	7.69761E-06	3.36857E-06	0	0.000263703
Babolroud	0.0021118	0.0021118	0.00158222	0

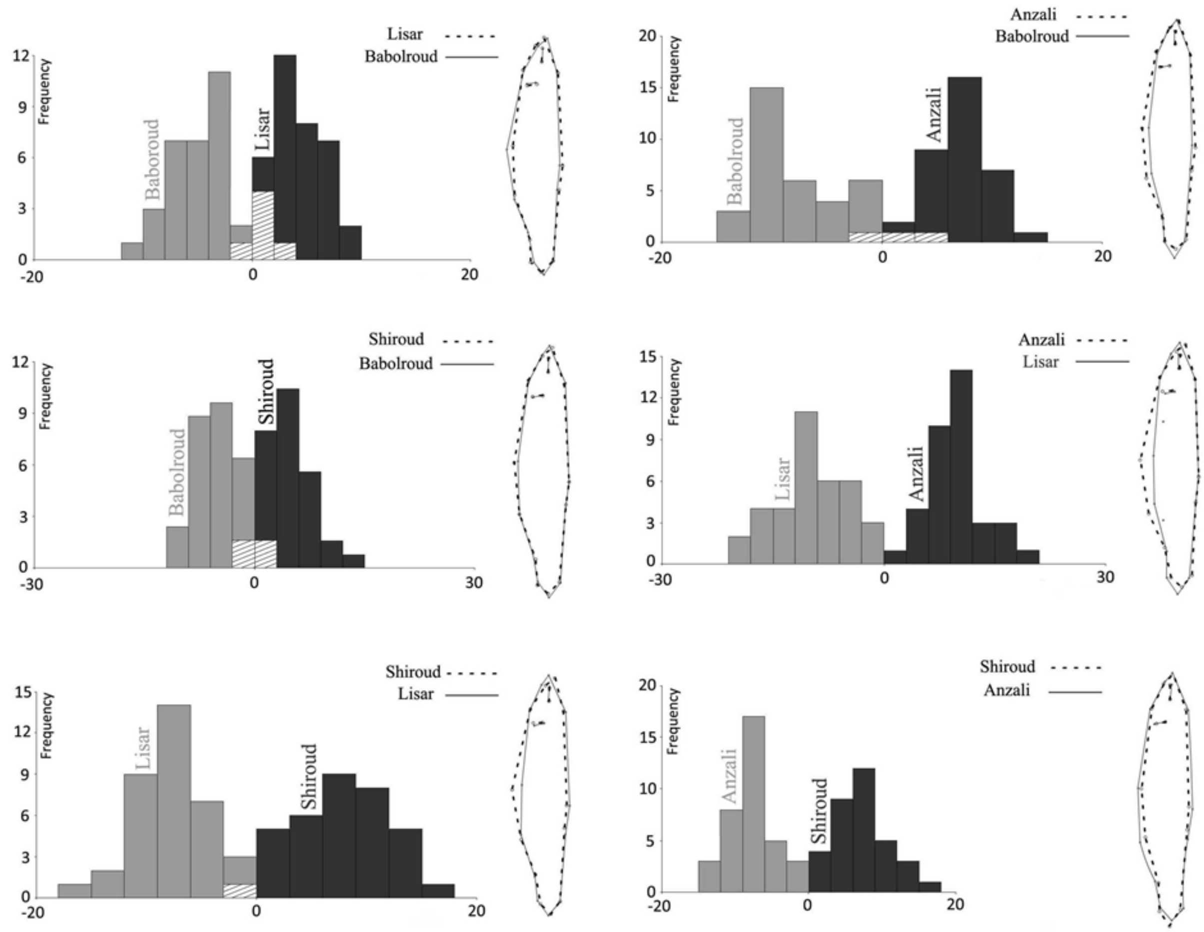

Figure 6. Histogram of discriminate analysis (DA) functions for pair wise competitions' between studied populations of *A. chalcoides*.

Table 3. Classification matrix showing the number and percentage of individuals that were correctly classified. (Bold values indicate correct classifications).

	Lisar	Anzali	Shiroud	Babolroud	Total
Original (%)					
Lisar	**88.9**	2.8	2.8	5.6	100
Anzali	.0	**97.2**	.0	2.8	100
Shiroud	2.9	2.9	**91.4**	2.9	100
Babolroud	11.1	11.1	5.6	**72.2**	100
Cross-validate (%)					
Lisar	**58.3**	2.8	16.7	22.2	100
Anzali	.0	**88.9**	5.6	5.6	100
Shiroud	11.4	11.4	**68.6**	8.6	100
Babolroud	13.9	11.1	13.9	**61.1**	100

3). Histogram of discriminant functions for pairwise groups has been shown in figure 6.

For distinguishing correlation between size and shape, the pearson product-moment correlation was used to find the highest correlation between the first three PC scores and CS. The scores of PC1 had the highest correlation (r=0.72; P<0.001). The growth trajectory related in PC1 clarifies high shape variability in small specimens followed by a better defined pattern of shape change in larger specimens.

Figure 8 shows the plot of PC1 versus CS and shapes related in the extreme values of axis, and it appears as a saturating curve. The major shape changes observed in fusiform shape of the fish. Gradually, the shape of larger fish is more fusiform, the anterior region sharpens and the caudal peduncle is longer and slimmer as they grow.

The UPMGA analysis for the studied populations showed that they divided into two major distinct groups. The first branch is included the Anzali's population and the second group is divided into Lisar's populations and another group including the Babolroud and Shiroud populations (Fig. 9).

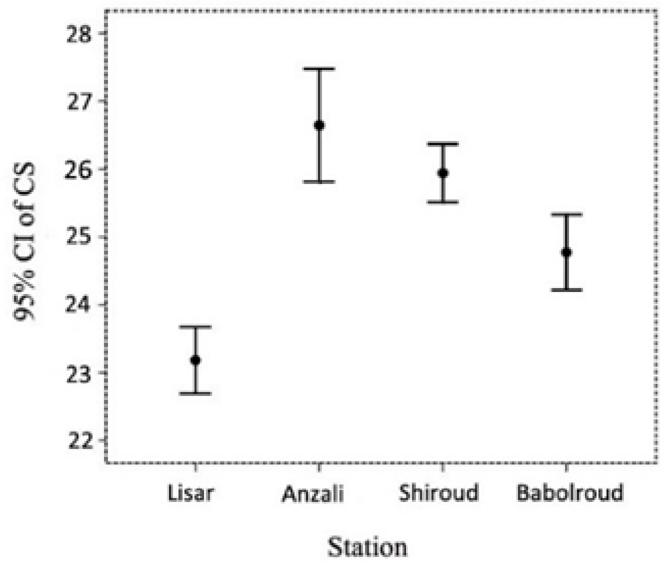

Figure 7. The 95% confidence intervals (CI) of Centroid Size (CS) vs. locations of *A. chalcoides*.

Discussion

In the present study, landmark-based geometric morphometrics tool was applied to compare and visualize the body shape changes as well as to display growth trajectories among four wild populations of Shemaya in the southern Caspian Sea. MANOVA, CVA and DFA showed a significant morphological difference in terms of body shape among populations. These discriminations between river populations and lagoon inhabitants is higher than those among river populations. This discriminations observed on three main morphological parts; (1) abdominal circumference, (2) caudal peduncle shape and (3) position of the mouth.

Comparison of the lagoon and river inhabitants specified that in similar ages, lagoon specimens have larger size, more fusiform body shape and slimmer caudal region. Comparison among three rivers populatons revealed that the Lisar population bear the bigger abdominal circumference, and upper position of mouth. Many fish species show morphological differences among habitats (Robinson and Wilson, 1994; Smith and Skulason, 1996; Taylor, 1999; Jonsson and Jonsson, 2001) and intraspecific polymorphism is typically believed to arise from divergent selection pressures among various environments (Robinson and Wilson, 1994; Smith and Skulason, 1996; Schluter, 2000). It is common that morphological characteristics can show high plasticity in response to different environmental circumstances (Wimberger, 1992).

Lagoons are fairly rich in terms of nutritional quality and quantity (Whitfield, 1999; Mariani et al., 2002) and their fishes live in a wide and deep water body with low flow water as seen in Anzali lagoon, whereas the Lisar is a river characterized with less depth, muddy bottom, high turbidity and fast-running water and less nutritious. On the other side the Shiroud and Babolroud rivers characterized with low turbidity, deeper, and more nutritious showing a better conditions than the Lisar. Hence, tough environmental conditions of the Lisar specimens may be led to smaller size of individuals. Insatiable condition takes more energy and results in low growth (Boily and Magnan, 2002).

It is commonly known that growth of lagoon fish is higher than that of river specimens (Warburton, 1979; Mariani et al., 2002). Coban et al. (2008) reported that there is no significant shape variation between cultured fish (that are always fed well) and lagoon caught. Also, the results of this study revealed that fish in a lagoon which is rich in terms of nutrition than rivers, are bigger in size.

Many fishes show distinct morphological differences between lotic and lentic habitats (Robinson and Wilson, 1994; Taylor et al., 1997;

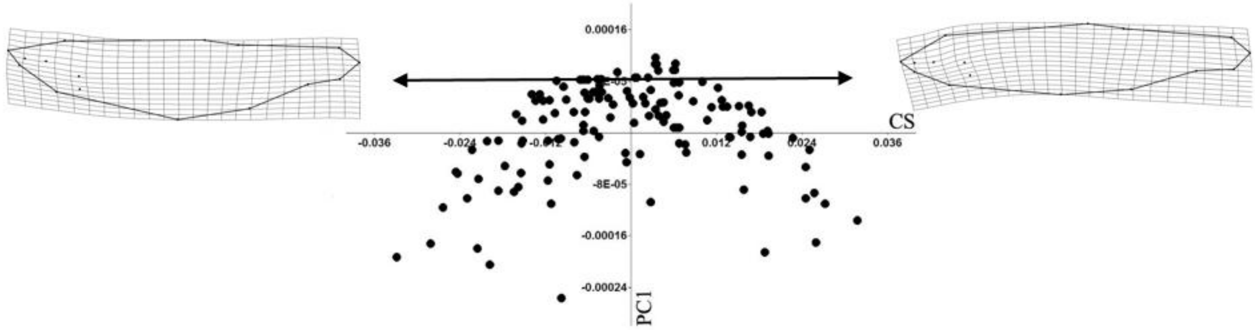

Figure 8. Relative Warp 1 (RW1) analogous to principal components of shape variability versus centroid size (CS).

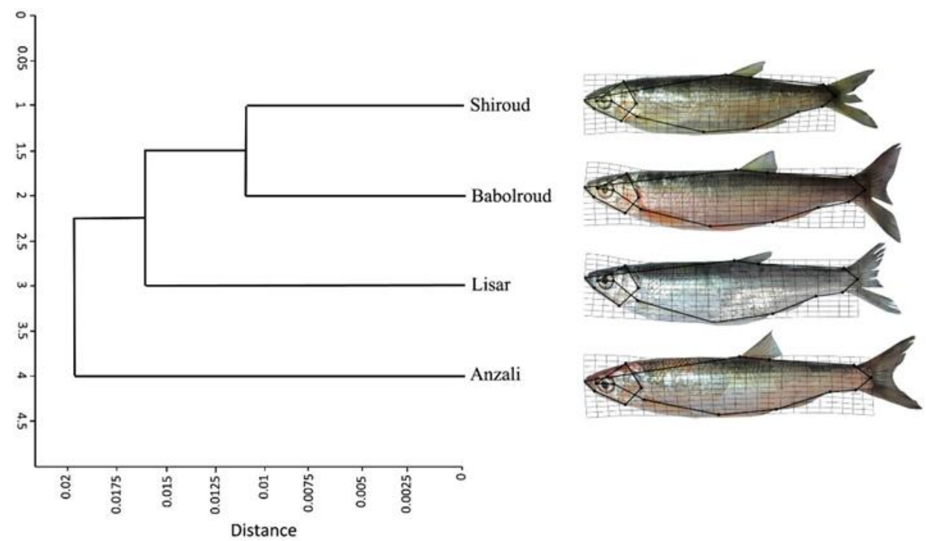

Figure 9. The UPGMA graph for four studied populations of *A. chalcoides*. Shape differences on the extremities of each population are presented.

Hendry et al., 2000; Pakkasmaa and Piironen, 2000; Brinsmead and Fox, 2002). Hydrodynamic theory prove that a more fusiform body shape decrease drag, and hence reduces the energetic expenditure essential to maintain position in the flowing water (Keast and Webb, 1966; Blake, 1983; Webb, 1984; Videler, 1993; Vogel, 1994). But the scenario in this study can be applied when nutrition in whole station be similar and analogous in similar ages, specimens contains better feeding, indicate better fusiform discrete from velocity of water flow (flowing of water in the Anzali lagoon is slow). Because as indicated, by growing the size of fish body form becoming more fusiform (Fig. 8). Bagherian and Rahmani (2007) studied two river inhabiting populations of Shemaya in the south Caspian Sea, expressing that more intensity of water flowing cause to be more slender body in this fish.

Intra-specific trophic diversification is also well known in fishes (Robinson and Wilson, 1994; Wimberger, 1994; Robinson and Wilson, 1995; Smith and Skulason, 1996; Ruzzante et al., 1998; Mittelbach et al., 1999; Holtmeier, 2001). The observed differences in mouth position among habitats would show discriminations in feeding, such as foraging mode, orientation or diet composition (Keast and Webb, 1966; Winemiller, 1992; Moyle and Cech, 2000). The results showed that Lisar specimens have upturned mouths but other populations have terminal mouths. The depth of Lisar river is low and maybe the fishes of this river are fed from surface. Other population might be expected to forage more frequently on these mid-water prey items in lagoon and rivers with enough depth. Mid-water foragers naturally show terminal mouths, benthic feeders exhibit sub-terminal mouths, and surface feeders have upturned mouths (Keast and Webb, 1966; Winemiller, 1992; Moyle and Cech, 2000).

The UPGMA graph shows two main branches, including Anzali's population as firs group and the rest in the second one. Further, the second branch is divided into two groups comprising (a) the Lisar and (b) the Babolroud and Shiroud populations.

As mentioned above, Anzali is a lagoon with different environmental condition rom rivers and this have been probably caused different body shape (Langerhans et al., 2003). Also, Lisar population is far from Shiroud and Babolroud ones and maybe little gene exchange between Lisar and others river populations (Via and Lande, 1985; West-Eberhard, 1989; Robinson and Wilson, 1994; Orr and Smith, 1998; Schluter, 2000), whereas, geographically, the Anzali and Lisar specimens are very close to each other, but showing a high shape differences. Hence, it seems that ecological pressures have more importance role in shape differences in Shemaya and gene exchange has less rate in equalization of the shape in populations. The member of branch including Shiroud and Babolroud have similar body shape with morphological common features. These two sites have similar environmental conditions rather than two others (Lisar and Anzali).

These results indicated that feeding habits (Coban, 2008; Langerhans, et al. 2003) and flow conditions (Langerhans, et al. 2003) along with geographical distance play an effective role in body shape variation in studied Shemaya populations and can be considered as main evolutionary drivers acting on aquatic biodiversity.

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References

Adriaens D. (2013). Aavailable from: http://www.funmorph.ugent.be.

Agrawal A.A. (2001). Phenotypic plasticity in the interactions and evolution of species. Science, 294: 321-326.

Alberch P., Gould S.J., Oster G.F., Wake D.B. (1979). Size and shape in ontogeny and phylogeny. Paleobiology, 1979: 296-317.

Bagherian A., Rahmani H. (2007). Morphological differentiation between two populations of the Shemaya, *Chalcalburnus chalcoides*: a geometrical morphometric approach. Zoology in the Middle East, 40: 53-62.

Balon E.K. (1993). Dynamics of biodiversity and mechanisms of change: a plea for balanced attention to form creation and extinction. Biological Conservation, 66: 5-16.

Blake R. (1983). Fish locomotion. Cambridge: Cambridge University Press.

Bogutskala N.G. (1997). Contribution of the knowledge of leucosis fishes of Asia Minor. Mitteilungen avs dem Hamburgischen Zoologischen Museum und Institiut, 94: 161–186.

Boily P., Magnan P. (2002). Relationship between individual variation in morphological characters and swimming costs in brook charr (*Salvelinus fontinalis*) and yellow perch (*Perca flavescens*). Journal of Experimental Biology, 205: 1031-1036.

Bookstein F.L. (1991). Morphometric Tools for Landmark Data. Geometry and Biology. Cambridge University Press.

Brinsmead J., Fox M. (2002). Morphological variation between lake-and stream-dwelling rock bass and pumpkinseed populations. Journal of fish biology, 61: 1619-1638.

Coban D., Saka S., Firat K. (2008). Morphometric Comparison of Cultured and Lagoon Caught Gilthead Seabream (*Sparus aurata* L. 1758). Turkish Journal of Zoology, 2008: 32: 337.

Endler J.A. (1977). Geographic variation, speciation, and clines. Princeton University Press.

Endler J.A. (1982). Convergent and divergent effects of natural selection on color patterns in two fish faunas. Evolution, 36: 178-188.

Gatz Jr A.J. (1979). Community organization in fishes as indicated by morphological features. Ecology, 1979: 711-718.

Hendry A.P., Wenburg J.K., Bentzen P., Volk E.C., Quinn T.P. (2000). Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon. Science, 290: 516-518.

Holtmeier C.L. (2001). Heterochrony, maternal effects, and phenotypic variation among sympatric pupfishes. Evolution, 55: 330-338.

Hugueny B., Pouilly M. (1999). Morphological correlates of diet in an assemblage of West African freshwater fishes. Journal of Fish Biology, 54: 1310-1325.

Jennions M., Telford S. (2002). Life-history phenotypes in populations of *Brachyrhaphis episcopi* (Poeciliidae) with different predator communities. Oecologia, 132: 44-50.

Johnson J.B., Belk M.C. (2001). Predation environment predicts divergent life-history phenotypes among populations of the live bearing fish *Brachyrhaphis rhabdophora*. Oecologia, 126: 142-149.

Jonsson B., Jonsson N. (2001). Polymorphism and speciation in Arctic charr. Journal of Fish Biology, 58: 605-638.

Kaneko K. (2002). Symbiotic sympatric speciation: consequence of interaction-driven phenotype differentiation through developmental plasticity. Population ecology, 44: 71-85.

Karr J.R., James F.C. (1975). Eco-morphological configurations and convergent evolution in species and communities. Cambridge, Ecology and evolution of communities. , 545p: 258-291.

Keast A., Webb D. (1966). Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. Journal of the Fisheries Board of Canada, 23: 1845-1874.

Klingenberg C.P. (1996). Multivariate allometry. In: Marcus, L.F., Corti, M., Loy, A., Naylor, G.J.P., Slice, D.E. (Eds.), Advances in Morphometrics. NATO ASI Series. Plenum Press, New York. 23–50.

Klingenberg C.P. (1998). Heterochrony and allometry: the analysis of evolutionary change in ontogeny. Biological Reviews, 73: 79-123.

Langerhans R.B., Layman C.A., Langerhans A.K., Dewitt T.J. (2003). Habitat-associated morphological divergence in two Neotropical fish species. Biological Journal of the Linnean Society, 80: 689-698.

Levins R. (1968). Evolution in Changing Environments: Some Theoretical Explorations. (MPB-2). Princeton University Press.

Losos J.B. (1996). Phylogenetic perspectives on community ecology. Ecology, 1995:1344-1354.

Losos J.B., Creer D.A., Glossip D., Goellner R., Hampton A., Roberts G., Haskell N., Taylor P., Ettling J. (2000). Evolutionary implications of phenotypic plasticity in the hindlimb of the lizard *Anolis sagrei*. Evolution, 54: 301-305.

Loy A., Mariani L., Bertelletti M., Tunesi L. (1998). Visualizing allometry: Geometric morphometrics in the study of shape changes in the early stages of the two-banded sea bream, *Diplodus vulgaris* (Perciformes, Sparidae). Journal of Morphology, 237: 137-146.

Magurran A.E. (1998). Population differentiation without speciation. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 353: 275-286.

Marcus L.F., Corti M., Loy A., Naylor G.J., Slice D.E. (1996). Advances in morphometrics. Plenum Press, New York. 587 p.

Mariani S., Maccaroni A., Massa F., Rampacci M., Tancioni L. (2002). Lack of consistency betweenthe trophic interrelationships of five sparid species in two adjacent central Mediterranean coastal lagoons. Journal of Fish Biology, 61: 138-147.

Matthews W.J. (1998). Patterns in Freshwater Fish Ecology. New York, Chapman and Hall: 757p.

Mittelbach G.G., Osenberg C.W., Wainwright P.C. (1999). Variation in feeding morphology between pumpkinseed populations: phenotypic plasticity or evolution? Evolutionary Ecology Research, 1: 111-128.

Moyle P.B., Cech, J. J. (2000). Prentice - Hall, Upper Saddle River 4th. New Jersey.

Orr M.R., Smith T.B. (1998). Ecology and speciation. Trends in Ecology and Evolution, 13: 502-506.

Pakkasmaa S., Piironen J. (2000). Water velocity shapes juvenile salmonids. Evolutionary Ecology, 14: 721-730.

Rice W.R., Hostert E.E. (1993). Laboratory experiments on speciation: what have we learned in 40 years? Evolution, 1993:1637-1653.

Robinson B.W., Wilson D.S. (1994). Character release and displacement in fishes: a neglected literature. American Naturalist, 1994: 596-627.

Robinson B.W., Wilson D.S. (1995). Experimentally induced morphological diversity in Trinidadian guppies (Poecilia reticulata). Copeia, 1995: 294-305.

Rohlf F.J. (1993). Relative warp analysis and example of its application to mosquito wings. p. 153-159. In: L. F. Marcus, I. Bello and A. Garcia-Valdecasas (Eds.), Contribution to Morphometrics. Museo Nacional de Ciencias Naturales, Madrid.

Rohlf F.J. (1998a). On applications of geometric morphometrics to studies of ontogeny and phylogeny. Systematic Biology, 47: 147- 158.

Rohlf F.J. (1998b). TpsREGR. New York. Department of Ecology and Evolution, State University, Stony Brook.

Rohlf F.J. (2003). TpsSmall–Thin Plate Spline Small Variation Analysis, Version 1.2 [Computer software]. Stony Brook: Dept. of Ecology and Evolution, State Univ. of New York.

Rohlf F.J. (2004). TpsDig–Thin Plate Spline Digitise, Version 1.4 [Computer software]. Stony Brook: Dept. of Ecology and Evolution, State Univ. of New York.

Rohlf F.J. (2008). TpsRelw. Version 1.46. Department of Ecology and Evolution, State University of New York at Stony Brook, New York.

Rohlf F.J., Marcus L.F. (1993). A revolution in morphometrics. Trend in ecology and evolution, 8: 129-133.

Ruzzante D.E., Walde S.J., Cussac V.E., Macchi P.J., Alonso M.F. (1998). Trophic polymorphism, habitat and diet segregation in *Percichthys trucha* (Pisces: Percichthyidae) in the Andes. Biological Journal of the Linnean Society, 65: 191-214.

Schluter D. (2000). The ecology of adaptive radiation. OUP Oxford.

Slastenenko E. (1959). Zoogeographical review of the Black Sea fish fauna. Hydrobiologia, 14: 177-188.

Slatkin M. (1987). Gene flow and the geographic structure of natural. Science, 236: 787-792

Smith T.B., Skulason S. (1996). Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. Annual Review of Ecology and Systematics, 1996: 111-133.

Sneath P.H., Sokal R.R. (1973). Numerical taxonomy. The principles and practice of numerical classification.

Taylor E., Harvey S., Pollard S., Volpe J. (1997). Postglacial genetic differentiation of reproductive ecotypes of kokanee *Oncorhynchus nerka* in Okanagan Lake, British Columbia. Molecular Ecology, 6: 503-517.

Taylor E.B. (1999). Species pairs of north temperate freshwater fishes: evolution, taxonomy, and conservation. Reviews in Fish Biology and Fisheries, 9: 299-324.

Van Buskirk J. (2002). A comparative test of the adaptive plasticity hypothesis: relationships between habitat and phenotype in anuran larvae. The American Naturalist, 160: 87-102.

Veasey E.A., Schammass E.A., Vencovsky R., Martins P.S., Bandel G. (2001). Germplasm characterization of *Sesbania accessions* based on multivariate analyses. Genetic Resources and Crop Evolution, 48: 79-91.

Via S., Lande R. (1985). Genotype-environment interaction and the evolution of phenotypic plasticity. Evolution, 1985: 505-522.

Videler J.J. (1993). Fish swimming. London:

Chapman and Hall.

Vogel S. (1994). Life in moving fluids: the physical biology of flow. Princeton, NJ: Princeton University Press.

Warburton K. (1979). Growth and production of some important species of fish in a Mexican coastal lagoon system. Journal of Fish Biology, 14: 449-455.

Watson D., Balon E. (1984). Ecomorphological analysis of fish taxocenes in rainforest streams of northern Borneo. Journal of Fish Biology, 25: 371-384.

Webb P. (1984). Body form, locomotion and foraging in aquatic vertebrates. American Zoologist, 24: 107-120.

West-Eberhard M.J. (1989). Phenotypic plasticity and the origins of diversity. Annual Review of Ecology and Systematics, 20: 249-278.

Whitfield A.K. (1999). Ichthyofaunal assemblages in estuaries: a South African case study. Reviews in Fish Biology and Fisheries, 9: 151-186.

Wimberger P.H. (1992). Plasticity of fish body shape. The effects of diet, development, family and age in two species of *Geophagus* (Pisces: Cichlidae). Biological Journal of the Linnean Society, 45: 197-218.

Wimberger P.H. (1994). Trophic polymorphisms, plasticity and speciation in vertebrates. In: Stouder DJ, Fresh KL, Feller RJ, eds. Theory and application in fish feeding ecology. Columbia: University of South Carolina Press, 1994: 9–43.

Winemiller K.O. (1991). Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. Ecological Monographs, 343-365.

Winemiller K.O. (1992). Ecomorphology of freshwater fishes. National Geographic Research and Exploration, 9: 344-357.