

## Research Article

# Phenotype-environment associations in common carp, *Cyprinus carpio* Linnaeus 1758, in the southern coast of the Caspian Sea

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### Abstract

The present study was done to investigate the phenotype-environment associations of common carp in the southern coast of the Caspian Sea (Gomishan, Miankaleh, Rezvanshahr, and Anzali Wetland) during winter 2016. The morphometric data of the specimens were procured from their left sides using the Image J and TpsDig2. Both geometric and morphometric methods were applied. The two-block partial least squares was used to examine the relationship between morphological and environmental characteristics. Significant positive correlation ( $p < 0.05$ ) was found between two data sets of morphology and environment, indicating a high level of adaptation for *C. carpio* in the southern basin of the Caspian Sea. The observed correlation between geometric and environmental data (0.74) was higher than the traditional morphometric-environment correlation (0.50). To the best of our knowledge, this is the first study trying to make a comparison between two methods of morphometric studies in relation to environment, by doing an evenness function on the raw data. The higher level of correlation obtained by geometric data with environmental parameters may imply its advantage in future morph-environment association studies. The obtained results in the present study also can provide basic required information for the wild population conservation strategies in common carp in the southern basin of the Caspian Sea.

**Keywords:** Body shape, Environmental adaptation, Geometric morphometric, Two-Block PLS analysis

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## Introduction

In different habitats, organisms face too different types of challenges, which together respond by phenotypical shifts. Various factors affect the shape and body form of fishes including physicochemical parameters (Crispo and Chapman, 2010), predation pressure (Andersson *et al.*, 2006; Langerhans, 2009), water flow (Langerhans, 2008) and feeding mode (Svanbäck and Eklöv, 2003; Andersson *et al.*, 2006; Ruehl and DeWitt, 2007). For example, fish inhabiting an environment with lentic water (e.g. wetlands) have a deep body with a well-developed caudal peduncle enhancing its maneuverability (Webb, 1982; Webb, 1984; Robinson and Wilson, 1994; Walker, 1997; Langerhans and Reznick, 2010; Ruehl *et al.*, 2011), while a fusiform body shape enables the fish to swim contiguously (Brönmark and Pettersson, 1994; Nilsson *et al.*, 1995; Domenici *et al.*, 2008). Thereby the observed phenotypes, are showing the effects of some environmental variants in addition to other evolutionary factors (gene flow, genetic drift, etc.).

Physicochemical parameters are the inevitable parts of habitats, which have a main role on intra- and inter-specific variations of fishes. In fact, environmental factors may have a different magnitude of effects on organisms in different habitats and their impacts are being influenced by other factors (Crispo and Chapman, 2010). Morphological variations of a species across the gradients of environmental

parameters may indicate environment-phenotype associations (Wainwright *et al.*, 1991). Analyzing the relationship between morphological characteristics and the environmental parameters would be worthwhile to comprehend the phenotype-environment associations (Caumul and Polly, 2005; Hoverman *et al.*, 2005; Langerhans *et al.*, 2007). In this regard, quantification of such association may be rather difficult. Such associations mostly have an adaptive nature (Schluter, 2000, Nyboer and Chapman, 2013) and reflect the processes that make and conserve variation of traits in natural populations as the main goal of evolutionary biology (West-Eberhard, 1989; Pigliucci, 2005; Langerhans, 2008; Pfennig *et al.*, 2010; Levis and Pfennig, 2016).

Finding and assessing these relationships are a bit difficult, for example, one environmental factor may have a direct positive effect on a specific trait but indirectly can reduce that trait by its effect on the other environmental factors (Pigliucci and Preston, 2004; Marks *et al.*, 2005). Morphological variations induced in organisms can be assessed either by considering some morphometric traits or the variations induced in the form of the fish's body. Therefore, it is probable to miss some morphological variations if the attention goes for one of them. In this study in order to investigate that the morphological variations occurred between different locations of common carp, both methods including traditional morphometric and Geometric

morphometric (Adams *et al.*, 2004) were applied.

*Cyprinus carpio* is a species with a worldwide range of distribution and is naturally well dispersed in the Caspian Sea (Mazaheri Kouhestani *et al.*, 2020). This species is present throughout the southern parts of the Caspian Sea and several population genetic studies using DNA markers have proposed different populations of common carp across the southern basin (Laloei *et al.*, 2013; Ghelichpour *et al.*, 2010). The southern parts of the Caspian Sea exhibit different environmental conditions regarding annual mean temperature, depth and shore flow type (Mehdipour *et al.*, 2015; Nouri *et al.*, 2008). Therefore, the extended distribution range of common carp in southern coast of the Caspian Sea can reflect its adaptation capability to the specific environmental conditions in these regions. Furthermore, the strain existing in the Anzali Wetland is accepted to be the permanent resident of the lagoon (the resident form), while the sea-form (migratory population) moves towards the shallow freshwater rivers to spawn between winter and spring (Vazirzadeh and Yelghi, 2015). Considering these facts, *C. carpio* can be a suitable model in phenotype-environment association studies. Hence, based on the current knowledge of the authors, the present study has been conducted for the first time to investigate the relationship between environmental factors and phenotypic traits of common carp in the southern coasts of the Caspian Sea

using both geometric and traditional morphometric approaches.

## Material and methods

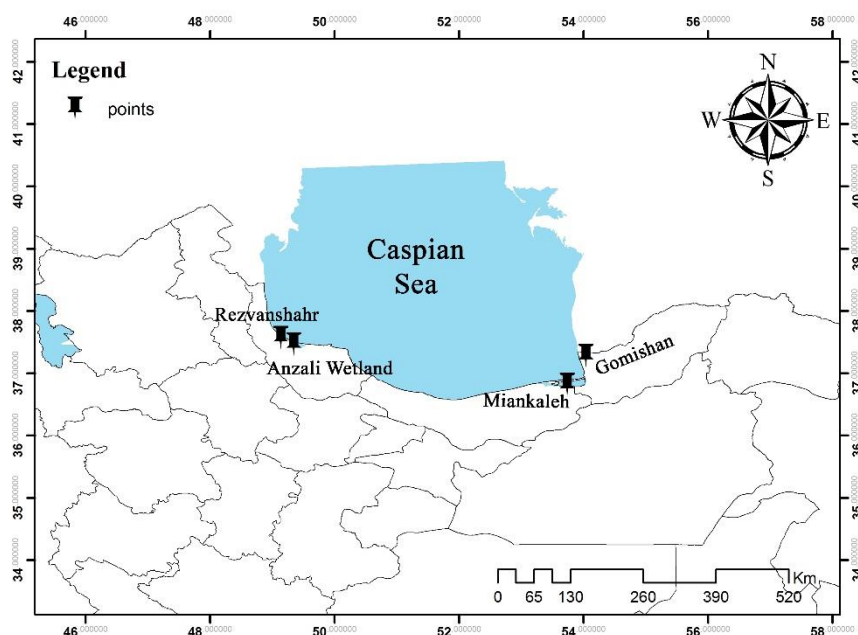
### Sampling

100 specimens were collected from four locations in the Southern Caspian Sea during winter 2016 (Fig. 1): Gomishan (GW; E: 53°29', N: 37°51'), Miankaleh (MK; E: 53°30', N: 36°52'), Rezvanshahr (RS; E: 49° 8', N: 37°34') and the Anzali wetland (AW; E: 49°26', N: 37°25'). The specimens were anesthetized using tricaine mesylate (MS-222, Syndel USA), and their left sides were photographed for morphometric analyses. Seven water samples were collected by random in each location to measure pH, total dissolved solids (TDS), total suspended solids (TSS), alkalinity, electrical conductivity (EC), salinity, PO<sub>4</sub>, NO<sub>3</sub>, NO<sub>2</sub>, NH<sub>3</sub>, temperature, and turbidity. Temperature, salinity, EC, pH, and turbidity were measured using an electronic device (<sup>®</sup>Wag tech, England). NO<sub>3</sub>, PO<sub>4</sub>, NO<sub>2</sub>, NH<sub>3</sub>, and alkalinity were measured using a photometer (Palin Test<sup>®</sup> photometer 7100). TSS was measured using a standard method (Rieger *et al.*, 2004).

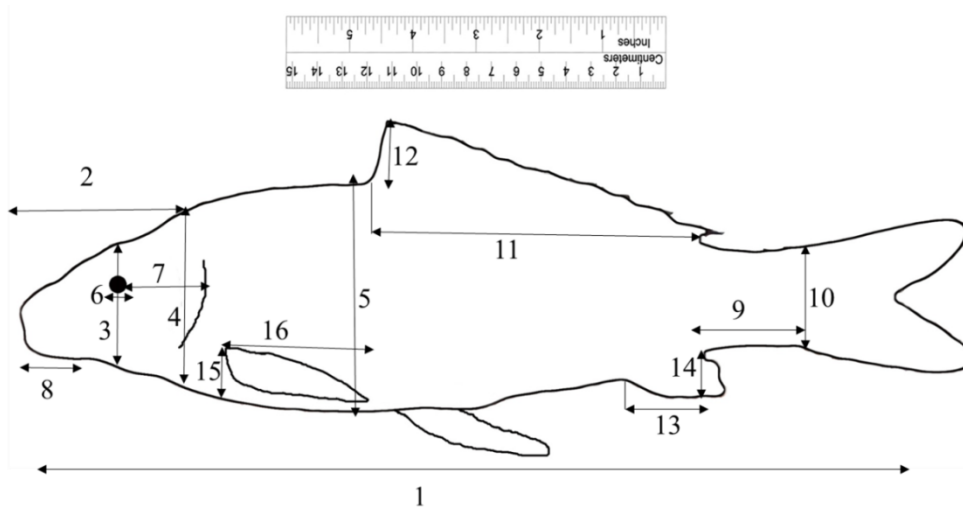
### Morphometric analysis

#### Traditional morphometrics

Sixteen morphometric distances were measured using Image J version 1.45s (Fig. 2). The size component from multivariate data sets of measured distances was removed based on the method described by Elliott *et al.* (1995) using the software PAST version 3 (Hammer *et al.*, 2001).



**Figure 1:** The investigated locations of common carp in the southern coast of the Caspian Sea.



**Figure 2:** Morphometric characteristics of the Caspian common carp; 1(FL): fork length, 2(HL): head length, 3(HH1): head height on eye area, 4(HH2): maximum head height, 5(BD): body depth, 6(ED): eye diameter, 7(POL): post orbital length, 8(ML): mouth width length, 9(CPL): caudal peduncle length, 10(CPH): caudal peduncle height, 11(DBL): dorsal base length, 12(DH): dorsal fin height, 13(ABL): anal base length, 14(AH): anal fin height, 15(PBL): pectoral base length, 16(PH): pectoral fin height.

### *Geometric morphometrics*

Fourteen landmark points were digitized on the images using the software TpsDig2 version 2.10 (Fig. 3). A generalized Procrustes analysis was used to remove the effects of size,

rotation, and translation from the landmark data ;( Rohlf and Slice, 1990; Rohlf, 2001; Klingenberg, 2011). The environmental parameters were standardized to have a range of 0-1 (Zuur *et al.*, 2007) because they had

different dimensions. A two-block partial least squares (PLS) was used to examine the covariation between morphometric data and environmental

parameters using the package Geomorph in R (Rohlf and Corti, 2000).

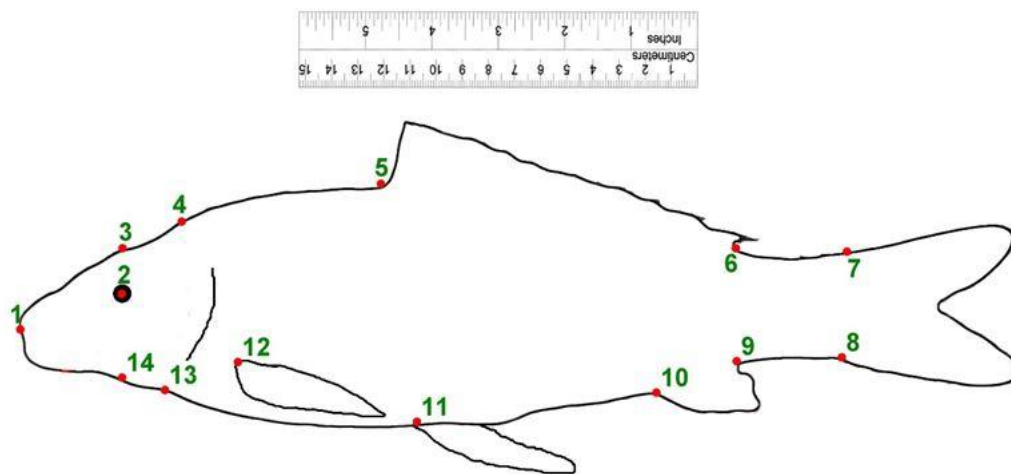


Figure 3: The digitized landmark points on the Caspian common carp.

## Results

Environmental and morphometric data are presented in Tables 1 and 2. The

highest mean ( $\pm$ SE) temperature ( $14.56\pm 0.24$ ) and nitrate concentration ( $0.37\pm 0.09$ ) were found in RS (Table 1).

Table 1: The mean ( $\pm$  SE) of the environmental parameters measured in the Southern Caspian Sea.

Location*	pH	Temperature (°C)	salinity (ppt)	EC ( $\mu$ s)	Turbidity (NTU)	NH <sub>3</sub> (mg/L)	NO <sub>3</sub> (mg/l)	NO <sub>2</sub> (mg/l)	Alkalinity (mg/L CaCO <sub>3</sub> )	PO <sub>4</sub> (mg/L)	TSS (mg/L)
MK	8.42 $\pm$ 0.01	13.29 $\pm$ 0.25	11.94 $\pm$ 0.31	547.22 $\pm$ 2.31	5.84 $\pm$ 1.07	5.40 $\pm$ 2.84	0.08 $\pm$ 0.04	0.46 $\pm$ 0.20	177.5 $\pm$ 10.30	3 $\pm$ 0.83	0.05 $\pm$ 0.01
GW	8.40 $\pm$ 0.003	12.71 $\pm$ 0.09	20.50 $\pm$ 2.07	594.75 $\pm$ 4.53	173.6 $\pm$ 63.59	3.38 $\pm$ 1.78	0.31 $\pm$ 0.10	0.00	152.5 $\pm$ 4.78	0.5 $\pm$ 0.07	0.65 $\pm$ 0.18
AW	8.34 $\pm$ 0.11	14.46 $\pm$ 0.46	0.45 $\pm$ 0.08	128.87 $\pm$ 6.05	3.42 $\pm$ 0.92	2.95 $\pm$ 1.28	0.27 $\pm$ 0.04	0.02 $\pm$ 0.003	123.33 $\pm$ 11.81	0.22 $\pm$ 0.13	0.10 $\pm$ 0.02
RS	8.46 $\pm$ 0.01	14.56 $\pm$ 0.24	5.87 $\pm$ 0.39	426.71 $\pm$ 54.64	10.12 $\pm$ 3.84	1.50 $\pm$ 0.88	0.37 $\pm$ 0.09	0.01 $\pm$ 0.006	171 $\pm$ 6.78	0.82 $\pm$ 0.28	0.19 $\pm$ 0.08

\*MK: Miankaleh, GW: Gomishan, AW: Anzali Wetland, RS: Rezvanshahr

For morphometric data, the highest ( $46.75\pm 2.26$ ) and lowest ( $28.07\pm 0.94$ ) mean values of the FL were found in RS and AW locations, respectively (Table 2). Three dimensions were extracted from the two-block PLS using the singular value and the relevant scree plot (Figure 4). There was a significant positive correlation between scores of the projected values on the first singular vectors of the traditional morphometric

data (morphometric distances) and the water parameters ( $r=0.498$ ,  $P=0.01$ ).

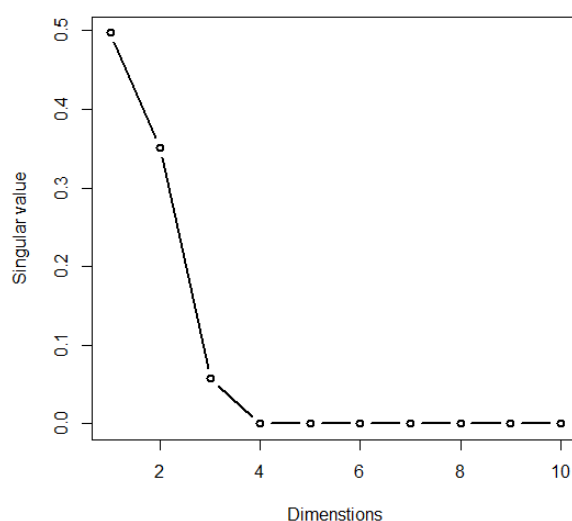
Nitrate was correlated with HH1, HL, pH, BD, POL, ED, and PBL. pH was correlated with HL and CPH. The temperature was highly correlated to the morphometric parameters FL, POL, DH, ABL, and pH. The attributes ED, FL, ML, and ABL, displayed high correlation with salinity. Ammonia, turbidity, and phosphate were correlated with the parameters HH2, HH1, and

BD, respectively. Alkalinity was correlated to ABL, BD, and PBL and the environmental parameter, nitrogen dioxide, had a positive correlation with CPL and DBL (Fig. 5).

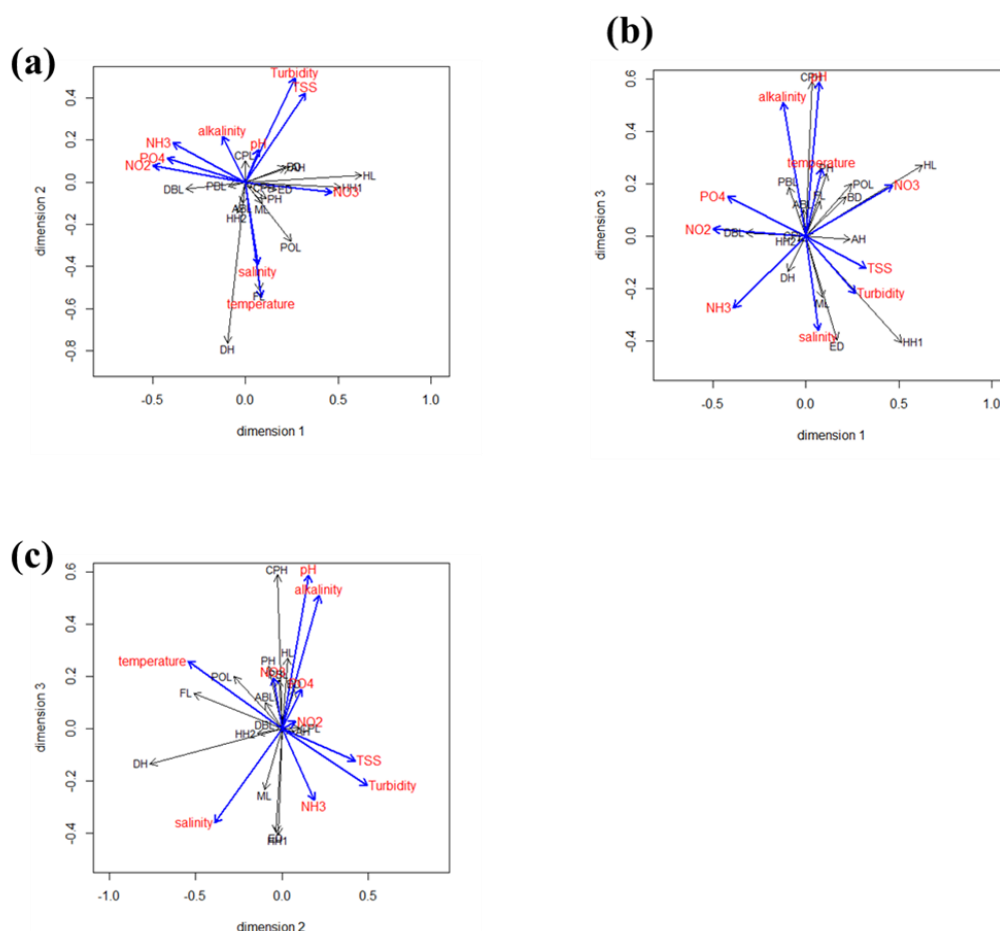
**Table 2: The mean (cm)  $\pm$  SE of morphometric parameters and weight measurements in *Cyprinus carpio* in the Southern Caspian Sea.**

Morphometric and weight characteristics	Mean $\pm$ SE			
	AW	MK	GW	RS
FL	28.07 $\pm$ 0.94	36.25 $\pm$ 1.53	32.93 $\pm$ 1.54	46.75 $\pm$ 2.26
HL	4.88 $\pm$ 0.31	5.76 $\pm$ 0.28	5.96 $\pm$ 0.23	9.09 $\pm$ 0.44
HH1	5.97 $\pm$ 0.22	6.99 $\pm$ 0.27	7.03 $\pm$ 0.31	9.88 $\pm$ 0.59
HH2	3.49 $\pm$ 0.13	4.28 $\pm$ 0.17	3.88 $\pm$ 0.20	5.28 $\pm$ 0.29
BD	7.86 $\pm$ 0.30	9.97 $\pm$ 0.41	9.35 $\pm$ 0.34	12.94 $\pm$ 0.58
ED	1.33 $\pm$ 0.04	1.35 $\pm$ 0.08	1.45 $\pm$ 0.05	1.88 $\pm$ 0.12
POL	3.32 $\pm$ 0.13	3.82 $\pm$ 0.18	3.66 $\pm$ 0.16	5.93 $\pm$ 0.30
ML	1.26 $\pm$ 0.07	1.36 $\pm$ 0.07	1.33 $\pm$ 0.08	1.89 $\pm$ 0.08
CPL	3.21 $\pm$ 0.18	4.56 $\pm$ 0.27	4.12 $\pm$ 0.24	5.90 $\pm$ 0.40
CPH	3.21 $\pm$ 0.11	4.17 $\pm$ 0.14	3.83 $\pm$ 0.15	5.68 $\pm$ 0.26
DBL	9.35 $\pm$ 0.31	12.47 $\pm$ 0.57	10.97 $\pm$ 0.49	14.70 $\pm$ 0.83
DH	2.91 $\pm$ 0.18	3.09 $\pm$ 0.27	2.45 $\pm$ 0.20	4.38 $\pm$ 0.27
ABL	2.10 $\pm$ 0.07	2.60 $\pm$ 0.10	2.34 $\pm$ 0.11	3.37 $\pm$ 0.28
AH	1.44 $\pm$ 0.17	1.76 $\pm$ 0.10	1.86 $\pm$ 0.09	2.82 $\pm$ 0.27
PBL	1.02 $\pm$ 0.07	1.43 $\pm$ 0.07	1.20 $\pm$ 0.06	1.70 $\pm$ 0.13
pH	4.56 $\pm$ 0.26	5.73 $\pm$ 0.26	5.34 $\pm$ 0.25	7.77 $\pm$ 0.42
W (gr)	344.78 $\pm$ 38.08	841.57 $\pm$ 112.44	694.44 $\pm$ 186.77	1653.8 $\pm$ 230.9

FL: Fork Length, HL: Head Length, HH1: Head Height in optical area, HH2: Maximum Head Height, BD: Body Depth, ED: Eye Diameter, POL: Post Orbital Length, ML: Mouth Length, CPL: Caudal Peduncle Length, CPH: Caudal Peduncle Height, DBL: Dorsal fin Base Length, DH: Dorsal Fin Height, ABL: Anal fin Base Length, AH: Anal fin Height, PBL: Pectoral fin Base Length, pH: Pectoral fin Height, W: Weight (gr).



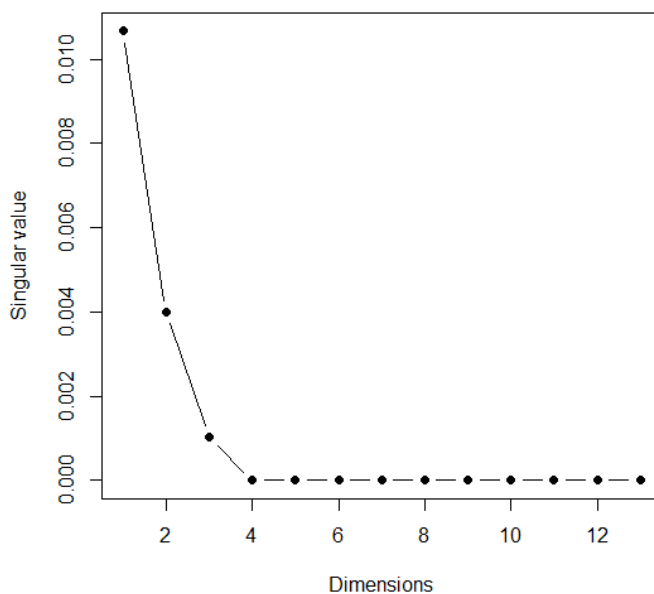
**Figure 4: The scree plot of the singular values from the two-block PLS calculated using the morphometric distance data (traditional morphometric).**



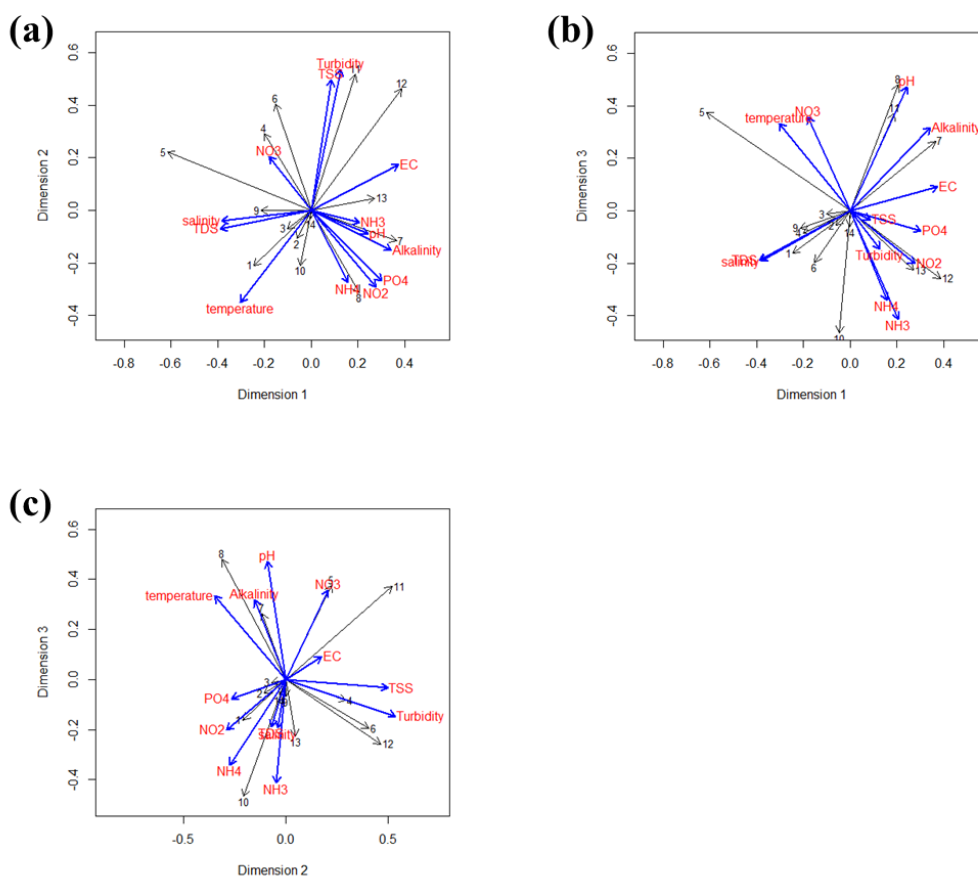
**Figure 5: The biplots of morphometric and environmental (water) data for the first three dimensions.**

Based on 1000 random permutation test through two-block PLS analysis ( $r=0.745$ ,  $p=0.001$ ), there was a significant positive correlation between scores of the projected values on the first singular vectors of the distance of the landmarks from the centroid and the water parameters. Three dimensions were extracted from the two-block PLS using the singular value and the relevant scree plot (Figure 6). Turbidity and Total Suspended Solids (TSS) had the highest correlation with the distance of the landmark 11 from the centroid (the position of the pelvic fin). Nitrate had the maximal correlation with the

centroid distance of the landmark 4 (related to the head position). Temperature was highly correlated with the distances of the landmarks of 1, 2, 3, 10, and 14 from the centroid and the highest correlation was seen with the centroid distance of the first landmark. In addition, salinity and TDS displayed high correlation with the distance of the landmark point 9 from the centroid (related to the anal fin). The relationships between these two sets of data (landmark points and environmental parameters) are available at a biplots under Fig. 7.



**Figure 6:** The scree plot of the singular values of the two-block PLS calculated from the distance between the landmark coordinate and the centroid (geometric morphometric).



**Figure 7:** The biplots of the landmark coordinates and environmental (water) data for the first three dimensions.



## Discussion

This study investigated the morphology association (traditional and geometric) data belonged to *Cyprinus carpio* with environmental parameters in the southern coast of the Caspian Sea. The two-block PLS has indicated that there was a significant correlation between morphological and environmental parameters as examined using both traditional and geometric data. In comparison with a traditional morphology, which is focused on linear distances, the geometric morphometric mostly considers the form of body based on landmark's coordinates. Adams *et al.* (2004) concluded that morphological variations through geometric approach is better than traditional approach, as we took out higher correlation and significance from this approach in this study (Zelditch *et al.*, 2012). A two-Block PLS on traditional data indicated that the caudal peduncle form (CPL and CPH) had positive correlations with pH, alkalinity, nitrate, and nitrogen dioxide. These environmental variables except nitrate had shown their correlations by variations in landmark points of caudal peduncle (7 and 8) through geometric approach (Figs. 5 and 7). The head morphology (head length and head height) showed high correlation with nitrate. Similarly, the geometric approach showed correlation between nitrate and landmarks as related to the head shape. Bouton *et al.* (2002), found that eight ecological variables influenced the head shape of haplochromines in the Lake Victoria.

Also, Crispo and Chapman (2010) investigated the effects of hypoxia on body shape variations of cichlid and found big heads in waters with low oxygen levels.

We found a high correlation between temperature and head morphology through two morphological methods, traditional and geometric methods. High temperature increases the oxygen demand of fishes. Dissolved oxygen was not measured in this study, however, the variations in the head size might have been related to the direct effect of oxygen demand which is in agreement with Crispo and Chapman (2010).

Phenotypic traits may show different correlations in different size and age classes (Nyboer and Chapman, 2013). In the study on Nile perch, *Lates niloticus*, the different size classes (small, medium, and large size classes) of *L. niloticus* were investigated the oxygen level in each location and by this approach; they could remove the effect of size and allometric growth on the observed variations. In this study, morphological (geometric and traditional based) and ecological data were first standardized, and then the associations were investigated. So the observed associations were not affected by the size of the variants.

The maximum value of nitrate was found in the RS (Guilan province, southwest of the Caspian Sea) which had the specimens with heads bigger than those of other specimens (higher values for the head length and height in eye area). Furthermore, the water

temperature at this location was higher than other locations increasing the oxygen demand. The role of nitrate in fish adaptation to hypoxia has been well identified (Dolomatov *et al.*, 2016), so the higher amount of nitrate may be one of the more important factors in fish adaptation in the southern coast of the Caspian Sea.

A distinctive negative correlation was found between salinity and the gill shape in both morphometric approaches (Figs. 5 and 7). Having a smaller gill in salt waters may be a function of adaptation for osmoregulation so that the fish can keep more salts and so keep their osmotic pressure close to the environment. Ecological factors can show their effects on phenotype directly and indirectly. Langerhans *et al.* (2007) found that water flow and dissolved oxygen have direct or indirect effects on gill size, body form and the shape of caudal fin on *Barbus neumayeri*. Also, temperature, as an important ecological variable, showed both positive and negative correlation with dorsal fin (in traditional morphometric) and the position of pectoral fin (In geometric morphometric) respectively, which is somehow in agreement by the results obtained from 88 samples of *Schizothorax richardsonii*. The observed difference between two methods of morphology is probably due to the difference of their views and visualizing of traits.

The results of this study show somewhat convergence between relationship of geometric and traditional

morphometric and the association of environmental parameters with the higher level of assurance for the geometric morphometric approach. The findings of this study present new information about morpho-environmental association across the southern coasts of the Caspian Sea for *C. Carpio* as a native species. It is therefore suggested that evaluating effects of ecological parameters may provide valuable information on stocks reestablishment and thus yearly investigation is recommended. This is the first investigation of phenotype environment association with two morphological methods performed in the Caspian Sea.

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#### References

- Adams, D.C., Rohlf, F.J. and Slice, D.E., 2004.** Geometric morphometrics: ten years of progress following the 'revolution'. *Italian Journal of Zoology*, 71, 5-16. DOI: 10.1080/11250000409356545
- Andersson, J., Johansson, F. and Södelund, T., 2006.** Interactions between predator-and diet-induced phenotypic changes in body shape of crucian carp. *Proceedings of the Royal Society of London B:*

- Biological Sciences*, 273, 431-437. DOI: 10.1098/rspb.2005.3343
- Bouton, N., Visser, J.D. and Barel, C.D., 2002.** Correlating head shape with ecological variables in rock-dwelling haplochromines (Teleostei: Cichlidae) from Lake Victoria. *Biological Journal of the Linnean Society*, 76, 39-48.
- Brönmark, C. and Pettersson, L.B., 1994.** Chemical cues from piscivores induce a change in morphology in crucian carp. *Oikos*. pp. 396-402.
- Caumul, R. and Polly, P.D., 2005.** Phylogenetic and environmental components of morphological variation: skull, mandible, and molar shape in marmots (Marmota, Rodentia). *Evolution*, 59, 2460-2472. DOI: 10.1111/j.0014-3820.2005.tb00955.x
- Vazirzadeh, A. and Yelghi, S., 2015.** Long-term changes in the biological parameters of wild carp (*Cyprinus carpio carpio*) from the south-eastern Caspian Sea. *Iranian Journal of Science and Technology (Sciences)*, 39(3), 391-397. DOI: 10.22099/IJSTS.2015.3262
- Crispo, E. and Chapman, L., 2010.** Geographic variation in phenotypic plasticity in response to dissolved oxygen in an African cichlid fish. *Journal of evolutionary Biology*, 23, 2091-2103. DOI: 10.1111/j.1420-9101.2010.02069.x
- Dolomatov, S., Zukow, W., Dzierzanowski, M., Mieszkowski, J., Muskieta, R. and Klimczyk, M., 2016.** Role of nitrates in the adaptation of fish to hypoxic conditions. *Water resources*, 43, 177-183. DOI: 10.1134/S0097807816120046
- Domenici, P., Turesson, H., Brodersen, J. and Brönmark, C., 2008.** Predator-induced morphology enhances escape locomotion in crucian carp. *Proceedings of the Royal Society of London B: Biological Sciences*, 275, 195-201. DOI: 10.1098/rspb.2007.1088
- Elliott, N.G., Haskard, K. and Koslow, J.A., 1995.** Morphometric analysis of orange roughy (*Hoplostethus atlanticus*) off the continental slope of southern Australia. *Journal of Fish Biology*, 46(2), 202-220. DOI: 10.1111/j.1095-8649.1995.tb05962.x
- Ghelichpour, M., Shabani, A. and Shabanpour, B., 2010.** Genetic diversity of the two populations of Common carp (*Cyprinus carpio*) in Gharahsu and Anzali regions using eight microsatellite markers. *Taxonomy and Biosystematics*, 2(5), 41-48.
- Hammer, Ø., Harper, D. and Ryan, P., 2001.** Paleontological statistics software: package for education and data analysis. *Palaeontologia Electronica*, 4(1), 1-9.
- Hoverman, J.T., Auld, J.R. and Relyea, R.A., 2005.** Putting prey back together again: integrating predator-induced behavior, morphology, and life history. *Oecologia*, 144, 481-491. DOI: 10.1007/s00442-005-0082-8
- Klingenberg, C.P., 2011.** MorphoJ: an integrated software package for

- geometric morphometrics. *Molecular ecology resources*, 11, 353-357. DOI: 10.1111/j.1755-0998.2010.02924.x.
- Laloei, F., Gilkolaei, S.R. and Taghavi, M.J., 2013.** Genetic diversity and differentiation of common carp (*Cyprinus carpio* L.) in the southern part of Caspian Sea by using microsatellite markers. *Asian Fisheries Science*, 26(2), 115-127. DOI: 10.33997/j.afs.2013.26.2.004
- Langerhans, R., Chapman, L. and Dewitt, T., 2007.** Complex phenotype-environment associations revealed in an East African cyprinid. *Journal of Evolutionary Biology*, 20, 1171-1181. DOI: 10.1111/j.1420-9101.2007.01282.x.
- Langerhans, R.B., 2008.** Predictability of phenotypic differentiation across flow regimes in fishes. *Integrative and Comparative Biology*, 48, 750-768. DOI:10.1093/icb/icn092
- Langerhans, R.B., 2009.** Trade-off between steady and unsteady swimming underlies predator-driven divergence in *Gambusia affinis*. *Journal of Evolutionary Biology*, 22, 1057-1075. DOI: 10.1111/j.1420-9101.2009.01716.x
- Langerhans, R.B. and Reznick, D.N., 2010.** Ecology and evolution of swimming performance in fishes: predicting evolution with biomechanics. *Fish Locomotion: An Eco-Ethological Perspective*, 200-248.
- Levis, N.A. and Peennig, D.W., 2016.** Evaluating 'plasticity-first' evolution in nature: key criteria and empirical approaches. *Trends in Ecology and Evolution*, 31, 563-574. DOI: 10.1016/j.tree.2016.03.012
- Marks, C., West, T.N., Bagatto, B. and Moore, F.B., 2005.** Developmental environment alters conditional aggression in zebrafish. *Copeia*, 2005, 901-908. DOI: 10.1643/0045-8511(2005)005[0901:DEACAI]2.0.CO;2
- Mazaheri Kouhanestani, Z., Ghorbani, R., Fujiwara, M., Rabbaniha, M., Amini, K. and Mahmoodi, S., 2020.** Identification of larval stages of fish in southeastern coastal waters of the Caspian Sea- Golestan Province. *Iranian Journal of Fisheries Sciences*. 19(1), 325-339. DOI: 10.22092/ijfs.2018.119806.
- Mehdipour, N., Gerami, M.H., Nemati, H., Rahnama, R. and Hamzehpour, A., 2015.** Spatial and Temporal Variation of Macroalgae along the Southern Coasts of the Caspian Sea Relating to Environmental Parameters. *Journal of the Persian Gulf*, 6, 65-73.
- Nilsson, P. A., Brönmark, C. and Pettersson, L.B., 1995.** Benefits of a predator-induced morphology in crucian carp. *Oecologia*, 104, 291-296.
- Nouri, J., Karbassi, A. and Mirkia, S., 2008.** Environmental management of coastal regions in the Caspian Sea. *International Journal of Environmental Science and*

- Technology*, 5, 43-52. DOI: 10.1007/BF03325996
- Nyboer, E.A. and Chapman, L.J., 2013.** Ontogenetic shifts in phenotype–environment associations in Nile perch, *Lates niloticus* (Perciformes: Latidae) from Lake Nabugabo, Uganda. *Biological Journal of the Linnean Society*, 110, 449-465. DOI: 10.1111/bij.12122
- Peennig, D.W., Wund, M.A., Snell-Rood, E.C., Cruickshank, T., Schlichting, C.D. and Moczek, A.P., 2010.** Phenotypic plasticity's impacts on diversification and speciation. *Trends in Ecology and Evolution*, 25, 459-467. DOI: 10.1016/j.tree.2010.05.006
- Pigliucci, M. and Preston, K., 2004.** *Phenotypic integration: studying the ecology and evolution of complex phenotypes*, Oxford University Press.
- Pigliucci, M., 2005.** Evolution of phenotypic plasticity: where are we going now? *Trends in Ecology and Evolution*, 20, 481-486. DOI: 10.1016/j.tree.2005.06.001
- Rieger, L., Langergraber, G., Thomann, M., Fleischmann, N. and Siegrist, H., 2004.** Spectral in-situ analysis of NO<sub>2</sub>, NO<sub>3</sub>, COD, DOC and TSS in the effluent of a WWTP. *Water Science and Technology*, 50(11), 143-152. DOI: 10.2166/wst.2004.0682
- Robinson, B.W. and Wilson, D.S., 1994.** Character release and displacement in fishes: a neglected literature. *The American Naturalist*, 144, 596-627.
- Rohlf, F.J. and Slice, D., 1990.** Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Biology*, 39, 40-59.
- Rohlf, F.J. and Corti, M., 2000.** Use of two-block partial least-squares to study covariation in shape. *Systematic Biology*, 49, 740-753.
- Rohlf, F.J., 2001.** Comparative methods for the analysis of continuous variables: geometric interpretations. *Evolution*, 55, 2143-2160.
- Rohlf, C.B. and DeWitt, T.J., 2007.** Trophic plasticity and foraging performance in red drum, *Sciaenops ocellatus* (Linnaeus). *Journal of Experimental Marine Biology and Ecology*, 349, 284-294. DOI: 10.1016/j.jembe.2007.05.017
- Ruehl, C.B., Shervette, V. and Dewitt, T.J., 2011.** Replicated shape variation between simple and complex habitats in two estuarine fishes. *Biological Journal of the Linnean Society*, 103, 147-158. DOI: 10.1111/j.1095-8312.2011.01626.x
- Schluter, D., 2000.** *The Ecology of Adaptive Radiation* (Oxford Series in Ecology and Evolution (Paper)).
- Svanbäck, R. and Eklöv, P., 2003.** Morphology dependent foraging efficiency in perch: a trade-off for ecological specialization? *Oikos*, 102, 273-284.
- Wainwright, P., Osenberg, C. and Mittelbach, G., 1991.** Trophic polymorphism in the pumpkinseed sunfish (*Lepomis gibbosus* Linnaeus): effects of environment on

ontogeny. *Functional Ecology*, 40-55.

**Walker, J.A., 1997.** Ecological morphology of lacustrine threespine stickleback *Gasterosteus aculeatus* L.(Gasterosteidae) body shape. *Biological Journal of the Linnean Society*, 61, 3-50.

**Webb, P.W., 1982.** Locomotor patterns in the evolution of actinopterygian fishes. *American Zoologist*, 22, 329-342.

**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.

**Zelditch, M.L., Swiderski, D.L. and Sheets, H.D., 2012.** *Geometric morphometrics for biologists: a primer*, Academic Press. DOI: 10.1016/B978-0-12-778460-1.X5000-5

**Zuur, A.F., Ieno, E.N. and Smith, G.M., 2007.** *Analysing Ecological Data*, USA, Springer.