

Morphological diversity and relationships of *Scardinius dergle* and *Scardinius plotizza* populations (Actinopteri; Cypriniformes) from Croatia and Bosnia and Herzegovina

Morfološka raznolikost i odnosi populacija *Scardinius dergle* i *Scardinius plotizza* (Actinopteri; Cypriniformes) iz Hrvatske i Bosne i Hercegovine

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ABSTRACT

Genus *Scardinius* (Cypriniformes, Actinopteri) belongs to the family Leuciscidae, subfamily Leuciscinae, and it includes 10 species. Phylogenetic and morphometric research conducted so far have shown a great taxonomic complexity within this genus. Therefore, the aim of this research was to determine the morphological diversity and contribute to the clarification of taxonomic relationships and status of *S. dergle* and *S. plotizza*. For the purpose of this research specimens of *S. dergle* and *S. plotizza* were collected from their whole distribution area in Croatia and Bosnia and Herzegovina. On each individual 25 morphometric characters were measured, standardized with allometric conversion and analysed using descriptive and inferential statistics. Results showed significant intra- and interspecific differences in investigated morphometric characters. In addition, distinct grouping of populations of each species and partial overlapping of some populations of both species was recorded, reflecting their possible relationships. Also, investigated meristic characters showed accordance with deterministic values for most investigated populations. Although this research has given indications of relationships and the status of populations of *S. dergle* and *S. plotizza*, in order to confirm the results and determine the exact taxonomic status, phylogenetic relationships and genetic diversity of these species, further phylogenetic research is needed.

Keywords: genus *Scardinius*, morphology, Adriatic basin, endemic species

SAŽETAK

Rod *Scardinius* (Cypriniformes, Actinopteri) pripada porodici Leuciscidae, potporodici Leuciscinae, a obuhvaća 10 vrsta. Do sada provedena filogenetička i morfometrijska istraživanja pokazala su veliku taksonomsku složenost unutar ovog roda. Stoga, cilj ovog istraživanja bio je utvrditi morfološku raznolikost i pridonijeti razjašnjenu taksonomskih odnosa i statusa *S. dergle* i *S. plotizza*. U svrhu ovog istraživanja uzorci *S. dergle* i *S. plotizza* prikupljeni su sa cijelog njihovog područja rasprostranjenosti u Hrvatskoj i Bosni i Hercegovini. Na svakoj jedinici izmjereno je 25 morfometrijskih značajki, koje su standardizirane alometrijskom pretvorbom i analizirane pomoću deskriptivne i inferencijalne statistike. Rezultati su pokazali značajne intra- i interspecifične razlike u ispitivanim morfometrijskim značajkama. Uz to, zabilježeno je zasebno grupiranje populacija svake vrste i djelomično preklapanje nekih populacija obje vrste, odražavajući njihove

moguće odnose. Također, zabilježene merističke značajke su u skladu s determinističkim vrijednostima za većinu istraživanih populacija. Iako je ovo istraživanje dalo indikacije odnosa i statusa populacija *S. dergle* i *S. plotizza*, kako bi se potvrdili rezultati i utvrdio točan taksonomski status, filogenetički odnosi i genetska raznolikost ovih vrsta, potrebna su daljnja filogenetička istraživanja.

Ključne riječi: rod *Scardinius*, morfologija, Jadranski slijev, endemske vrste

INTRODUCTION

Genus *Scardinius* (Cypriniformes, Actinopteri) belongs to the family Leuciscidae, subfamily Leuciscinae, and includes 10 species: *S. acarnicus* Economidis, 1991; *S. dergle* Heckel & Kner, 1858; *S. elmaliensis* Bogutskaya, 1997, *S. erythrophthalmus* (Linnaeus, 1758), *S. graecus* Stephanidis, 1937, *S. hesperidicus* Bonaparte, 1845, *S. knezevici* Bianco & Kottelat, 2005, *S. plotizza* Heckel & Kner, 1858, *S. racovitzai* Müller, 1958, and *S. scardafa* (Bonaparte, 1837) (Bogutskaya, 1997; Kottelat and Freyhof, 2007; Fricke et al., 2020). Nominal species, the common Rudd *S. erythrophthalmus*, is widespread, while other species have a narrow geographic distribution. Due to the great morphological similarity of these species, as well as the lack of the detailed phylogenetic research, taxonomic position and the exact distribution of species within this genus have long been the subject of discussions and are still not fully clarified (Karaman, 1928; Vuković and Ivanišević, 1962; Ketmaier et al., 2003, 2004; Bianco and Kottelat, 2005; Perea et al., 2010).

Species *S. dergle* and *S. plotizza* are regional endemic species of the Adriatic basin, with an area of distribution limited to the territory of Croatia and Bosnia and Herzegovina. Species *S. dergle* inhabits karst springs and channels in the Livanjsko Karst Field and Buško and Mandečko Lakes in Bosnia and Herzegovina, and Krka and Cetina River basins in Croatia. Distribution area of *S. plotizza* is limited to the middle and lower parts of the Neretva River basin in both countries, and in Croatia this species also inhabits Desne, Kuti and Baćinska Lakes, as well as the Norin River (Mrakovčić et al., 2006; Kottelat and Freyhof, 2007; Čaleta et al., 2015, 2019). Both species prefer slower parts of river catchments, river tributaries and flood zones with a well-developed vegetation, and can tolerate lower oxygen concentrations and higher water temperatures (Čaleta et al., 2015). All water bodies

inhabited by *S. plotizza* and *S. dergle* are typical karstic rivers, so it can be expected that species adopted to this unique environment also have morphological adaptations.

Recent morphological and phylogenetic analyses of these species are scarce, and often include only small number of populations and samples from their distribution area. For example, Šprem et al. (2010) published a paper on morphometric and meristic characters of one specimen of the common Rudd from the Vrana Lake on the Cres Island, but since the Vrana Lake on the Cres Island is not a natural distribution area of this species, and there is no historical data supporting any introductions of the common Rudd, it can be concluded that authors made an incorrect determination. Furthermore, investigation of morphological characters of some *S. dergle* and *S. plotizza* populations from Croatia and Bosnia and Herzegovina was conducted by Martinović (1995), Topić Popović et al. (2001), Valić et al. (2013), Dulčić et al. (2009), Ivanković (2016) and Salaj (2017), while phylogenetic analyses were also conducted only on few populations and a small sample size by Freyhof et al. (2005), Perea et al. (2010), Valić et al. (2013) and Ivanković (2016). The lack of scientific data is the principal reason for still not fully resolved taxonomy of this genus in the Adriatic basin. Namely, taxonomic position of several populations is still not certain and their pertinence to different species has been proposed by various authors. The most problematic seems to be taxonomic position of the population from the Vrana Lake on the Cres Island. Valić et al. (2013) based on their research suggest that this population belongs to *S. hesperidicus*, while Perea et al. (2010) list the population from the Krka River also as *S. hesperidicus*. Based on the older reports, *S. hesperidicus* is not distributed in Croatia (Kottelat and Freyhof, 2007).

Since there is a lack of data on the diversity and phylogenetic relationships and even the taxonomic status

of several populations of the Adriatic *Scardinius* species, the conservation of their populations cannot be effective. This fact is extremely important, especially in the context of today's negative human pressures on freshwater ecosystems due to the habitat degradation and loss, the introduction of invasive alien species, and the global climate change. These pressures across Europe and the world lead to the accelerated extinction of freshwater fish species (Crivelli and Maitland, 1995; Helfman et al., 2009), and endemic species are the most vulnerable group due to narrow distribution areas and the low ability to adapt to changes in environmental factors (Mrakovčić et al., 2006; Čaleta et al., 2015). The problem of the ineffective conservation of these endemic species is even more pronounced because their distribution ranges are not well described, due to already explained taxonomic uncertainties.

Based on the above mentioned, the aim of this research was to determine the morphological diversity and clarify relationships and status of *S. dergle* and *S. plotizza* populations from their entire distribution area in Croatia and Bosnia and Herzegovina. Specimens of the common Rudd were used for the comparison purposes with investigated *S. dergle* and *S. plotizza* populations. This research is the first comprehensive investigation of the morphological diversity of these species.

STUDY AREA

Specimens of *S. dergle* were collected from the Vrana Lake on the Cres Island, the Visovac Lake, the Ruda River, the Guduča River and the Vransko Lake near Biograd in Croatia, and the Veliki Ždralovac Channel in Bosnia and Herzegovina, while specimens of *S. plotizza* were collected from the Kuti Lake in Croatia and Hutovo blato and Ravno karst field localities in Bosnia and Herzegovina. All these river basins form parts of the Adriatic watershed and are formed in karstic environments. For comparison purposes, specimens of *S. erythrophthalmus* were collected from Plitvice Lakes in Croatia. The whole area of distribution of *S. dergle* and *S. plotizza* is located within the Dinaric Karst, which stretches from northwest to southeast from the southern Alps to the Prokletije mountain range in

the border area between Montenegro and Albania. The Dinaric Karst also includes islands of the Adriatic coast, and extends to the territory of Bosnia and Herzegovina. It is characterized by a specific process which includes circulation of water through soluble rocks, primarily limestone. By sinking, water dissolves the limestone, cracks deepen and widen, and as water flows, a complex system of underground caves and connections between water bodies develop (Roglić, 2004).

Plitvice Lakes are located in the alpine biogeographical region. The lakes are fed by the groundwater of Crna and Bijela rivers, and they remain on the surface because of tufa deposits which prevent water from sinking through existing limestone cracks. All lakes together are 8 km long and cover a total of 1.98 km² (Božičević, 1992). Important to mention, unlike the endemic *Scardinius* species on the remaining localities included in this research, *S. erythrophthalmus* is non-native for the Plitvice Lakes water system. It was introduced here from unknown localities in the Danube River basin in Croatia. The Visovac Lake is located on the Krka River between two tufa barriers, Roški slap on north and Skradinski buk on south (Crkvenčić et al., 1974). The Guduča River is one of 6 tributaries of the Krka River, and it flows into the Krka River in the area of the Prokljansko Lake, which is a submerged river canyon (Božičević, 1992). The Ruda River is one of the main tributaries of the Cetina River, and it is located in the Sinjsko karst field (Tadić, 2019). The Veliki Ždralovac Channel is situated in the Livanjsko karst field in the Ždralovac marsh, and was built for agricultural purposes (Nijaz and Ćerić, 2014). The Kuti Lake is a small, shallow, brackish karst lake in the Neretva River basin, which is mainly fed by freshwater from karst springs, and to a lesser extent from the Neretva River (Jurina Tokić, 2013). Hutovo blato is a wetland located in the lower part of the Neretva River basin, about 15 km upstream from the Neretva River delta. Karst sinkholes and surface waters from the surrounding areas create a larger number of lakes and provide a high groundwater level, which affects the occurrence of permanent and occasional springs (PC Nature Park Hutovo blato, 2020). The Ravno karst field is located in the Trebišnjica River

basin. It is a complex system of surface and underground waterflows in Herzegovina, whose final destination is the Ombla River near Dubrovnik, in the Adriatic Basin (Božićević, 1992). Localities Vrana Lake on the Cres Island and the Vransko Lake near Biograd are isolated from other investigated localities. The Vrana Lake is a freshwater lake on the Cres Island, and its reserves of the freshwater come primarily from the rainfall (Božićević, 1992; Ožanić and Rubinić, 1994). The Vransko Lake near Biograd is a shallow, brackish lake that is supplied with water from several freshwater springs, and has a connection with the sea since 1770, when an 850 m long canal was dug through for agricultural purposes (Božićević, 1992).

MATERIALS AND METHODS

In total 154 specimens were collected from 10 localities (Figure 1, Table 1). Fish were collected using electrofishing

and gill nets. Specimens were over-anesthetized with the MS-222 (tricaine methanesulfonate). All individuals were preserved in 4% formaldehyde for 72 hours, after which they were transported into the 70% ethanol, where they were deposited until measuring. Therefore, since all conditions were the same for all individuals, comparison of their body shapes was not affected by artefact measurements. To distinguish between investigated species the number of scales in lateral line, as well as the number of branched rays in the anal fin were used as deterministic values (according to Kottelat and Freyhof, 2007).

On each individual 25 morphometric characters were measured in millimeters (mm): total length (TL), standard length (SL), head length (c), distance between head tip and anal aperture (Pan), preanal distance (aA), distance between ventral fins and anal aperture (Van), preventral

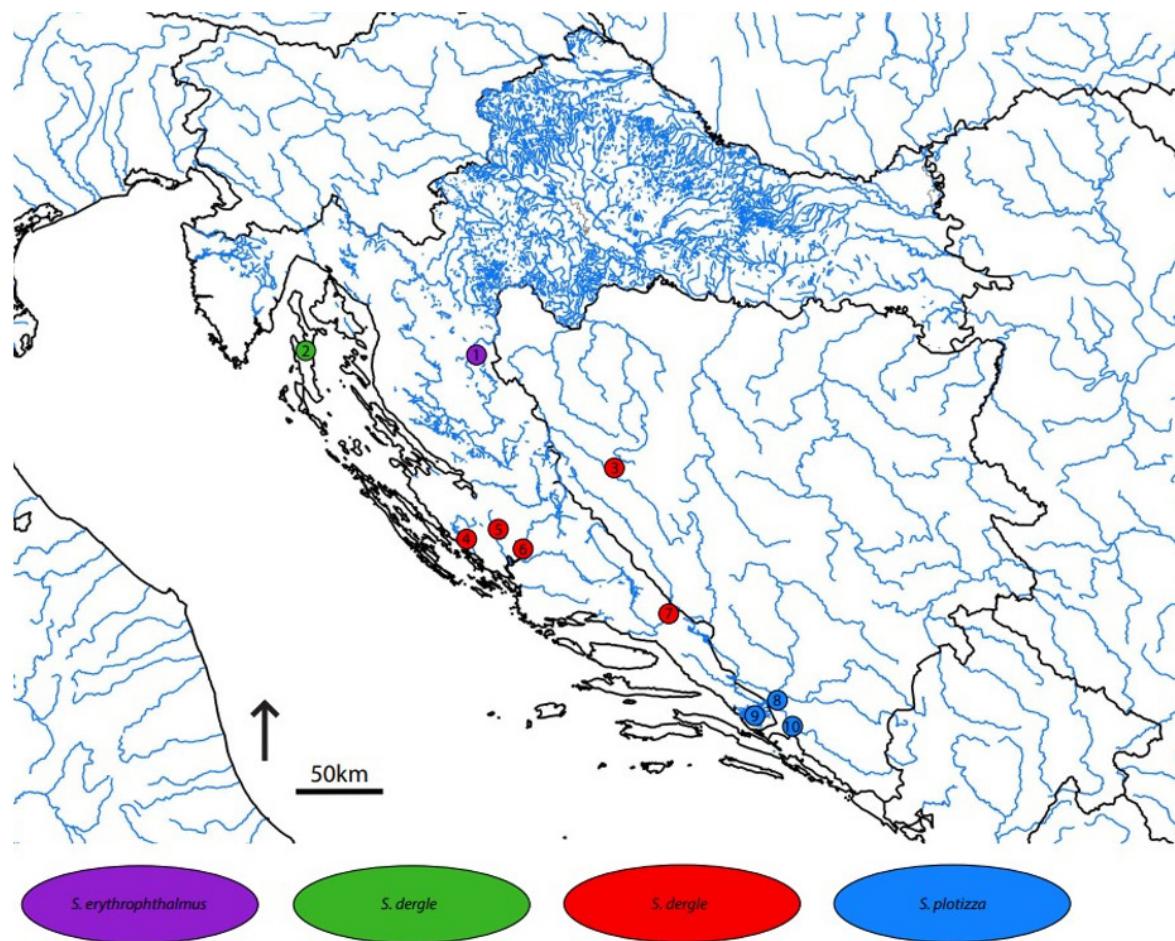


Figure 1. The map of sampling localities (purple locality - *S. erythrophthalmus*, red and green localities - *S. dergle*, blue localities - *S. plotizza*; 1- Plitvice Lakes, 2- Vrana Lake Cres Island, 3- Veliki Ždralovac Channel in Livanjsko karst field, 4- Vransko Lake near Biograd, 5- Guduča River, 6- Visovac Lake, 7- Ruda River, 8- Hutovo blato, 9- Kutje Lake, 10 - Ravno (Popovo) karst field)

distance (aV), prepectoral distance (aP), predorsal pectoral distance (aD), caudal peduncle length (lpc), length of dorsal (ID), anal (IA), caudal (IC), pectoral (IP), and ventral fin (IV), maximum head height (hco), maximum (H), and minimum body height (h), maximum head (laco), and body width (lac), distance between eyes (io), eye diameter (Oh), distance between the beginning of the head and the beginning of the eye (prO), distance between the end of the eye and the end of the operculum (poO), and length of the middle part of caudal fin (lsr. rp).

All measurements were standardized with the allometric conversion, since morphometric ratios are known to poorly remove the body size effects from data sets (Reist, 1985; Lleonart et al., 2000; Baur and Leuenberger, 2011), and analysed using descriptive (mean, range, standard deviation) and inferential statistics (ANOVA and principal component analysis - PCA). In all statistical tests, level of significance $p=0.05$ was used. The allometric conversion was performed according to the formula $M_s = M \cdot (L_s/L_o)b$, where M_s is the standardized

measure, M is the measured character, L_s is the mean value of SL of all specimens, L_o is SL of the individual, and b the slope of the linear regression curve ($\log M$ to $\log L_o$) of all individuals from the sample (Reist, 1985; Elliot et al., 1995; Turan, 2004).

ANOVA is based on dividing the total variance into variance within and between samples. Samples have two sources of variability, variability around each mean value within the sample and variability between samples due to differences between the mean values of the population from which the samples are taken (Fowler et al., 1998; Dytham, 2010). This analysis was used to determine whether there is a significant statistical difference in standardized morphometric characters within and between investigated populations. For this purposes, post hoc Fisher's test was used.

PCA is a multivariate analysis used to determine the relative importance of variables in explaining data. This is done by evaluating the influence of linear combinations of variables (so-called Principal components - PC) on

Table 1. Localities and sampling dates, number of specimens per species, label and color markings used in PCA, average value (\bar{x}), range and standard deviation (s.d.) of TL of investigated populations of genus *Scardinius*

Locality	Species	N	Label and color marking	Average (\bar{x}), range and s.d. of TL
Plitvice Lakes (CRO) ^a /March 2017	<i>S. erythrophthalmus</i>	15	PL	$\bar{x}= 156,8$ (119-236) s.d.= 25,37
Vrana Lake Cres Island (CRO)/August 2016	<i>S. dergle</i>	20	CR	$\bar{x}= 271,40$ (155-329) s.d.= 47,25
Veliki Ždralovac Canal in Livanjsko karst field (BAH) ^b /June 2016	<i>S. dergle</i>	10	VZ	$\bar{x}= 114,43$ (55,56-163) s.d.= 37,21
Visovac Lake (CRO)/October 2010	<i>S. dergle</i>	22	VI	$\bar{x}= 197,57$ (177-230) s.d.= 14,57
Ruda River (CRO)/November 2014	<i>S. dergle</i>	9	RU	$\bar{x}= 160,63$ (145-176) s.d.= 12,05
Guduča River (CRO)/March 2015	<i>S. dergle</i>	20	GU	$\bar{x}= 150,03$ (92-269) s.d.= 63,88
Vransko Lake near Biograd (CRO)/March 2014	<i>S. dergle</i>	10	VR	$\bar{x}= 223,90$ (207-231) s.d.= 7,37
Ravno (Popovo) karst field (BAH)/September 2010	<i>S. plotizza</i>	22	RA	$\bar{x}= 56,92$ (48,22-69,47) s.d.= 5,37
Hutovo blato (BAH)/January 2009	<i>S. plotizza</i>	11	HB	$\bar{x}= 154,89$ (141-173) s.d.= 10,28
Kuti Lake (CRO)/September 2014	<i>S. plotizza</i>	15	KU	$\bar{x}= 110,27$ (81-261) s.d.= 53,55

^a CRO – Croatia

^b BAH – Bosnia and Herzegovina

the variation of data. The goal of PCA is to identify the combination of variables that explain the largest amount of the variation in multivariate data settings. The main components are organized so that the first main component (PC1) explains the largest amount of the variation, PC2 the next largest amount, etc. The basic premise is that a small number of main components explains so much variation in data that the remaining main components can be ignored, so that data can be described with only a few components instead of a large number of variables (Fowler et al., 1998; Dytham, 2010). In this research PCA was used to determine which standardized morphometric characters contribute the most to the main PCA components, as well as to detect possible relations of investigated populations based on those characters. For analyses Statistica 13.1. software and Microsoft Office Excel 2010 were used.

Additionally, meristic characters were measured, which included the number of scales in lateral line and the number of unbranched and branched rays in caudal, pectoral, ventral, dorsal, and anal fins on all specimens. Also, for the purposes of this research, the population from the Vrana Lake on the Cres Island is treated as *S. dergle*.

RESULTS

Box-plots of the standard length (SL) for all populations are shown in Figure 2. Results show that the greatest variability in SL for *S. dergle* is recorded on localities the Vrana Lake on the Cres Island and the Guduča River, and the lowest on localities the Vransko Lake near Biograd, the Ruda River and the Visovac Lake. For *S. plotizza* the greatest variability in SL is recorded on locality Kuti and the lowest on locality Ravno. Maximum TL (329 mm) is recorded for *S. dergle* from the Vrana Lake on the Cres Island, and minimum TL (48.22 mm) for *S. plotizza* from Ravno.

ANOVA F-test results of the standardized data show that there is a significant difference ($P<0.05$) in all standardized morphometric characters, and post hoc Fisher's test confirmed that there is a significant intra-

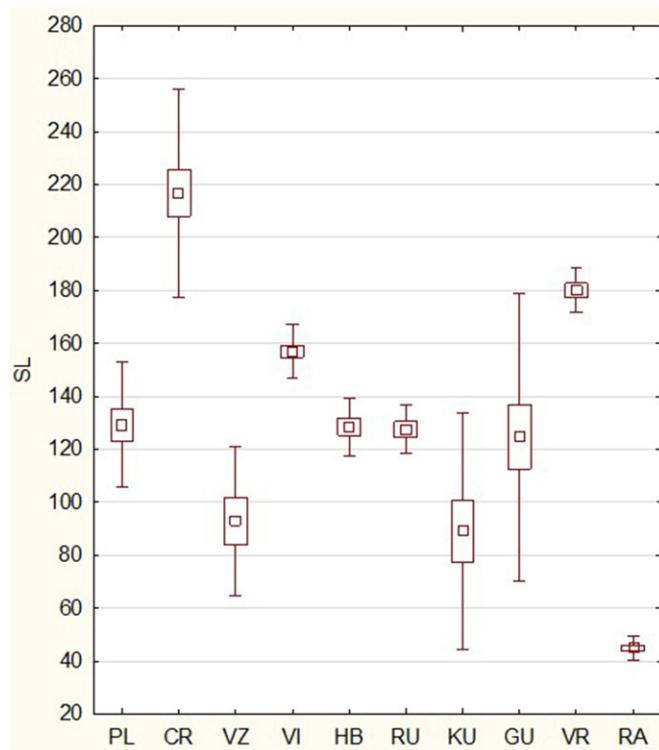


Figure 2. Box plots of standard length (SL) in mm of populations from all localities (*S. erythrophthalmus*: PL-Plitvice Lakes; *S. dergle*: CR-Vrana Lake (Cres), VZ-Veliki Ždralovac, VI-Visovac Lake (Krka), RU-Ruda, GU-Guduča, VR-Vransko Lake (Biograd); *S. plotizza*: HB-Hutovo blato, KU-Kuti, RA-Ravno). Box-plots show average (square), average +/- standard error (rectangle) and range of average +/- standard deviation

and interspecies difference ($P<0.05$) in all morphometric characters between most of investigated populations. Results of post hoc Fisher's test are available in supplement materials (Table SI_1_1). Populations from Hutovo blato, as well as Ruda and Guduča rivers show the similarity with the population from Plitvice Lakes in almost all standardized characters. Also, populations from the Veliki Ždralovac Channel and the Kuti Lake are similar in more than half measured morphometric characters. The most distinct population is the one from Ravno, since it does not show any similarities with other investigated populations. Populations from the Vrana Lake on the Cres Island and the Vransko Lake near Biograd, show similarities with other populations in only one (the Vransko Lake) and two (the Vrana Lake) investigated characters.

The PCA projection of standardized measures defined by factors 1 and 2 is shown in Figure 3.

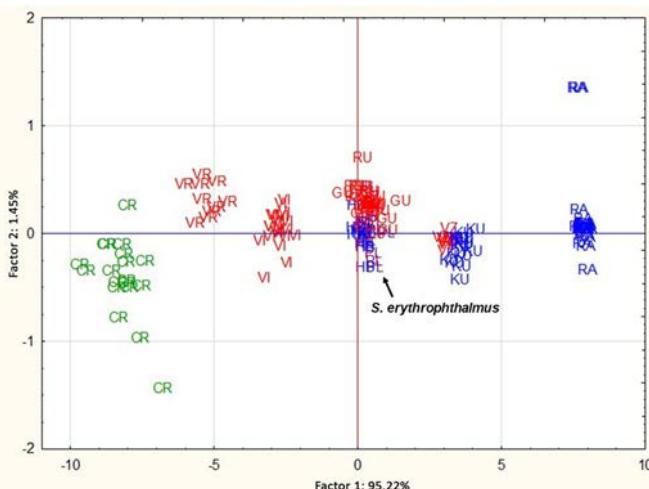


Figure 3. PCA results of standardized morphometric characters (red = *S. dergle*; green = *S. dergle* from the Cres Island; blue = *S. plotizza*; purple = *S. erythrophthalmus*). Eigenvalue for factor 1 was 22.85, and eigenvalue for factor 2 was 0.35

Factor 1 contains 95.22 % of the total variance and it is mostly defined by standardized measures M(Pan), M(aA), M(aV), M(hco) and M(H), while factor 2 contains 1.44% of the total variance and is mostly defined by measures M(Oh), M(prO), M(c) and M(poO). Eigenvalues

and relationships of factors and standardized measures are available in supplement materials (Table SI_1_2, Table SI_1_3). The PCA projection shows that populations of *S. dergle* from the Vrana Lake on the Cres Island, the Vransko Lake near Biograd and the Visovac Lake, and the population of *S. plotizza* from Ravno separate from other investigated populations. Populations of *S. dergle* from the Veliki Ždralovac Channel and *S. plotizza* from Kuti, as well as populations of *S. erythrophthalmus* from Plitvice Lakes, *S. dergle* from Guduča and Ruda rivers, and *S. plotizza* from Hutovo blato are grouped together.

Meristic characters of all investigated populations are shown in Table 2. The pronounced variability in the number of scales in lateral line, as well as in the number of soft rays in caudal and pectoral fin is recorded. Specimens of *S. erythrophthalmus* have a significant variability in the number of branched rays in the anal fin. Main deterministic characters in genus *Scardinius* are the number of scales in lateral line, as well as the number of branched rays in the anal fin.

Table 2. The number of scales in the lateral line and the number of unbranched and branched rays in the anal (A), caudal (C), ventral (V), pectoral (P), and dorsal (D) fin of investigated populations

Species and locality	N of scales in lateral line	N of unbranched and branched rays in fins				
		A	C	V	P	D
<i>S. erythrophthalmus</i>						
Plitvice Lakes	(40)41(42)	III 10% (11%) (121/2)	18(19)	II (7) 8	I 14 (15)	III 8(9)
<i>S. dergle</i>						
Vrana Lake (Cres)	(39)40-41(42)	III 10%	(18)19(20)(21)	II 7-8	I 14 (15)	III 8(9)
Veliki Ždralovac	40(41)	III 10%	19(20)	II 7-8	I 14-15	III (8)9
Visovac Lake	(39)40(41)(42)	III (9%)10%	(18)19(20)	II (7)8	I (13)14(15)(16)	III (7)8(9)
Ruda River	(40)41(42)	III (9%)10%	(18)19	II (7)8	I (13)14(15)	III 8(9)
Guduča River	(39)40-41(42)(43)	III 10%	(17)(18)19(20)	II 7(8)	I (13)14(15)(16)	III 8(9)
Vransko Lake (Biograd)	40(41)(42)	III 10%	19(20)	II (7)8	I (14)15(16)	III 8(9)
<i>S. plotizza</i>						
Hutovo blato	(37)38(39)(40)	III 9½	(18)19(21)	II (7)8	I (12)(13)14(15)	III 8
Ravno karst field	(37)(38)(39)40	III 9½/2	18)19(20)	II 7(8)	I 14(15)	III (7)8(9)
Kuti Lake	37(38)(39)(40)	III 9½/2	(17)(18)19(20)	II 7-8	I (13)(14)15(16)	III 8(9)

For populations of *S. erythrophthalmus*, *S. plotizza*, and most populations of *S. dergle* recorded meristic characters are in line with their deterministic values, while for specimens of *S. dergle* from the Visovac Lake and the Ruda River deviation from deterministic values of the number of branched rays in anal fin is noticed (9% instead of 10%). Also, for specimens of *S. dergle* from the Vrana Lake on the Cres Island, the Visovac Lake and the Guduča River 39 scales (instead of 40-43) in lateral line are recorded.

DISCUSSION

On the interspecific level, *S. dergle* populations from the Vrana Lake on the Cres Island, the Visovac Lake, the Vransko Lake and the Guduča River show higher maximum values of SL than investigated populations of *S. plotizza*. Populations of *S. dergle* from the Vrana Lake on the Cres Island, the Veliki Ždralovac Channel and the Guduča River, as well as the population of *S. plotizza* from the Kuti Lake show the higher range of measured SL values, while other investigated populations of these species have a quite narrow range of SL. This is especially the case with the population of *S. plotizza* from Ravno, where investigated individuals were all juvenile, with maximum SL of 54.60 mm. Although the highest maximum value of SL (273 mm) was recorded for *S. dergle* from the Vrana Lake, other authors have recorded even higher SL values for this population: 274 mm (Valić et al., 2013), 325 mm (Topić Popović et al., 2001), and 541 mm (Šprem et al., 2010). In general, specimens from the Vrana Lake on the Cres Island have the largest recorded body size compared to other populations (Šprem et al., 2010). Also, Valić et al. (2013) have recorded even higher range of SL values for the population of *S. dergle* from the Krka River (86-198 mm), than it was recorded in this research (146-181 mm). For specimens of *S. plotizza* from Hutovo blato the recorded range of TL was 141-173 mm, which is significantly lower than values recorded by Dulčić et al. (2009) for specimens of this species from Hutovo blato (99-390 mm), and values recorded by Ivanković (2016) and Salaj (2017) for specimens of *S. plotizza* from the Deransko Lake in Bosnia and Herzegovina (142-404 mm).

Similarities between populations from Hutovo blato, Ruda and Guduča rivers and Plitvice Lakes detected with post hoc Fisher's test could be the result of morphological adaptations of these populations to similar environmental conditions (Marčić et al., 2011), since all these locations are characterized by complex hydrological processes specific for the karst. Also, geographically closer populations, which is the case for populations from Veliki Ždralovac and the Kuti Lake, show more similarities than more distant populations. This could be the result of the connection of these hydrological systems in the past. Finally, populations which are geographically the most isolated show none, as it is the case with the population from Ravno, or very low number of similarities with other investigated populations, which is the case with populations from the Vrana Lake on the Cres Island and the Vransko Lake. Although results of ANOVA F-test of standardized data showed that there is a significant difference ($P<0.05$) in all standardized morphometric characters, and post hoc Fisher's test confirmed that there is a significant intra- and interspecies difference ($P<0.05$) in all morphometric characters between most of investigated populations, PCA results indicate possible relationships between these populations. Populations of *S. dergle* from the Vrana Lake on the Cres Island, and *S. plotizza* from Ravno separate the farthest from other investigated populations, which might imply their gradual divergence or different taxonomic status. Valić et al. (2013), based on phylogenetic analysis of cytochrome b gene, state that the population of *S. dergle* from Vrana Lake is actually *S. hesperidicus*. Although this is a valid assumption, which could be explained by the geological history of the Adriatic basin and past connections of rivers in this area (Colantoni et al., 1984), further phylogenetic research, especially determination of genetic distance between these species, is needed in order to firmly support this assumption.

This research confirmed that recorded meristic characters for populations of *S. erythrophthalmus*, *S. plotizza*, and most populations of *S. dergle* are in line with their deterministic values (number of scales in lateral line and number of branched rays in anal fin). The only

discrepancy from deterministic values was recorded for specimens of *S. dergle* from the Visovac Lake and the Ruda River, where in some specimens the number of branched rays in anal fin was 9% instead of 10%, and for some specimens of this species from the Vrana Lake on the Cres Island, the Visovac Lake and the Guduča River where 39 scales in lateral line, instead of 40-43, were recorded. Ivanković (2016) recorded discrepancy in the number of scales in the lateral line for specimens of *S. plotizza* from the Deransko Lake, 37-43 instead of 37-40, which confirms the variability of meristic characters in natural populations.

CONCLUSIONS

Based on results, this research confirmed the exact distribution area of *S. dergle* and *S. plotizza*. Regarding the population from the Vrana Lake on the Cres Island, the taxonomic position of this population remains questionable. There is an obvious influence of the isolation on this population, since a very low number of similarities with other investigated populations was detected, which could be the result of morphological adaptation, but also probably has a genetic basis, which should be confirmed with further phylogenetic analysis.

Although this research gave valuable new information on morphological variability and possible relationships of populations of *S. dergle* and *S. plotizza* in their entire distribution area in Croatia and Bosnia and Herzegovina, analysis such as ANOVA and PCA, as well as investigation of deterministic meristic characters can only give an indication of possible phylogenetic relationships and the status of these populations. Since the combination of results of morphological and phylogenetic analyses is the most reliable method to answer questions regarding the systematic position of populations and their relationships, additional phylogenetic research, which will also determine genetic diversity of these species, is needed. It is important to emphasise that, in the light of significant negative human impacts on freshwater ecosystems, it is of great importance to gather more scientific data on these species as soon as possible, in order to determine the status of these populations, and implement appropriate

conservation measures.

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SUPPLEMENT INFORMATION

Table SI_1_1. Results of post hoc Fisher's test for all morphometric measures of all investigated populations standardized with allometric conversion (statistically significant differences ($P<0.05$) are marked red). *S. erythrophthalmus*: PL-Plitvice Lakes; *S. dergle*: CR-Vrana Lake (Cres), VZ-Veliki Ždralovac, VI-Visovac Lake (Krka), RU-Ruda, GU-Guduča, VR-Vransko Lake (Biograd); *S. plotizza*: HB-Hutovo blato, KU-Kuti, RA-Ravno

Standardized measure: M (lsr. rp)										
Population	PL	CR	VZ	VI	HB	RU	KU	GU	VR	RA
PL		0.0000	0.0314	0.0167	0.8327	0.2945	0.0046	0.6539	0.0000	0.0000
CR	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0452	0.0000
VZ	0.0314	0.0000		0.0000	0.0346	0.0063	0.7204	0.0090	0.0000	0.0025
VI	0.0167	0.0000	0.0000		0.0668	0.4228	0.0000	0.0374	0.0151	0.0000
HB	0.8327	0.0000	0.0346	0.0668		0.4374	0.0075	0.8708	0.0003	0.0000
RU	0.2945	0.0000	0.0063	0.4228	0.4374		0.0010	0.4614	0.0085	0.0000
KU	0.0046	0.0000	0.7204	0.0000	0.0075	0.0010		0.0007	0.0000	0.0023
GU	0.6539	0.0000	0.0090	0.0374	0.8708	0.4614	0.0007		0.0000	0.0000
VR	0.0000	0.0452	0.0000	0.0151	0.0003	0.0085	0.0000	0.0000		0.0000
RA	0.0000	0.0000	0.0025	0.0000	0.0000	0.0000	0.0023	0.0000	0.0000	
Standardized measure: M (TL)										
Population	PL	CR	VZ	VI	HB	RU	KU	GU	VR	RA
PL		0.0000	0.0000	0.0000	0.7673	0.3313	0.0000	0.0052	0.0000	0.0000
CR	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
VZ	0.0000	0.0000		0.0000	0.0000	0.0000	0.1213	0.0000	0.0000	0.0000
VI	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
HB	0.7673	0.0000	0.0000	0.0000		0.5249	0.0000	0.0071	0.0000	0.0000
RU	0.3313	0.0000	0.0000	0.0000	0.5249		0.0000	0.0016	0.0000	0.0000
KU	0.0000	0.0000	0.1213	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000
GU	0.0052	0.0000	0.0000	0.0000	0.0071	0.0016	0.0000		0.0000	0.0000
VR	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000
RA	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	
Standardized measure: M (c)										
Population	PL	CR	VZ	VI	HB	RU	KU	GU	VR	RA
PL		0.0000	0.0000	0.0000	0.0000	0.4977	0.0000	0.0858	0.0000	0.0000
CR	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
VZ	0.0000	0.0000		0.0000	0.0000	0.0000	0.0530	0.0000	0.0000	0.0000
VI	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
HB	0.0000	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000
RU	0.4977	0.0000	0.0000	0.0000	0.0000		0.0000	0.0417	0.0000	0.0000
KU	0.0000	0.0000	0.0530	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000
GU	0.0858	0.0000	0.0000	0.0000	0.0000	0.0417	0.0000		0.0000	0.0000
VR	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000
RA	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	

Continued

Standardized measure: M (Pan)										
Population	PL	CR	VZ	VI	HB	RU	KU	GU	VR	RA
PL		0.0000	0.0000	0.0000	0.0881	0.0778	0.0000	0.5277	0.0000	0.0000
CR	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
VZ	0.0000	0.0000		0.0000	0.0000	0.0000	0.0271	0.0000	0.0000	0.0000
VI	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
HB	0.0881	0.0000	0.0000	0.0000		0.0027	0.0000	0.0213	0.0000	0.0000
RU	0.0778	0.0000	0.0000	0.0000	0.0027		0.0000	0.1806	0.0000	0.0000
KU	0.0000	0.0000	0.0271	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000
GU	0.5277	0.0000	0.0000	0.0000	0.0213	0.1806		0.0000	0.0000	0.0000
VR	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000
RA	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	
Standardized measure: M (aA)										
Population	PL	CR	VZ	VI	HB	RU	KU	GU	VR	RA
PL		0.0000	0.0000	0.0000	0.2988	0.0743	0.0000	0.0309	0.0000	0.0000
CR	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
VZ	0.0000	0.0000		0.0000	0.0000	0.0000	0.0949	0.0000	0.0000	0.0000
VI	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
HB	0.2988	0.0000	0.0000	0.0000		0.0134	0.0000	0.0038	0.0000	0.0000
RU	0.0743	0.0000	0.0000	0.0000	0.0134		0.0000	0.8749	0.0000	0.0000
KU	0.0000	0.0000	0.0949	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000
GU	0.0309	0.0000	0.0000	0.0000	0.0038	0.8749		0.0000	0.0000	0.0000
VR	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000
RA	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	
Standardized measure: M (Van)										
Population	PL	CR	VZ	VI	HB	RU	KU	GU	VR	RA
PL		0.0000	0.0000	0.0000	0.8589	0.7941	0.0000	0.0031	0.0000	0.0000
CR	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
VZ	0.0000	0.0000		0.0000	0.0000	0.0000	0.0309	0.0000	0.0000	0.0000
VI	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
HB	0.8589	0.0000	0.0000	0.0000		0.9295	0.0000	0.0066	0.0000	0.0000
RU	0.7941	0.0000	0.0000	0.0000	0.9295		0.0000	0.0096	0.0000	0.0000
KU	0.0000	0.0000	0.0309	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000
GU	0.0031	0.0000	0.0000	0.0000	0.0066	0.0096		0.0000	0.0000	0.0000
VR	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000
RA	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	

Continued

Standardized measure: M (aV)										
Population	PL	CR	VZ	VI	HB	RU	KU	GU	VR	RA
PL		0.0000	0.0000	0.0000	0.4964	0.0862	0.0000	0.0001	0.0000	0.0000
CR	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
VZ	0.0000	0.0000		0.0000	0.0000	0.0000	0.0495	0.0000	0.0000	0.0000
VI	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
HB	0.4964	0.0000	0.0000	0.0000		0.0341	0.0000	0.0001	0.0000	0.0000
RU	0.0862	0.0000	0.0000	0.0000	0.0341		0.0000	0.2001	0.0000	0.0000
KU	0.0000	0.0000	0.0495	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000
GU	0.0001	0.0000	0.0000	0.0000	0.0001	0.2001		0.0000	0.0000	0.0000
VR	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000	0.0000
RA	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000
Standardized measure: M (aP)										
Population	PL	CR	VZ	VI	HB	RU	KU	GU	VR	RA
PL		0.0000	0.0000	0.0000	0.0000	0.1375	0.0000	0.0000	0.0000	0.0000
CR	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
VZ	0.0000	0.0000		0.0000	0.0000	0.0000	0.3730	0.0000	0.0000	0.0000
VI	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
HB	0.0000	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000
RU	0.1375	0.0000	0.0000	0.0000	0.0000		0.0000	0.0112	0.0000	0.0000
KU	0.0000	0.0000	0.3730	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000
GU	0.0000	0.0000	0.0000	0.0000	0.0000	0.0112		0.0000	0.0000	0.0000
VR	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000	0.0000
RA	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000
Standardized measure: M (aD)										
Population	PL	CR	VZ	VI	HB	RU	KU	GU	VR	RA
PL		0.0000	0.0000	0.0000	0.7313	0.9636	0.0000	0.0002	0.0000	0.0000
CR	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
VZ	0.0000	0.0000		0.0000	0.0000	0.0000	0.0212	0.0000	0.0000	0.0000
VI	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
HB	0.7313	0.0000	0.0000	0.0000		0.8058	0.0000	0.0041	0.0000	0.0000
RU	0.9636	0.0000	0.0000	0.0000	0.8058		0.0000	0.0037	0.0000	0.0000
KU	0.0000	0.0000	0.0212	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000
GU	0.0002	0.0000	0.0000	0.0000	0.0041	0.0037		0.0000	0.0000	0.0000
VR	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000	0.0000
RA	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000

Continued

Population	Standardized measure: M (lpc)									
	PL	CR	VZ	VI	HB	RU	KU	GU	VR	RA
PL		0.0000	0.0000	0.0000	0.0001	0.0000	0.0000	0.0027	0.0000	0.0000
CR	0.0000		0.0000	0.1449	0.0000	0.0000	0.0000	0.0000	0.0040	0.0000
VZ	0.0000	0.0000		0.0000	0.0000	0.0000	0.5169	0.0000	0.0000	0.0000
VI	0.0000	0.1449	0.0000		0.0000	0.0000	0.0000	0.0000	0.0001	0.0000
HB	0.0001	0.0000	0.0000	0.0000		0.1403	0.0000	0.1316	0.0000	0.0000
RU	0.0000	0.0000	0.0000	0.0000	0.1403		0.0000	0.0025	0.0000	0.0000
KU	0.0000	0.0000	0.5169	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000
GU	0.0027	0.0000	0.0000	0.0000	0.1316	0.0025		0.0000	0.0000	0.0000
VR	0.0000	0.0040	0.0000	0.0001	0.0000	0.0000	0.0000	0.0000		0.0000
RA	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	
Standardized measure: M (ID)										
Population	PL	CR	VZ	VI	HB	RU	KU	GU	VR	RA
PL		0.0000	0.0010	0.0000	0.0079	0.0000	0.0000	0.0000	0.0000	0.0000
CR	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
VZ	0.0010	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
VI	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
HB	0.0079	0.0000	0.0000	0.0000		0.0040	0.0000	0.1215	0.0000	0.0000
RU	0.0000	0.0000	0.0000	0.0000	0.0040		0.0000	0.0579	0.0000	0.0000
KU	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000
GU	0.0000	0.0000	0.0000	0.0000	0.1215	0.0579		0.0000	0.0000	0.0000
VR	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000
RA	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	
Standardized measure: M (IA)										
Population	PL	CR	VZ	VI	HB	RU	KU	GU	VR	RA
PL		0.0000	0.0000	0.0000	0.0000	0.3819	0.0000	0.5454	0.0000	0.0000
CR	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0006	0.0000
VZ	0.0000	0.0000		0.0000	0.0039	0.0000	0.0000	0.0000	0.0000	0.0000
VI	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
HB	0.0000	0.0000	0.0039	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000
RU	0.3819	0.0000	0.0000	0.0000	0.0000		0.0000	0.1694	0.0000	0.0000
KU	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000
GU	0.5454	0.0000	0.0000	0.0000	0.0000	0.1694		0.0000	0.0000	0.0000
VR	0.0000	0.0006	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000
RA	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	

Continued

Population	Standardized measure: M (IC)									
	PL	CR	VZ	VI	HB	RU	KU	GU	VR	RA
PL		0.0000	0.0000	0.0000	0.8506	0.6524	0.0000	0.0000	0.0000	0.0000
CR	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
VZ	0.0000	0.0000		0.0000	0.0000	0.0000	0.2539	0.0000	0.0000	0.0000
VI	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
HB	0.8506	0.0000	0.0000	0.0000		0.8013	0.0000	0.0000	0.0000	0.0000
RU	0.6524	0.0000	0.0000	0.0000	0.8013		0.0000	0.0000	0.0000	0.0000
KU	0.0000	0.0000	0.2539	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000
GU	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000	0.0000
VR	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000
RA	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	
Standardized measure: M (IP)										
Population	PL	CR	VZ	VI	HB	RU	KU	GU	VR	RA
PL		0.0000	0.0000	0.0000	0.3624	0.0098	0.0000	0.0435	0.0000	0.0000
CR	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
VZ	0.0000	0.0000		0.0000	0.0000	0.0000	0.1264	0.0000	0.0000	0.0000
VI	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
HB	0.3624	0.0000	0.0000	0.0000		0.1083	0.0000	0.0080	0.0000	0.0000
RU	0.0098	0.0000	0.0000	0.0000	0.1083		0.0000	0.0000	0.0000	0.0000
KU	0.0000	0.0000	0.1264	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000
GU	0.0435	0.0000	0.0000	0.0000	0.0080	0.0000	0.0000		0.0000	0.0000
VR	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000
RA	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	
Standardized measure: M (IV)										
Population	PL	CR	VZ	VI	HB	RU	KU	GU	VR	RA
PL		0.0000	0.0000	0.0000	0.1444	0.0072	0.0000	0.0000	0.0000	0.0000
CR	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
VZ	0.0000	0.0000		0.0000	0.0000	0.0000	0.0584	0.0000	0.0000	0.0000
VI	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
HB	0.1444	0.0000	0.0000	0.0000		0.0003	0.0000	0.0046	0.0000	0.0000
RU	0.0072	0.0000	0.0000	0.0000	0.0003		0.0000	0.0000	0.0000	0.0000
KU	0.0000	0.0000	0.0584	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000
GU	0.0000	0.0000	0.0000	0.0000	0.0046	0.0000	0.0000		0.0000	0.0000
VR	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000
RA	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	

Continued

Population	Standardized measure: M (hco)									
	PL	CR	VZ	VI	HB	RU	KU	GU	VR	RA
PL		0.0000	0.0000	0.0000	0.0158	0.3775	0.0000	0.5184	0.0000	0.0000
CR	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
VZ	0.0000	0.0000		0.0000	0.0000	0.0000	0.2473	0.0000	0.0000	0.0000
VI	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
HB	0.0158	0.0000	0.0000	0.0000		0.2169	0.0000	0.0024	0.0000	0.0000
RU	0.3775	0.0000	0.0000	0.0000	0.2169		0.0000	0.1572	0.0000	0.0000
KU	0.0000	0.0000	0.2473	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000
GU	0.5184	0.0000	0.0000	0.0000	0.0024	0.1572	0.0000		0.0000	0.0000
VR	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000
RA	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	
Standardized measure: M (H)										
Population	PL	CR	VZ	VI	HB	RU	KU	GU	VR	RA
PL		0.0000	0.0000	0.0000	0.0032	0.6319	0.0000	0.2056	0.0000	0.0000
CR	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
VZ	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
VI	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
HB	0.0032	0.0000	0.0000	0.0000		0.0038	0.0000	0.0000	0.0000	0.0000
RU	0.6319	0.0000	0.0000	0.0000	0.0038		0.0000	0.6203	0.0000	0.0000
KU	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000
GU	0.2056	0.0000	0.0000	0.0000	0.0000	0.6203	0.0000		0.0000	0.0000
VR	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000
RA	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	
Standardized measure: M (h)										
Population	PL	CR	VZ	VI	HB	RU	KU	GU	VR	RA
PL		0.0000	0.0002	0.0000	0.8087	0.1728	0.0000	0.7485	0.0000	0.0000
CR	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0004	0.0000
VZ	0.0002	0.0000		0.0000	0.0003	0.0000	0.1979	0.0000	0.0000	0.0000
VI	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
HB	0.8087	0.0000	0.0003	0.0000		0.2993	0.0000	0.9830	0.0000	0.0000
RU	0.1728	0.0000	0.0000	0.0000	0.2993		0.0000	0.2449	0.0000	0.0000
KU	0.0000	0.0000	0.1979	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000
GU	0.7485	0.0000	0.0000	0.0000	0.9830	0.2449	0.0000		0.0000	0.0000
VR	0.0000	0.0004	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000
RA	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	

Continued

Population	Standardized measure: M (laco)									
	PL	CR	VZ	VI	HB	RU	KU	GU	VR	RA
PL		0.0000	0.0000	0.0000	0.0590	0.8225	0.0000	0.6540	0.0000	0.0000
CR	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
VZ	0.0000	0.0000		0.0000	0.0000	0.0000	0.0084	0.0000	0.0000	0.0000
VI	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
HB	0.0590	0.0000	0.0000	0.0000		0.1670	0.0000	0.1117	0.0000	0.0000
RU	0.8225	0.0000	0.0000	0.0000	0.1670		0.0000	0.9061	0.0000	0.0000
KU	0.0000	0.0000	0.0084	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000
GU	0.6540	0.0000	0.0000	0.0000	0.1117	0.9061	0.0000		0.0000	0.0000
VR	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000
RA	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	
Standardized measure: M (lac)										
Population	PL	CR	VZ	VI	HB	RU	KU	GU	VR	RA
PL		0.0000	0.0000	0.0000	0.3994	0.4676	0.0000	0.0000	0.0000	0.0000
CR	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
VZ	0.0000	0.0000		0.0000	0.0000	0.0000	0.0020	0.0000	0.0000	0.0000
VI	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
HB	0.3994	0.0000	0.0000	0.0000		0.1733	0.0000	0.0000	0.0000	0.0000
RU	0.4676	0.0000	0.0000	0.0000	0.1733		0.0000	0.0003	0.0000	0.0000
KU	0.0000	0.0000	0.0020	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000
GU	0.0000	0.0000	0.0000	0.0000	0.0000	0.0003	0.0000		0.0000	0.0000
VR	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000
RA	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	
Standardized measure: M (io)										
Population	PL	CR	VZ	VI	HB	RU	KU	GU	VR	RA
PL		0.0000	0.0001	0.0000	0.7403	0.0000	0.0000	0.0000	0.0000	0.0000
CR	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.4276	0.0000
VZ	0.0001	0.0000		0.0000	0.0001	0.0000	0.0142	0.0000	0.0000	0.0000
VI	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000	0.0001	0.0000	0.0000
HB	0.7403	0.0000	0.0001	0.0000		0.0004	0.0000	0.0000	0.0000	0.0000
RU	0.0000	0.0000	0.0000	0.0000	0.0004		0.0000	0.0004	0.0000	0.0000
KU	0.0000	0.0000	0.0142	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000
GU	0.0000	0.0000	0.0000	0.0001	0.0000	0.0004	0.0000		0.0000	0.0000
VR	0.0000	0.4276	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000
RA	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	

Continued

Population	Standardized measure: M (Oh)									
	PL	CR	VZ	VI	HB	RU	KU	GU	VR	RA
PL		0.0000	0.0000	0.0000	0.3594	0.0000	0.0000	0.0000	0.0000	0.0000
CR	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
VZ	0.0000	0.0000		0.0000	0.0000	0.2522	0.0152	0.0000	0.0000	0.0000
VI	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000	0.5526	0.0000
HB	0.3594	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000
RU	0.0000	0.0000	0.2522	0.0000	0.0000		0.3104	0.0022	0.0000	0.0000
KU	0.0000	0.0000	0.0152	0.0000	0.0000	0.3104		0.0107	0.0000	0.0000
GU	0.0000	0.0000	0.0000	0.0000	0.0000	0.0022	0.0107		0.0000	0.0000
VR	0.0000	0.0000	0.0000	0.5526	0.0000	0.0000	0.0000	0.0000		0.0000
RA	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	
Standardized measure: M (prO)										
Population	PL	CR	VZ	VI	HB	RU	KU	GU	VR	RA
PL		0.0000	0.0000	0.0000	0.0001	0.2366	0.0000	0.1467	0.0000	0.0000
CR	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
VZ	0.0000	0.0000		0.0000	0.0000	0.0000	0.3878	0.0000	0.0000	0.0000
VI	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
HB	0.0001	0.0000	0.0000	0.0000		0.0178	0.0000	0.0025	0.0000	0.0000
RU	0.2366	0.0000	0.0000	0.0000	0.0178		0.0000	0.9279	0.0000	0.0000
KU	0.0000	0.0000	0.3878	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000
GU	0.1467	0.0000	0.0000	0.0000	0.0025	0.9279	0.0000		0.0000	0.0000
VR	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000
RA	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	
Standardized measure: M (poO)										
Population	PL	CR	VZ	VI	HB	RU	KU	GU	VR	RA
PL		0.0000	0.0000	0.0000	0.0000	0.1033	0.0000	0.2348	0.0000	0.0000
CR	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
VZ	0.0000	0.0000		0.0000	0.0000	0.0000	0.3099	0.0000	0.0000	0.0000
VI	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
HB	0.0000	0.0000	0.0000	0.0000		0.0003	0.0000	0.0000	0.0000	0.0000
RU	0.1033	0.0000	0.0000	0.0000	0.0003		0.0000	0.0095	0.0000	0.0000
KU	0.0000	0.0000	0.3099	0.0000	0.0000	0.0000		0.0000	0.0000	0.0000
GU	0.2348	0.0000	0.0000	0.0000	0.0000	0.0095	0.0000		0.0000	0.0000
VR	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		0.0000
RA	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	

Table SI_1_2. Results of the principal component analysis – eigenvalues. % of total variance, cumulative eigenvalue and cumulative %

Factor	Eigenvalue	% total variance	Cumulative eigenvalue	Cumulative %
1	22.85367	95.22363	22.85367	95.2236
2	0.34759	1.4483	23.20126	96.6719
3	0.23924	0.99682	23.4405	97.6687
4	0.11001	0.4584	23.55051	98.1271
5	0.07313	0.30472	23.62365	98.4319
6	0.06827	0.28447	23.69192	98.7163
7	0.05199	0.21663	23.74391	98.933
8	0.04745	0.19771	23.79136	99.1307
9	0.04064	0.16934	23.832	99.3
10	0.02377	0.09903	23.85577	99.399
11	0.02184	0.09098	23.87761	99.49
12	0.02029	0.08455	23.8979	99.5746
13	0.01875	0.07813	23.91665	99.6527
14	0.01549	0.06452	23.93214	99.7172
15	0.01407	0.05864	23.94621	99.7759
16	0.0119	0.04959	23.95811	99.8255
17	0.01128	0.04702	23.9694	99.8725
18	0.00869	0.03622	23.97809	99.9087
19	0.00833	0.03473	23.98642	99.9434
20	0.00528	0.02201	23.99171	99.9655
21	0.00479	0.01994	23.99649	99.9854
22	0.00225	0.00935	23.99874	99.9947
23	0.0008	0.00334	23.99954	99.9981
24	0.00046	0.00192	24	100

Table SI_1_3. Results of the principal component analysis – factors and standardized measures defining them

Measure/factor	F1	F2	F3	F4	F5	F6	F7	F8
M (Isr. rp)	-0.8200	0.5648	0.0889	0.0069	-0.0041	0.0035	0.0104	-0.0095
M (TL)	-0.9912	-0.0275	0.0218	0.0179	0.0078	0.0260	-0.0310	0.0189
M (c)	-0.9904	-0.0476	0.0951	0.0262	-0.0110	-0.0009	0.0345	-0.0372
M (Pan)	-0.9962	-0.0107	0.0357	-0.0112	-0.0171	-0.0150	-0.0481	-0.0095
M (aA)	-0.9961	-0.0141	0.0414	-0.0063	-0.0177	-0.0076	-0.0498	-0.0014
M (Van)	-0.9874	0.0220	-0.0026	-0.0541	-0.0173	-0.0226	-0.1029	-0.0055
M (aV)	-0.9937	-0.0202	0.0567	0.0107	-0.0204	-0.0188	-0.0319	-0.0115
M (aP)	-0.9901	-0.0335	0.0928	0.0564	-0.0067	-0.0109	-0.0098	-0.0333
M (aD)	-0.9854	-0.0206	0.0069	0.0324	0.0618	-0.0980	0.0234	-0.0392
M (lpc)	-0.9246	0.0362	-0.3090	0.1956	-0.0775	0.0305	-0.0037	-0.0403
M (ID)	-0.9768	0.0073	-0.1099	-0.0067	0.0745	-0.1047	0.0824	0.0072
M (IA)	-0.9704	0.0089	-0.1592	-0.0076	0.1114	-0.0785	-0.0669	0.0307
M (IC)	-0.9838	-0.0178	0.0430	0.0611	0.0569	0.0582	0.0065	0.0893
M (IP)	-0.9868	-0.0163	0.0142	0.0280	0.0047	0.0604	0.0723	0.0761
M (IV)	-0.9894	-0.0146	-0.0244	0.0231	0.0136	0.0445	0.0055	0.0962
M (hco)	-0.9921	-0.0321	0.0230	-0.0263	-0.0311	0.0339	0.0432	0.0113
M (H)	-0.9921	0.0030	-0.0127	-0.0857	0.0206	-0.0144	-0.0214	0.0348
M (h)	-0.9678	-0.0169	-0.0669	-0.0639	0.1223	0.1611	-0.0116	-0.1062
M (laco)	-0.9898	-0.0378	0.0527	-0.0237	-0.0311	-0.0100	0.0160	0.0091
M (lac)	-0.9837	-0.0317	-0.0528	-0.1139	-0.0633	0.0290	-0.0267	0.0192
M (io)	-0.9645	0.0093	-0.1554	-0.1417	-0.1230	-0.0183	0.0418	-0.0087
M (Oh)	-0.9626	-0.0955	0.1584	0.1028	-0.0468	-0.0191	-0.0549	-0.0156
M (prO)	-0.9817	-0.0761	0.0790	-0.0340	0.0238	-0.0264	0.0703	-0.0549
M (poO)	-0.9876	-0.0426	0.0723	0.0254	-0.0339	0.0007	0.0546	-0.0263

Continued

Measure/factor	F9	F10	F11	F12	F13	F14	F15	F16
M (Isr. rp)	0.0127	-0.0088	0.0005	0.0000	-0.0012	0.0041	0.0070	0.0000
M (TL)	-0.0212	0.0516	0.0276	0.0446	-0.0247	-0.0306	0.0562	-0.0017
M (c)	-0.0229	-0.0153	-0.0256	0.0024	0.0123	-0.0039	-0.0005	-0.0030
M (Pan)	-0.0341	0.0173	0.0036	-0.0172	-0.0041	-0.0119	0.0020	0.0022
M (aA)	-0.0339	0.0165	0.0075	-0.0103	0.0021	-0.0116	-0.0055	0.0025
M (Van)	-0.0537	0.0151	-0.0385	-0.0360	-0.0086	0.0028	-0.0278	-0.0071
M (aV)	-0.0210	0.0213	0.0395	-0.0006	0.0025	-0.0242	-0.0018	0.0028
M (aP)	-0.0346	0.0076	-0.0050	0.0124	0.0220	-0.0180	0.0110	-0.0061
M (aD)	0.0094	-0.0015	0.0845	0.0159	-0.0053	0.0253	-0.0473	0.0200
M (lpc)	-0.0232	0.0018	-0.0035	-0.0015	-0.0133	0.0243	-0.0039	-0.0067
M (ID)	0.0258	0.0535	-0.0592	-0.0050	-0.0371	-0.0145	0.0208	0.0250
M (IA)	0.0229	-0.0495	0.0001	0.0059	0.0661	-0.0062	0.0282	-0.0216
M (IC)	-0.0198	-0.0608	-0.0043	0.0581	-0.0482	-0.0117	-0.0154	-0.0134
M (IP)	0.0093	0.0350	0.0232	-0.0570	0.0470	0.0155	0.0117	-0.0321
M (IV)	-0.0058	-0.0123	-0.0055	-0.0492	-0.0107	-0.0210	-0.0312	0.0360
M (hco)	0.0151	0.0246	0.0398	0.0117	0.0209	0.0130	0.0110	0.0210
M (H)	0.0119	0.0156	-0.0054	-0.0037	-0.0189	0.0344	-0.0229	0.0008
M (h)	0.0423	0.0090	-0.0056	-0.0041	-0.0011	-0.0104	-0.0120	0.0042
M (laco)	0.0339	0.0436	-0.0390	0.0536	0.0115	0.0289	-0.0366	-0.0528
M (lac)	-0.0041	-0.0256	-0.0038	0.0233	-0.0016	0.0662	0.0392	0.0363
M (io)	0.0447	-0.0338	0.0225	0.0031	-0.0098	-0.0601	-0.0118	-0.0192
M (Oh)	0.1432	-0.0242	-0.0125	-0.0282	-0.0205	0.0034	0.0160	0.0050
M (prO)	-0.0604	-0.0544	0.0047	-0.0451	-0.0413	0.0222	0.0291	-0.0337
M (poO)	-0.0292	-0.0306	-0.0465	0.0259	0.0605	-0.0149	-0.0140	0.0406

Continued

Measure/factor	F17	F18	F19	F20	F21	F22	F23	F24
M (Isr. rp)	-0.0018	0.0037	-0.0023	-0.0010	0.0009	-0.0005	-0.0001	-0.0001
M (TL)	-0.0530	0.0187	0.0040	0.0040	-0.0130	-0.0046	-0.0009	0.0003
M (c)	0.0137	-0.0108	0.0225	-0.0225	-0.0212	-0.0328	-0.0024	0.0033
M (Pan)	0.0212	0.0027	-0.0044	0.0113	0.0072	-0.0043	0.0232	0.0056
M (aA)	0.0260	0.0060	0.0012	0.0084	0.0052	-0.0085	-0.0011	-0.0182
M (Van)	-0.0405	-0.0376	0.0107	0.0041	0.0125	0.0013	-0.0068	0.0031
M (aV)	0.0526	0.0201	-0.0107	0.0160	0.0074	0.0021	-0.0140	0.0085
M (aP)	0.0142	-0.0103	0.0120	-0.0422	-0.0063	0.0285	0.0017	-0.0012
M (aD)	-0.0241	0.0032	0.0234	-0.0027	0.0066	-0.0010	0.0017	-0.0003
M (lpc)	0.0024	0.0008	-0.0067	0.0031	-0.0060	0.0000	-0.0002	0.0000
M (ID)	0.0168	-0.0100	0.0071	0.0020	0.0107	0.0016	-0.0010	-0.0004
M (IA)	0.0000	0.0019	-0.0149	-0.0030	-0.0007	-0.0044	-0.0003	0.0003
M (IC)	0.0162	-0.0261	0.0109	0.0112	0.0078	0.0025	0.0007	0.0001
M (IP)	-0.0011	-0.0060	0.0362	0.0138	0.0029	0.0035	0.0001	0.0003
M (IV)	-0.0156	0.0353	-0.0214	-0.0284	0.0040	-0.0029	-0.0004	0.0008
M (hco)	-0.0019	-0.0537	-0.0527	-0.0065	0.0047	-0.0044	-0.0001	-0.0005
M (H)	0.0133	0.0005	-0.0082	0.0099	-0.0544	0.0091	0.0004	-0.0001
M (h)	0.0035	0.0038	0.0035	0.0009	0.0043	0.0014	0.0000	-0.0001
M (laco)	-0.0062	0.0271	-0.0192	-0.0084	0.0163	-0.0027	0.0007	0.0002
M (lac)	0.0120	0.0136	0.0247	-0.0092	0.0157	0.0011	-0.0010	0.0009
M (io)	-0.0047	-0.0039	0.0124	-0.0028	-0.0025	0.0022	0.0009	-0.0006
M (Oh)	-0.0069	-0.0035	0.0008	0.0062	0.0000	0.0017	-0.0002	-0.0004
M (prO)	-0.0137	0.0137	-0.0259	0.0044	0.0032	0.0038	-0.0012	-0.0010
M (poO)	-0.0233	0.0114	-0.0031	0.0315	-0.0051	0.0074	0.0002	-0.0003