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EVIDENCES OF MULTICOMPONENT STRUCTURE OF THE MIGRATORY STOCK AND MORPHOLOGICAL DISTINCTIONS OF SHADS FROM THE GENUS *ALOSA* (CLUPEAFORMES, ALOSIINAE) OF THE SEA OF AZOV

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Evidences of Multicomponent Structure of the Migratory Stock and Morphological Distinctions of Shads from the Genus *Alosa* (Clupeaformes, Alosiinae) of the Sea of Azov. Mezhzherin S. V., Vernygora O. V. — Migratory stocks of shads passing through the Kerch strait during their seasonal migrations consist of three groups of specimens, that can be identified based on the number of gill rakers on the first arch. These are so called Kerch shad *A. maeotica* (50.2 %), Pontic shad *A. immaculata* (48.7 %) and Caspian shad *A. caspia* (1.1 %). This ratio of species in the region remains stable for the last 60 years. Populations of Kerch and Pontic shads have similar age structure and sex ratio with a shift toward females 52–54 %. Specimens of *A. maeotica* have greater linear size and weight than those of *A. immaculata*, that indicates higher growth rate of the former. Analysis of 26 body measurements shows definite differences between these shads in their absolute features, there are also some differences in the proportions of the head. Nevertheless, degree and reproducibility of interspecific differences during various periods of time, do not allow for the reliable discrimination of specimens of these species assumed by some researchers.

Key words: pontic shad, *Alosa*, stock structure, morphometry, ecomorphs.

Доказательства многокомпонентности структуры миграционного стада и морфологические особенности пузанковых сельдей (Clupeaformes, Alosiinae) Азовского моря. Межжерин С. В., Вернигора О. В. — Миграционные стада пузанковых сельдей, проходящие в период сезонных миграций через Керченский пролив, состоят из особей трёх групп, которые можно идентифицировать по числу жаберных тычинок на 1-й дуге. Это так называемая керченская сельдь, *A. maeotica* (50,2 %), черноморско-азовская сельдь, *A. immaculata* (48,7 %), и пузанок, *A. caspia* (1,1 %). Такое соотношение между этими видами в регионе остаётся стабильным на протяжении последних 60 лет. Популяции керченской и черноморско-азовской сельдей имеют одинаковую возрастную структуру и соотношение полов, при котором самки составляют 52–54 %. Особи *A. maeotica* отличаются от *A. immaculata* большими линейными размерами и массой, что свидетельствует о более высоком темпе их роста. Использование 26 промеров тела показывает определённые различия между этими сельдями по абсолютным признакам, также отмечаются некоторые различия и в пропорциях головы. Тем не менее масштаб и низкая воспроизводимость межвидовых различий в разные периоды не позволяют надёжно дискриминировать особей этих предполагаемых некоторых исследователями видов.

Ключевые слова: черноморские сельди, *Alosa*, структура стада, морфометрия, экоморфы.

Alosa shads traditionally attracted attention of ichthyologists of the Black Sea and Sea of Azov. And that is not accidental, because this is one of the most valuable commercial groups of fish in the region. Numerous scientific studies were done on this group of fish, including those dealing with problems of systematics. Nevertheless, there are still some disputable questions including the species composition of the genus *Alosa* Linck, 1790 in the Black sea and Sea of Azov. Many researchers (Knipovitch, 1923; Tret'yakov, 1947; Ambroz, 1956; Pavlov, 1959a, 1959b; Vinogradov, 1960; Vasil'eva, 1996) stated that there were three species of shads in the Black Sea and Sea of Azov: *Alosa immaculata* E. T. Bennett, 1835, *A. maeotica* (Grimm, 1901), and *A. caspia* (Eichwald, 1838). Others (Vladimirov, 1961; Svetovidov, 1964) argued that there were only *A. immaculata* and *A. caspia* present, uniting *A. maeotica* and *A. immaculata* into one species. Moreover, in some publications few unidentified species were added to the last two species of shads, based on the single catches of individuals that

differed in their morphology and electrophoresis specters (Svetovidov, 1964; Mezhzherin, Fedorenko, Dobrovolov et al., 2012).

Lately the idea about the identity of the three proposed species of the genus *Alosa* in the Azov-Black sea basin became widely accepted. These results are based on the genetic analysis at the level of allozyme markers as well as on the DNA sequencing of anadromous and resident shads of the Atlantic that did not show any clear differences among species and forms (Boisneau et al., 1992; Bentzen et al., 1993; Faria et al., 2006; Bowen et al., 2008). Consequently, these three species should only be considered ecomorphs. Herewith, *A. immaculata* — large anadromous form with 40 to 60 gill-rakers that spawns in rivers; *A. maeotica* — large shad (20 to 49 gill rakers) that, unlike *A. immaculata*, spawns in brackish waters of the Sea of Azov; and *A. caspia* — resident small shad with number of gill rakers varying in the range from 60 to 80. Presence of both anadromous and resident ecomorphs is common for species of the Holarctic, and special morphological and genetic analyses (Ferguson et al., 1978. Hecht et al., 1987, Østbye et al., 2005) have showed that just like shads these ecomorphs have different number of gill rakers and size, whereas anadromous forms are significantly larger than resident forms, even though they are genetically identical to each other.

It is known that shads with fewer number of gill rakers, identified as *A. maeotica*, are only abundant in the Sea of Azov (Pavlov, 1959 a). Detailed morphological analysis, not only of the recent years (Fedorenko, 2006; Mezhzherin, Fedorenko, 2007), but also of the first half and middle of the XX century (Pavlov, 1959 a, 1959 b), has showed that shads with less than 36 gill-rakers are almost absent in the basins of the Danube, Dnepr, and Dniester rivers, meaning that *A. maeotica* is tightly connected to the Sea of Azov. Based on the number of gill-rakers this shad can be clearly distinguished not only from the species of the Danube, Dnepr, and Dniester stocks, but also from so called Don shads that spawn in the Don river. Therefore, even if *A. maeotica* is not a separate species, it can still be considered an independent unit of reproduction and feeding. Nevertheless, Kerch (Azov) shad and Pontic shad that spawns in the Don river are still not differentiated not only in commercial catches, but also during the period of feeding, and therefore the ratio of Kerch shad in the Sea of Azov is unknown. The question about the degree of differences of other morphological characteristics between these two forms remains unclear. Available comparative morphological descriptions of shads were made according to the standards of 50s of the XX century, and therefore require revision and specification according to the modern standards of statistical analysis.

Material and methods

Present research was based on the series of shad samples collected from commercial catches in the period from December 2009 to May 2011 in the Kerch strait near the station Zavetnoe. Samples, total of 623 specimens, were collected evenly throughout the seasons.

Besides the biological analysis: determining of size-weight values, sex, and age; the latter was done according to the method specific for shad (Miklashevskaya, 1953); the detailed morphological analysis of all fish was performed. The scheme of 26 body measurements was used for this purpose (Pavlov, 1953 a): Smith's length (L), maximum body height (H), minimum body height (h), antedorsal distance (D), postdorsal distance (pD), anteventral distance (V), anteanal distance (A), distance between pectoral and ventral fins ($P-V$), distance between ventral and anal fins ($V-A$), length of caudal peduncle (pl), length of dorsal fin base (ID), height of dorsal fin (hD), length of anal fin base (IA), height of anal fin (hA), length of pectoral fin (IP), length of ventral fin (IV), length of the upper lobe of caudal fin (IC_1), length of the lower lobe of caudal fin (IC_2), head length (HL), head height (Hh), snout length (ae), eye diameter (gh), postorbital distance (fd), upper jaw length (ak), lower jaw length (al), head width (wi). Indexation of body and fin measurements was done relatively to the body length, and indices of head measurements were calculated relatively to the head length. Besides that, number of gill-rakers on the first arch ($sp. br.$) was counted for each fish.

Statistical analysis of the material was performed using the Statistica V.6 package.

Results and discussion

Number of gill rakers on the first arch in the total sample of shads varied from 25 to 75, with the distribution being quite uniform without any definite modal value (fig. 1). Therefore, based on this feature, three species can be identified among the studied fish. Individuals with number of gill rakers from 26 to 40 should be considered *A. maeotica* (313 specimens, 50.2 %), from 40 to 60 — *A. immaculata* (304 specimens, 48.7 %), and more than 60 — *A. caspia* (7 specimens, 1.1 %). Worth to mention that there is no hiatus between groups of shads identified as *A. maeotica* and *A. immaculata*. That means, that despite decrease of the number of individuals with 39–40 gill rakers, this feature cannot be used for the differentiation of these two ecomorphs. Unreliability of this feature for the differentiation of so called marine and anadromous forms has been mentioned previously (Vladimirov, 1961). The fact that specimens with less than 39 gill-rakers are absent in the Dnepr and lower Danube rivers (fig. 1) gives a reason to consider shads

with a small number of gill-rakers to be specific to the Sea of Azov. This means that more than a half of the shad stock in the Sea of Azov is formed of the Kerch shad that apparently spawns in the Sea of Azov. It should be emphasized that the same ratio of this species was present in catches in the Kerch strait during the late 40s of the XX century, found in Pavlov's works (Pavlov, 1959 a). Nearly the same ratio of Azov shads in the previous catches was noted by other authors (Sirotenko, 1966).

Comparison of biological characteristics of *A. maeotica* and *A. immaculata* (table 1) shows that *A. maeotica* has slightly larger size and body weight, while these two groups of shads have the same age value, and this proves greater growth rates of *A. maeotica*. There is also no difference in the condition of the two species, estimated with Fulton's condition coefficient (1.32 ± 0.013 and 1.31 ± 0.014 for *A. maeotica* and *A. immaculata* respectively). Sex ratio is nearly equal, slightly shifted toward females (table 1).

Specimens with more than 60 gil rakers were identified as *A. caspia*, but apparently this group included both *A. caspia* and *A. immaculata* with a big number of gill rakers. This idea is supported by extremely high individual variations of the size and age values of some specimens.

Comparison of the mean values of individual body measurements revealed highly significant differences of a number of characteristics, with *A. maeotica* always having greater values than *A. immaculata*, and that is quite natural because the former shads are larger than the latter (table 2). Range of variability of some characteristics that differ with a high level of significance overlap for the two species and thus none of the characteristics can be used for the clear differentiation of *A. maeotica* and *A. immaculata*. In regard to indices, these species are much less different in their body proportions and only some head indices are significantly different. Particularly, *A. maeotica* has relatively greater snout length, eye diameter, length of lower jaw, and head width. However, in this case as well, variation of these indices of the two species overlap and therefore cannot be used to obtain reliable diagnostics of the individual specimens of *A. immaculata* and *A. maeotica*.

Insignificance of morphological differences between *A. maeotica* and *A. immaculata* is also supported by multidimensional analysis. When using the factor analysis, almost

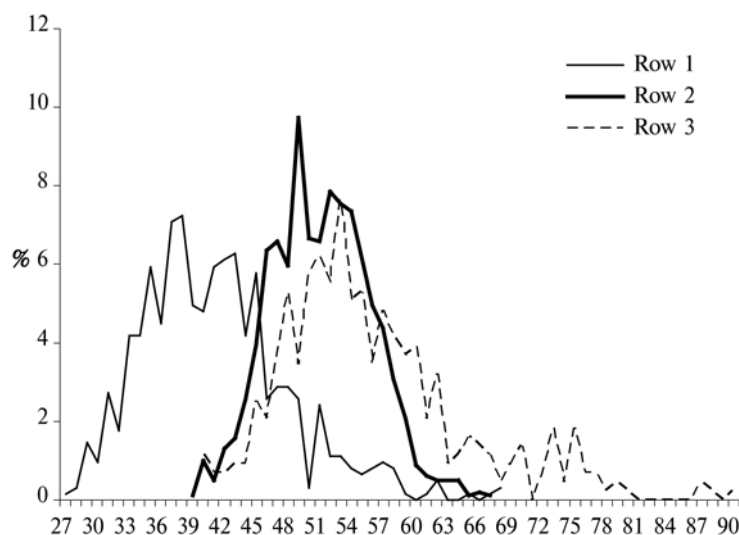


Fig. 1. Distribution of number of gill rakers on the first arch in shads of the genus *Alosa*: row-1 — Azov shads (Kerch strait, 2009–2011s), row-2 — Danube shad (2005–2008s); row-3 — Dnepr shads after: Ambroz, 1956 (1937).

Рис. 1. Распределение пузанковых сельдей рода *Alosa* по числу жаберных тычинок на первой дуге: ряд 1 — азовская сельдь (Керченский пролив, 2009–2011-е гг.); ряд 2 — дунайская сельдь (2005–2008-е гг.); ряд 3 — днепровская сельдь по: Ambroz, 1956 (1937 г.).

Table 1. Basic biological characteristics of shads identified to species based on the number of gill rakers on the first arch

Таблица 1. Основные биологические показатели у сельдей, определённых до вида, по числу жаберных тычинок на первой дуге

Characteristic	N	M	min	max	m
26–40 (<i>A. maeotica</i>)					
Age	294	3.37	1	6	0.05
L, cm	313	24.7	107	324	0.23
P, g	313	222.85	10	550	4.88
♀, %	277	0.52			0.03
41–60 (<i>A. immaculata</i>)					
Age	278	3.38	1	6	0.06
L, cm	304	23.8	105	303	0.27
P, g	304	201.68	8	398	5.37
♀, %	253	0.54			0.03
61–75 (<i>A. caspia</i>)					
Age	9	2.88	1	5	0.40
L, cm	9	16.9	140	287	0.17
P, g	9	76.67	22	320	31.9
♀, %	7	0.57			0.19

Table 2. Mean values (M) and their standard errors (SE), minimum (min) and maximum (max) values of characteristics, and statistical significance (p) calculated by one-way ANOVA for the two supposed species of shads
Таблица 2. Средние значения (M) и их стандартная ошибка (SE), минимальные (min) и максимальные (max) значения признаков и степень достоверности (p) различий средних по критерию (one-way ANOVA) для двух предполагаемых видов сельдей

Characteristic	<i>A. immaculata</i>				<i>A. maeotica</i>				p
	M	min	max	SE	M	min	max	SE	
<i>sp. br.</i>	46.3	41	75	0.29	35.8	27	40	0.17	0.000000
<i>H</i> , mm	59.5	20	90	0.88	62.6	21	95	0.80	0.009080
<i>h</i> , mm	17.5	6	26	0.24	18.3	6	24	0.21	0.005030
<i>aD</i> , mm	112.0	44	144	1.31	117.2	48	161	1.15	0.003090
<i>lD</i> , mm	31.2	13	44	0.38	32.7	12	47	0.34	0.005003
<i>hD</i> , mm	28.6	9	42	0.40	30.4	12	42	0.36	0.001081
<i>lA</i> , mm	35.9	14	47	0.42	37.5	15	50	0.37	0.006249
<i>hA</i> , mm	15.8	5	24	0.22	16.7	5	28	0.21	0.002177
<i>lC_1</i> , mm	47.2	22	64	0.51	49.2	20	65	0.45	0.004003
<i>lC_2</i> , mm	54.1	28	68	0.56	56.1	25	74	0.50	0.007656
<i>HL</i> , mm	54.1	24	69	0.57	56.1	24	77	0.49	0.007931
<i>ae</i> , mm	14.8	4	21	0.20	15.8	4	22	0.18	0.000188
<i>gh</i> , mm	9.8	3	15	0.16	10.7	3	15	0.15	0.000035
<i>pl</i> , mm	31.2	11	43	0.39	32.9	13	45	0.34	0.000886
<i>wi</i> , mm	10.2	2	16	0.19	11.1	2	17	0.17	0.000284
<i>al</i> , mm	10.8	8	15	0.09	10.3	8	16	0.09	0.000303
<i>ae/HL</i> , %	27.1	16	34	0.18	28.0	15	33	0.18	0.000639
<i>gh/HL</i> , %	17.9	10	25	0.18	18.8	10	25	0.17	0.000224
<i>al/HL</i> , %	57.4	37	71	0.27	58.5	48	73	0.27	0.002590
<i>wi/HL</i> , %	18.4	7	26	0.23	19.4	7	27	0.20	0.000669

complete overlapping of scatter plots of *A. maeotica* and *A. immaculata* specimens in the space of the first two factors obtained from the analysis of the variability of 25 body indices (fig. 2) is observed. Moreover, discriminant analysis shows that accuracy of identifying individual specimens by a complex of indices is only 63 % (table 3), that does not meet the level of interspecific morphological differentiation.

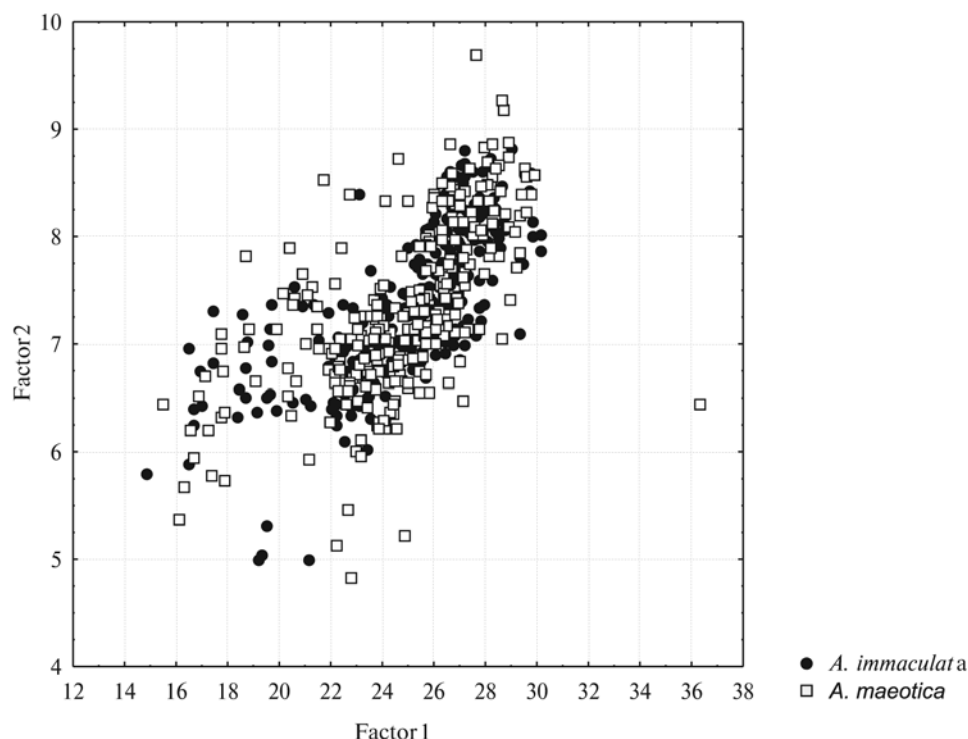


Fig. 2. Scatter plot of the two species of shads in the space of two principal components based on 25 body and head indices (Factor-1 — 28 % of the total variability, Factor-2 — 13.5 %).

Рис. 2. Рассеивание отдельных особей двух видов пузанковых в пространстве первых двух главных компонент по 25 индексам туловища и головы (Factor-1 — 28% общей изменчивости; Factor-2 — 13,5%).

Previously, researchers have noted that differentiation of Don and Kerch shads based on their body measurements is not reliable and stable. Particularly, the artificiality of differentiation between *A. maeotica* and *A. immaculata* is supported by the fact that differences of body indices between Kerch (marine) and Don (anadromous) shads of the sea of Azov were significantly smaller than between populations of marine shads with a small number of gill rakers, identified as *A. maeotica*, in different parts of the Azov-Black Sea basin, Danube region of the Black sea and the Sea of Azov in particular (Pavlov, 1959). Researchers of that time explained this paradox by close similarity of the feeding conditions of anadromous and marine shads in the Sea of Azov. Thus number of gill rakers on the first arch has always been the only feature for identifying *A. maeotica* and *A. immaculata*. However distribution of the number of gill rakers in the samples of shads is quite uniform without any hiatus and therefore decision to draw a line between species at the mark of 40 gill-rakers would be rather disputable.

Differences of body indices between *A. maeotica* and *A. immaculata* are not stable in time and probably depend on the individual researcher doing the measurements. Analysis

Table 3. Classification matrix of the discriminant analysis of shads of the Sea of Azov, based on 25 body and head indices (rows — observed classification, columns — expected)

Таблица 3. Классификационная матрица дискриминантного анализа пузанковых сельдей Азовского моря по 25 индексам туловища и головы (по рядам — наблюдаемая классификация, по столбикам — ожидаемая)

Species	%	<i>A. maeotica</i>	<i>A. immaculata</i>
<i>A. maeotica</i>	67.1	210	103
<i>A. immaculata</i>	60.3	121	184
Total	63.7	331	287

Table 4. Comparison of a number of morphological features between shads of the modern stocks and those of the 40–50s of the XX century

Таблица 4. Сравнительная характеристика ряда морфометрических параметров сельдей современного стада и по материалам 40–50-х годов XX ст.

Characteristic, % (except <i>L</i>)	<i>A. maeotica</i>				<i>A. immaculata</i>			
	2009/2011		40–50s XX c. *		2009/2011		40–50s XX c. *	
	M	m	M	m	M	m	M	m
<i>L</i> , cm	24.7	0.23	20.8	0.26	23.8	0.27	20.1	0.17
<i>al/L</i>	10.3	0.09	12.1	0.08	10.8	0.09	12.0	0.13
<i>hD/L</i>	12.2	0.07	12.5	0.08	12.0	0.08	12.2	0.1
<i>hA/L</i>	6.7	0.06	6.2	0.06	6.6	0.06	5.9	0.11
<i>IP/L</i>	13.8	0.06	—	—	13.9	0.07	15.4	0.17
<i>IV/L</i>	8.8	0.04	—	—	8.9	0.05	9.5	0.07
<i>IC_1/L</i>	19.9	0.07	19.0	0.08	20.0	0.07	19.0	0.11
<i>IC_2/L</i>	22.7	0.07	20.7	0.07	22.9	0.08	20.7	0.11
<i>Hh/HI</i>	81.7	0.3	70.0	0.21	82.3	0.36	72.0	0.48
<i>fd/HI</i>	58.5	0.19	53.3	0.14	57.9	0.20	54.5	0.27
<i>ak/HI</i>	50.1	0.16	46.0	0.16	49.6	0.18	46.1	0.24
<i>al/HI</i>	58.5	0.27	59.9	0.14	57.4	0.27	60.0	0.24
<i>wi/HI</i>	19.4	0.21	16.4	0.13	18.4	0.23	15.97	0.16

* According to P. I. Pavlov (Pavlov, 1959 a).

of the modern material showed the maximum differences between the two species in *al/HI*, *wi/HI*, *fd/HI*, *Hh/HI* ratios (tables 2, 4), with *A. maeotica* having greater values of the first three indices and lower value of the last index. While in the samples of shads collected 50–60 years ago, differences between these species were much less and were observed for different indices and for the same indices had different direction (table 4). Significant changes of morphological features have also occurred during the compared period of time. Not only has the size of fish become larger, but also a number of body proportions has changed, especially: *al/HI*, *ak/HI*, *wi/HI*, and *fd/HI*. Moreover, these changes have occurred parallel of the same indices and in the same degree in the stocks of Azov and Don shads.

Thus, the present research provides evidences that, indeed, there are shads with a small number of gill rakers in the Sea of Azov that some researchers have viewed as a separate species *A. maeotica* and that has currently disappeared in the North-Western region of the Black Sea. Just as 50–60 years ago this form comprises about a half of all shads. Morphological analysis of a number of indices showed that plastic features of individual specimens identified as *A. maeotica* and *A. immaculata* had only slight differences and nature of these differences was not stable in time and space.

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