1871
ИнБЮМ – IBSS

Морской биологический журнал, 2020, том 5, № 1, с. 99–110
Marine Biological Journal, 2020, vol. 5, no. 1, pp. 99–110
https://mbj.marine-research.org; doi: 10.21072/mbj.2020.05.1.10
ISSN 2499-9768 print / ISSN 2499-9776 online

UDC 576.893.1:597.2/.5(262.5+262.54+262.81)

HISTORY OF FORMATION AND PECULIARITIES OF PONTO-CASPIAN FISH MYXOSPOREAN FAUNA

© 2020 **V. M. Yurakhno[1] and A. N. Özer[2]**

[1]A. O. Kovalevsky Institute of Biology of the Southern Seas of RAS, Sevastopol, Crimea
[2]Sinop University, Sinop, Turkey
E-mail: *viola_taurica@mail.ru*

Received by the Editor 18.07.2019; after revision 20.09.2019;
accepted for publication 27.03.2020; published online 31.03.2020.

History of formation of Ponto-Caspian basin fish myxosporean fauna is examined. This work is based on our own material on myxosporean parasites of fish from the Black Sea (collected in 1987–2018) and the Sea of Azov (1997–2016). Totally, we have investigated 15 368 specimens of 87 species of fish (14 297 specimens of 80 species of fish in the Black Sea and 1071 specimens of 19 species of fish in the Sea of Azov). The material was collected by the method of incomplete parasitological dissections and treated by generally accepted methods. Also, all available literary sources on the myxosporean parasites of fish from the Black Sea, the Sea of Azov, and the Caspian Sea are analyzed (references list contains the most significant publications). A comparative analysis of fish myxosporean fauna in the Black Sea, the Sea of Azov, and the Caspian Sea is performed. It is stated that 108 parasite species are known in the Black Sea, 42 – in the Sea of Azov, and 68 – in the Caspian Sea. Number of myxosporean parasite species common for the Sea of Azov and the Black Sea is 32, for the Caspian and Black seas – 32, and for the Sea of Azov and the Caspian Sea – 20. Totally 16 species of myxosporean parasites are registered in all the mentioned seas. To date, of 108 myxosporean species of Black Sea region, 29 are registered only in freshwater fish in the estuaries with considerable brackish water. For 79 myxosporean species, marine fish species serve as hosts; they are registered mainly in full-salt sea part, and 17 of them are of freshwater origin: 7 species are registered in freshwater fish and in euryhaline mullets; 1 parasitizes on freshwater and marine salmon fishes; the only hosts for 9 species are mullets or other marine fish species. Marine forms are represented by Pontic (22 species), Ponto-Azov (3), and Ponto-Caspian (2) endemics, as well as by Mediterranean invaders (35). Among freshwater myxosporeans, only 1 species is Black Sea endemic; 1 species is Ponto-Azov endemic, and most other species are widely represented in freshwater reservoirs. Among Mediterranean invaders, 23 species found in the Mediterranean Sea should be noted; 12 species still have not been registered in the Mediterranean Sea, mainly due to very few studies on this group of parasites. The fauna of Sea of Azov fish parasites includes 42 myxosporean species; 32 of them are found in the Black Sea, 20 – in the Caspian Sea. Totally 19 species belong to freshwater ones, and they are parasitic only in freshwater fish species. Ten species are of freshwater origin but can be registered in marine fish species (mostly in mullets, and one – in gobies). Of the freshwater species, one is Ponto-Azov endemic. Totally 13 myxosporean species are marine ones: 2 species are Sea of Azov endemics; 3 species are Ponto-Azov endemics; 8 species are Mediterranean invaders. Caspian Sea fauna includes 68 species of myxosporeans: 8 are marine ones (1 is ancient marine species; 1 is Ponto-Caspian endemic; 6 are brackish-water myxosporeans), and 60 are freshwater species. Five endemics of the Caspian Sea are known (2 of marine origin and 3 of freshwater origin). When moving from west to east (from the Black Sea to the Caspian Sea), a gradual impoverishment of marine myxosporean fauna and its replacement by freshwater myxosporean species are observed. Impoverishment of Myxosporea species composition of the Sea of Azov and the Caspian Sea in comparison with the Black Sea one is also found.

Keywords: fauna, Myxosporea, fish, Black Sea, Sea of Azov, Caspian Sea

History of formation of the Ponto-Caspian basin fish myxosporean fauna is connected with a complex geological past of the southern seas. At the Paleogene at the site of the Mediterranean, Black, and Caspian seas, as well as the Sea of Azov, there laid a full-salt sea Tethys, connected openly with the ocean [2, 32, 33, 42, 43]. At Miocene, it gradually isolated, becoming Sarmat basin; it was accompanied by strong desalination. Sharp stratification of waters appeared, leading to development of hydrogen sulfide zone at depth. Under new conditions, rapid extinction of almost the entire fauna in the Sarmat basin and wide development of peculiar mactric fauna took place. Between Sarmat and Pliocene periods, the Meotic basin also connected with the ocean was formed. In its turn, this led to changes in the fauna: Sarmat species began to vanish, and typical Mediterranean species appeared. In the eastern part of the Meotic basin, hydrological conditions were very similar with those of modern Black Sea, and there was a deep-water part contaminated with hydrogen sulfide [1]. The Meotic basin eastern part has separated during Pliocene period. Vast inner brackish-water Pontic Lake was a sea with brackish-water fauna. By the end of Tertiary and the beginning of Quaternary period, this sea split, forming now existing the Black Sea, the Sea of Azov, the Caspian Sea, and the Aral Sea. The last two of them preserved brackish-water character with appropriate fauna, while the Black Sea underwent one more transformation. Being connected with the Mediterranean Sea, it underwent great salinization. As a result, brackish-water fauna partially died out, and its remnants remained in the estuaries and in the Sea of Azov. All the other parts of the sea were inhabited by Mediterranean fauna. Due to low water salinity and uninhabited Black Sea depth resulting from hydrogen sulfide presence, many Mediterranean species and their parasites could not settle there; nevertheless, of fish, only Gobiidae, Atherinidae, Clupeidae, Syngnathidae, and Acipenseridae originate from the brackish water basin mentioned above and are common for the Caspian Sea [17]. All other fish resettled in the Black Sea from the Mediterranean Sea [37].

Absence of many Mediterranean parasite species in Black Sea fish parasite fauna was noted by V. A. Dogel [5]; he based on the results of his own research and data of S. U. Osmanov [22], A. V. Reshetnikova [30], and Z. S. Donets [7, 8] who wrote about impoverishment of Black Sea fish myxosporeans compared to Atlantic and Mediterranean basins fish myxosporeans. A. Reshetnikova relying on myxosporeans origin proposed to divide Black Sea species into following zoogeographic groups: global, arctic-boreal, boreal-Atlantic, Mediterranean, freshwater, and Black Sea endemics. N. N. Naidenova [21] studying parasites of gobies from the Black Sea and the Sea of Azov isolated some other zoogeographic groupings. So, freshwater species are divided into paleo-arctic, Ponto-Caspian-Aral, Black Sea endemics, characteristic for the area and common with Amur species, and Mediterranean with not clear areal. Marine parasites are divided into arctic-boreal, boreal (boreal-Atlantic, amphi-boreal), Mediterranean, Ponto-Azov endemics, tropic-boreal, global, and with not clear areal. In general, according to N. Naidenova, the fauna of gobies parasites unites the following zoogeographic groupings of species: 1 – Mediterranean; 2 – widely spread geographically (arctic and boreal); 3 – freshwater; 4 – characteristic only for the Black Sea and the Sea of Azov. N. Naidenova attributed *Sphaeromyxa sevastopoli*, *Fabespora nana*, and neoendemic *Myxidium melanostomi* to the last paleo-endemics.

Faunistic complexes and groups of the freshwater myxosporeans have another history and, therefore, adhere to different laws. For the southern water basins of the former USSR, they are given in detail by Z. Donets [6], and that is why we will limit ourselves to a brief presentation. In Black Sea area of Ponto-Caspian-Aral province, this problem was studied by Z. Donets mostly for myxosporean fauna of big rivers coming into the Black Sea and the Sea of Azov, as well as Crimean water reservoirs. Z. Donets emphasizes that Ponto-Caspian-Aral province is the richest region with freshwater myxosporeans within the Euro-Asian part of Golarctics, but in this province, when moving from west to east, gradual impoverishment of parasites species composition is observed, especially pronounced in the Aral Sea.

Formation of myxosporean fauna in southern seas of the former USSR is also analyzed by Z. Donets [7, 8]. It is proposed to consider the Black Sea fauna to be impoverished marine with not considerable admixtures of freshwater elements. In the Black Sea, 32 species were divided by Z. Donets into the following groups: ancient-marine (1 species), Ponto-Caspian endemics of marine origin (6), Mediterranean invaders (19), parasites of Gasterosteidae (1), freshwater species (4), and Ponto-Caspian endemics of freshwater origin (1). Analysis of the Caspian and Aral seas myxosporeans has been given [7].

All the authors named above marked that zoogeographical characteristic of parasites is in good accordance with zoogeography of Black Sea free-living organisms. In 1987, a bit different idea on the richness of Black Sea fish myxosporean fauna appeared. M. G. Kolesnikova and Z. S. Donets [18] presented their belief that the idea of fauna's extreme impoverishment is a bit out reality. They supposed that a great number of new species found in the Black Sea can be also found in the Mediterranean Sea. Based on their data (description of 4 new myxosporean species), we continued and made description of 15 new species increasing considerably the list of fish myxosporeans in the Ponto-Azov basin. *Myxidium pulchrum* described in 1991 for the Black Sea was later found in the Adriatic Sea [19]. *Alataspora solomoni* – Black Sea species new for science described by V. Yurakhno in 1988 – was later found in the Ionian Sea [4]. *Zschokkella admiranda* considered previously as Black Sea species was found in the Mediterranean Sea near coast of Spain [39]. The data on species richness of Black Sea fish myxosporean fauna became fuller due to Pacific and Atlantic oceans species, as well as Mediterranean, Red, and Adriatic seas species found in the Pontic basin. Myxosporean species known for the Atlantic Ocean (*Chloromyxum schulmani*, *Sinuolinea rebae*), for the Atlantic and Pacific oceans (*Ch. ovatum*, *Ortholinea orientalis*) [25, 26, 34], and for the Mediterranean and Red seas and for the Pacific Ocean (*Enteromyxum leei*) [28] were later found in the Black Sea. *Ceratomyxa beloneae* – a species described earlier in the Adriatic Sea – was later found by us in the Black Sea [29, 34]. Myxosporean parasites *Sphaerospora dicentrarchi*, *Sphaerospora mugilis*, *Myxobolus spinacurvatura*, *M. ichkeulensis* [23, 39], and *Myxobolus episquamalis* [3, 31] found earlier in Mediterranean Sea mullet were later registered in the Black Sea and in the Sea of Azov. Many myxosporean species were found in new hosts and geographical areas, and their lists of hosts and areas were widened.

In this regard, it is of interest to give modern comparative characteristics of the Ponto-Caspian basin fish parasite fauna, since myxosporeans constitute one of the most interesting groups in it.

MATERIAL AND METHODS

This work is based on our own material on the myxosporeans of fish from the Black Sea collected in 1987–2018 and from the Sea of Azov collected in 1997–2016. Totally, we have investigated 15 368 specimens of 87 species of fish (14 297 specimens of 80 species of fish in the Black Sea and 1071 specimens of 19 species of fish in the Sea of Azov).

The material was collected by the method of incomplete parasitological dissections and treated by generally accepted methods. Also, all available literary sources on the myxosporean parasites of fish from the Black Sea, the Sea of Azov, and the Caspian Sea were analyzed (references list contains only the most significant publications).

RESULTS AND DISCUSSION

Comparison of species composition of Black Sea, Sea of Azov, and Caspian Sea fish myxosporean parasites has shown that 108 species are known in the Black Sea, 42 – in the Sea of Azov, and 68 – in the Caspian Sea (Table 1) [41, modern data]. Number of myxosporean parasite species common for the Sea of Azov and the Black Sea is 32, for the Caspian and the Black seas – 32, and for the Sea of Azov and the Caspian Sea – 20. Totally 16 myxosporean species are registered in all three seas.

Table 1. Myxosporean species of Black Sea, Sea of Azov, and Caspian Sea fishes (according to literary and own data)

Myxosporean species	The Black Sea	The Sea of Azov	The Caspian Sea
Alataspora solomoni	+		
Ceratomyxa agilis	+		
C. arcuata	+		
C. beloneae	+		
C. caspia			+
C. elegans	+		
C. globulifera	+		
C. hepseti	+	+	
C. inaequalis	+		
C. informis	+		
C. markewichi	+		
C. merlangi	+		
C. parva	+		
C. peculiaria	+		
C. reticularis	+		
Chloromyxum cristatum	+		+
Ch. esocinum	+		
Ch. fluviatile	+		+
Ch. legeri	+		+
Ch. osmanovi	+		
Ch. ovatum	+		
Ch. partistriatus	+		
Ch. psetti	+		
Ch. schulmani	+		
Ch. trachuri	+		
Ch. truttae			+
Ch. varicorhini			+
Enteromyxum leei	+		
Fabespora nana	+		
Henneguya chaibulaevi			+
H. creplini	+		
H. gigantea	+		
H. lobosa	+		+
H. oviperda	+		
H. psorospermica	+		+
H. schizura		+	
H. sinova	+		
Hoferellus conifer		+	
H. jurachni	+		
Gadimyxa ovale	+		
Kudoa anatolica	+		

Continue on next page…

Myxosporean species	The Black Sea	The Sea of Azov	The Caspian Sea
K. niluferi	+		
K. nova	+	+	
K. quadratum	+		
K. stellula	+		
Myxidium cochleatum	+		
M. benthophili		+	
M. gadi	+	+	
M. incurvatum	+		
M. lieberkühni	+	+	+
M. macrocapsulare	+		+
M. melanostomi	+	+	
M. parvum	+		
M. pfeifferi	+	+	+
M. pulchrum	+		
M. rhodei	+		+
M. salmonis	+		
M. schulmani			+
Myxobilatus convexum	+		
M. gasterostei	+		+
M. medius	+	+	+
M. platessae	+		
M. varicorhini			+
Myxobolus adeli	+	+	
M. albovae	+		+
M. alburni			+
M. alievi			+
M. anurus	+		
M. asymmetricus	+		
M. bliccae		+	+
M. bramae	+	+	+
M. branchialis	+		+
M. carassii			+
M. chondrostomi			+
M. circulus	+		+
M. cycloides			+
M. cyprini	+	+	+
M. cyprinicola			+
M. dispar	+	+	+
M. diversicapsularis			+
M. dogieli		+	+
M. donecae			+
M. dujardini			+
M. elegans	+		
M. ellipsoides	+	+	+

Continue on next page…

Myxosporean species	The Black Sea	The Sea of Azov	The Caspian Sea
M. episquamalis	+	+	
M. exiguus	+	+	+
M. gigas			+
M. ichkeulensis	+	+	
M. infundibulatus			+
M. karelicus	+		+
M. kubanicus		+	
M. kuleminae			+
M. lobatus			+
M. macrocapsularis	+	+	+
M. magnus		+	
M. minutus			+
M. muelleri	+	+	+
M. musajevi			+
M. musculi	+	+	+
M. najdenovae	+	+	
M. nemachili			+
M. obesus	+		+
M. oviformis	+	+	+
M. parvus	+	+	
M. percarinae	+		
M. pfeifferi			+
M. pseudodispar	+	+	+
M. rotundus	+		+
M. rutili	+	+	+
M. saidovi			+
M. samgoricus			+
M. sandrae	+	+	+
M. schulmani			+
M. squamae			+
M. sphaericus	+		
M. spinacurvatura	+	+	
M. truttae			+
Myxodavisia cornuta		+	
M. ophidioni	+		
Ortholinea antipae	+		
O. divergens	+		
O. gobiusi	+	+	
O. mullusi	+		
O. orientalis	+		
Pseudalataspora pontica	+		
Sigmomyxa sphaerica	+		
Sinuolinea rebae	+		
S. sakinachanumae	+		+

Continue on next page…

Myxosporean species	The Black Sea	The Sea of Azov	The Caspian Sea
Sphaeromyxa atherinae	+		
S. balbiani	+		
S. incurvata	+		
S. sabrazesi	+		
S. sevastopoli	+	+	
Sphaerospora bergi	+		
S. carassii			+
S. caspialosae	+		+
S. caudata	+	+	
S. dicentrarchi	+	+	
S. donecae			+
S. elegans	+		+
S. mugilis	+	+	
Thelohanellus misgurni			+
T. pyriformis		+	+
Zschokkella admiranda	+		
Z. dogieli	+		
Z. iskovi	+		
Z. nova	+	+	+
Z. striata		+	
Z. sturionis		+	+

Black Sea fish myxosporean fauna was depicted earlier in key manuals [9, 16]. Origin and composition of Black Sea fish myxosporean fauna were considered later by V. M. Yurakhno in Russian, Georgian, Abkhazian, and Ukrainian waters [35, 37]. New data on Black Sea fauna were obtained near Turkish shores [12, 24, 27, 28, etc.], as well as in Ukrainian and Moldavian waters of Lower Danube and Dniester basins (for Clupeidae fishes) [20]. New data on Sea of Azov fauna were obtained for the Taganrog Gulf [36, 38]. New information was received for myxosporeans of Mugilidae in the Black Sea and the Sea of Azov [39, 40]. Comparison of the myxosporean fauna in the Black Sea and adjacent seas using Czekanowski – Sørensen index [35] has shown that fish myxosporean fauna in the Black Sea, the Sea of Azov, and the Caspian Sea forms one cluster. It is not quite homogenous by hydrological conditions and hosts species composition. Water salinity in the main part of the Black Sea is of 17–18.5 ‰. The Sea of Azov and the Caspian Sea have highly brackish waters with salinities of 10–14 ‰ and 12.7–12.8 ‰ (less often of 13.2 ‰), respectively. In the Sea of Azov near estuary areas, salinity is of 2–4 ‰ and even lower, and in the Caspian Sea – of 1–2 ‰ (in the north-west).

To date, of 108 myxosporean species of the Black Sea region, 29 are registered only in freshwater fish in the estuaries with considerable brackish water (*Myxidium lieberkühni*, *M. macrocapsulare*, *M. pfeifferi*, *M. rhodei*, *Chloromyxum cristatum*, *Ch. esocinum*, *Ch. fluviatile*, *Ch. legeri*, *Myxobolus albovae*, *M. anurus*, *M. cyprini*, *M. dispar*, *M. elegans*, *M. ellipsoids*, *M. karelicus*, *M. macrocapsularis*, *M. musculi*, *M. obesus*, *M. oviformis*, *M. percarinae*, *M. pseudodispar*, *M. rutili*, *M. sandrae*, *M. sphaericus*, *Henneguya creplini*, *H. gigantea*, *H. lobosa*, *H. oviperda*, and *H. psorospermica*). For 79 myxosporean species, marine fish species serve as hosts; they are registered mainly in full-salt sea part. Totally 17 of them are of freshwater origin: 7 species (*Zschokkella nova*, *Myxobolus branchialis*, *M. bramae*, *M. circulus*, *M. exiguus*, *M. muelleri*, and *M. rotundus*) are registered in freshwater fish and in euryhaline mullets; 1 (*Myxidium salmonis*)

parasitizes on freshwater and marine salmon fishes; the only hosts for 9 species are mullets (for *Myxobolus adeli*, *M. episquamalis*, *M. ichkeulensis*, *M. parvus*, and *M. spinacurvatura*) or other marine fish species (for *Myxobolus asymmetricus*, *M. najdenovae*, *Hoferellus jurachni*, and *Henneguya sinova*).

Marine forms are represented by Pontic (22 species), Ponto-Azov (3), and Ponto-Caspian (2) endemics, as well as by Mediterranean invaders (35). Among freshwater myxosporeans, only 1 species (*M. percarinae*) is Black Sea endemic; 1 species (*Myxobolus najdenovae*) is Ponto-Azov endemic, and most other species are widely represented in freshwater reservoirs. Of the marine forms, Pontic endemics are: *Sphaeromyxa atherinae*, *Myxidium cochleatum*, *M. parvum*, *Fabespora nana*, *Gadimyxa ovale*, *Myxodavisia ophidioni*, *Ceratomyxa merlangi*, *C. markewichi*, *C. peculiaria*, *Myxobilatus convexum*, *Chloromyxum osmanovi*, *Ch. partistriatus*, *Ch. psetti*, *Ch. trachuri*, *Ortholinea antipae*, *Ortholinea mullusi*, *Sphaerospora bergi*, *Zschokkella dogieli*, *Pseudalataspora pontica*, *Kudoa anatolica*, *K. niluferi*, and *K. stellula*. Ponto-Azov endemics are: *Sphaeromyxa sevastopoli*, *Myxidium melanostomi*, and *Ortholinea gobiusi*. Ponto-Caspian endemics are *Sphaerospora caspialosae* and *Sinuolinea sakinachanumae*. Among Mediterranean invaders, 23 species were found in the Mediterranean Sea (*Sphaeromyxa balbiani*, *S. incurvata*, *S. sabrazesi, Myxidium gadi*, *M. incurvatum*, *M. pulchrum*, *Sigmomyxa sphaerica*, *Enteromyxum leei*, *Zschokkella admiranda*, *Ortholinea divergens*, *Ceratomyxa arcuata*, *C. beloneae*, *C. globulifera*, *C. inaequalis*, *C. parva*, *C. reticularis*, *C. agilis*, *C. hepseti*, *Sphaerospora dicentrarchi*, *S. mugilis*, *Alataspora solomoni*, *Kudoa nova*, and *K. quadratum*). The rest 12 species (*Sinuolinea rebae*, *Ortholinea orientalis*, *Zschokkella iskovi*, *Ceratomyxa elegans*, *C. informis*, *Sphaerospora caudata*, *S. elegans*, *Myxobilatus medius*, *M. gasterostei*, *M. platessae*, *Chloromyxum ovatum*, and *Ch. schulmani*) still have not been found in the Mediterranean Sea, mainly due to very few studies on this group of parasites. Meanwhile, identification of most of the species mentioned above in close regions of the World Ocean allows suggesting that they penetrated the Black Sea only through the Mediterranean Sea. As for *Ceratomyxa elegans* from *Scorpaena porcus*, as well as for *Myxobolus parvus*, *M. episquamalis*, *M. exiguus*, and *M. spinacurvatura* from mullets, they can also become parasites for Pacific Ocean fishes. Taking into consideration that at the end of Neogenic period of Cainozoan era, the Atlantic and the Pacific oceans were connected by a wide strait for some time [44], we can assume presence of each of these parasites in a common large areal in the past which then was split due to powerful geological transformations on our planet. To our opinion, this also applies to widely spread brackish-water species *Myxobilatus medius*, *M. gasterostei*, and *Sphaerospora elegans* having marine origin that penetrated the Ponto-Caspian basin from the Mediterranean Sea many years ago. Possibly in the future, *Zschokkella sturionis* – a parasite for sturgeons whose parasite fauna in the Black Sea has not been studied well – will also be found in the Black Sea.

Of 46 myxosporean species of freshwater origin found in the Black Sea, most species (29) inhabit freshwater fish in the region of Dnieper Delta, as well as Dnieper and Dnieper-Bug estuaries with water salinity of 0.08–0.5 to 3–4 ‰ (less often of 6–8 ‰) within the main territory. Freshwater hosts are mostly carps, bass, and pike. There are also euryhaline hosts: Black Sea salmon (of freshwater origin); sea herring and mullet; brackish-water Gasterosteidae (of marine origin). Parasites for euryhaline fish are also registered in other full-salt sea parts, where pure marine myxosporean species also survive. Brackish-water forms (*Sphaerospora caspialosae* and *S. elegans*) are represented in the gulfs. *S. caspialosae* is also registered in the Kerch Strait – a region with salinity of 10–14 ‰ to depth of 50 m.

The fauna of Sea of Azov fish parasites includes 42 myxosporean species [3, 9, 36, 37]; 32 of them are found in the Black Sea, 20 – in the Caspian Sea. Totally 19 species (*Henneguya schizura*, *Hoferellus conifer*, *Myxidium lieberkühni*, *M. pfeifferi*, *Myxobolus bliccae*, *M. cyprini*, *M. dispar*, *M. dogieli*, *M. ellipsoides*, *M. kubanicus*, *M. macrocapsularis*, *M. magnus*, *M. musculi*, *M. oviformis*, *M. pseudodispar*, *M. rutili*, *M. sandrae*, *Thelohanellus pyriformis*, and *Zschokkella striata*) are freshwater species, and they are parasitic

only on freshwater fish species. Ten species are of freshwater origin but can be registered in marine fish species (mostly in mullets – *Myxobolus adeli*, *M. bramae*, *M. episquamalis*, *M. exiguus*, *M. ichkeulensis*, *M. muelleri*, *M. parvus*, *M. spinacurvatura*, and *Zschokkella nova*; one in gobies – *M. najdenovae*). Of the freshwater species, *Myxobolus najdenovae* is Ponto-Azov endemic. Totally 13 myxosporean species are marine ones: 2 species (*Myxodavisia cornuta* and *Myxidium bentophili*) are Sea of Azov endemics; 3 species (*Shaeromyxa sevastopoli*, *Myxidium melanostomi*, and *Ortholinea gobiusi*) are Ponto-Azov endemics; 8 species (*Ceratomyxa hepseti*, *Kudoa nova*, *Myxidium gadi*, *Myxobilatus medius*, *Sphaerospora caudata*, *S. dicentrarchi*, *S. mugilis*, and *Zschokkella sturionis*) are Mediterranean invaders.

Number of myxosporean species common for the Sea of Azov and the Black Sea is 32. Totally 12 are freshwater parasites on freshwater fish; 9 are parasites on euryhaline mullets; 1 is gobies parasite found in full-salt waters; 10 are marine species (2 of them are brackish-water forms).

The Caspian Sea fauna is well described in works of A. A. Gazimagomedov [10, 11] and Sh. R. Ibragimov [13, 14, 15, etc.]. On its myxosporean fauna, the Caspian Sea is very similar to the Black Sea. In the fauna composition, there are 68 myxosporean species with 8 having marine origin (1 (*Zschokkella sturionis*) is ancient marine species; 1 (*Sinuolinea sakinachanumae*) is Ponto-Caspian endemic; 6 (*Sphaerospora caspailosae*, *S. donecae*, *S. elegans*, *Ceratomyxa caspia*, *Myxobilatus gasterostei*, and *M. medius*) are brackish-water myxosporeans) and 60 being freshwater species. The researchers mentioned above reported 5 Caspian Sea endemics, with *Ceratomyxa caspia* and *Shaerospora donecae* being of marine origin and *Myxobolus saidovi*, *M. alievi*, and *Henneguya chaibulaevi* – of freshwater origin.

Common fauna of such different water basins as the Black Sea and the Caspian Sea can be explained by the fact that connection between them exists mostly due to freshwater forms (27 species). Among marine species, only 5 are common (4 of them are of brackish-water origin).

The Caspian Sea and the Sea of Azov have 18 common freshwater parasites and 2 marine parasites (one of them is of brackish-water type). Unlike the Caspian Sea, the Sea of Azov is characterized by presence of Mediterranean invaders who could penetrate it from the Black Sea after the separation of the Caspian Sea, which became an independent basin.

Conclusion. When moving from west to east (from the Black Sea to the Caspian Sea), a gradual impoverishment of marine myxosporean fauna and its replacement by freshwater species are observed. In the Black Sea, correlation of marine and freshwater forms is approximately equal. In the Sea of Azov, elements of freshwater fauna begin to dominate. They reach considerable priority in the Caspian Sea where marine species are represented mainly by freshwater forms. As for impoverishment of abundance of myxosporean species directed from the Black Sea to the Caspian Sea (it was marked by Z. Donets), it does occur.

Part of this work conducted by V. M. Yurakhno was carried out within the framework of government research assignment of IBSS no. AAAA-A18-118020890074-2.

REFERENCES

1. Arkhangelsky A. D. Hydrogen sulfide contamination of some Tertiary sea basins of the Crimea and Caucasus region and its connection with the origin of petroleum. *Neftyanoe khozyaistvo*, 1926, vol. 10, iss. 4, pp. 483–486. (in Russ.)
2. Arkhangelsky A. D., Strakhov N. M. *Geological History of the Black Sea.* Moscow ; Leningrad : Izd-vo AN SSSR, 1938, 226 p. (in Russ.)
3. Bortnikov E. S., Strizhakova T. V., Boiko N. E., Ruzhinskaya L. P., Shevkoplyasova N. N. Myxobolosis of the flathead grey mullet *Mugil cephalus* in the Russian waters of the Black Sea. In: *Contemporary Problems of Theoretical and Marine Parasitology : Coll. of Sci. Papers* / K. V. Galaktionov, A. V. Gaevskaya (Eds). Sevastopol : Izd-l' Bondarenko N. Yu., 2016, pp. 211–213. (in Russ.)

4. Campbell N. The myxosporean parasitofauna of the Atlantic horse mackerel, *Trachurus trachurus* (L.) in the North-East Atlantic Ocean and Mediterranean Sea. *Acta Parasitologica*, 2005, vol. 50, no. 2, pp. 97–101.
5. Dogel V. A. *General Parasitology*. Leningrad : Izd-vo Leningr. un-ta, 1962, 464 p. (in Russ.)
6. Donets Z. S. Zoogeographical analysis of myxosporeans in the USSR southern water reservoirs. *Trudy Zoologicheskogo instituta AN SSSR*, 1979, vol. 87, pp. 65–90. (in Russ.)
7. Donets Z. S. Formation of myxosporeans fauna in the USSR southern seas. *Trudy Zoologicheskogo instituta AN SSSR*, 1981, vol. 107, pp. 74–79. (in Russ.)
8. Donets Z. S. *Myxosporeans of the USSR Southern Rivers Basins* : avtoref. diss. … d-ra biol. nauk. Leningrad, 1982, 43 p. (in Russ.)
9. Gaevskaya A. V., Gusev A. V., Delyamure S. L., Donets Z. S., Iskova N. I., Kornyushin V. V., Kovaleva A. A., Margaritov N. M., Markevich A. P., Mordvinova T. N., Naidenova N. N., Nikolaeva V. M., Parukhin A. M., Pogoreltseva T. P., Smogorzhevskaya L. A., Solonchenko A. I., Shteyn G. A., Schulman S. S. (Contrs). *Opredelitel' parazitov pozvonochnykh Chernogo i Azovskogo morei. Paraziticheskie bespozvonochnye ryb, ryboyadnykh ptits i morskikh mlekopitayushchikh*. Kiev : Naukova dumka, 1975, 552 p. (in Russ.)
10. Gazimagomedov A. A. To the study of parasitic Protozoa of the Caspian Sea fish. In: *Sbornik nauchno-issledovatelskikh rabot Dagestanskogo nauchno-issledovatel'skogo veterinarnogo instituta.* Makhachkala, 1970, vol. 4, pp. 291–293. (in Russ.)
11. Gazimagomedov A. A. New species of mucous sporozoans of the Caspian Sea fish. In: *Voprosy fiziologii, biokhimii, zoologii, parazitologii* : sbornik nauchnykh soobshchenii kafedry fiziologii cheloveka i zhivotnykh, zoologii i biokhimii. Makhachkala, 1970, pp. 72–76. (in Russ.)
12. Gürkanlı C., Okkay S., Çiftçi Y., Yurakhno V., Özer A. Morphology and molecular phylogeny of *Ortholinea mullusi* sp. nov. (Myxozoa) in *Mullus barbatus* from the Black Sea. *Diseases of Aquatic Organisms*, 2018, vol. 127, pp. 117–124. https://doi.org/10.3354/dao03192
13. Ibragimov Sh. R. *Caspian Sea Fish Parasites (Species Composition, Ecology, Origin and Fauna Formation)* : avtoref. dis. … d-ra biol. nauk. Baku, 1991, 47 p. (in Russ.)
14. Ibragimov Sh. R. Zoogeographical status of Caspian Sea with consideration of the data on fish parasites. In: *Sovremennye problemy biologicheskikh resursov Kaspiiskogo morya* : materialy mezhdunar. konf., posvyashch. 90-letiyu Azerb. NIIRKh, 15–17 Sept., 2003. Baku, 2003, pp. 224–228. (in Russ.)
15. Ibragimov Sh. R. Parasite fauna of the Caspian Sea for long period of observations. In: *Problemy ikhtiopatologii v nachale XXI veka* : materialy mezhdunar. nauch. konf. Saint Petersburg, 2009, pp. 65–78. (in Russ.)
16. Iskov M. P. Myxosporeans (Myxosporea). In: *Fauna Ukrainy*. Kiev : Naukova dumka, 1989, vol. 37, iss. 4, 210 p. (in Russ.)
17. Kessler K. F. Fish inhabiting and occurring in Aral-Caspian-Pontian ichthyological region. *Trudy Aralo-Kaspiyskoi ekspeditsii,* 1877, iss. 4, 360 p. (in Russ.)
18. Kolesnikova M. G., Donets Z. S. Fauna of myxosporeans in the Crimean coast fish. In: *Parazitologiya i patologiya morskikh organizmov* : tez. dokl. 14-go Vsesoyuzn. simp. Kaliningrad, 1987, pp. 89–90. (in Russ.)
19. Lubat V., Radujkovic B., Marques A., Bouix G. Parasites des poissons marins du Montenegro: Myxosporidies. *Acta Adriatica*, 1989, vol. 30, no. 1/2, pp. 31–50.
20. Moshu A. Ja., Trombitsky I. D. New parasites (Apicomplexa, Cnidospora) of some Clupeidae fishes from the Danube and Dniester basins. In: *Academician Leo Berg – 130 : Coll. of Sci. Articles.* Bendery : Eco-TIRAS ; Tipogr. "ELAN POLIGRAF", 2006, pp. 95–103.
21. Naidenova N. N. *Parazitofauna ryb semeistva bychkovykh Chernogo i Azovskogo morei.* Kiev : Naukova dumka, 1974, 182 p. (in Russ.)
22. Osmanov S. U. Materials for the Black Sea fish parasitic fauna. *Uchenye zapiski Leningradskogo pedinstituta im. Gertsena*, 1940, vol. 30, pp. 187–265. (in Russ.)
23. Ovcharenko M., Yurakhno V., Tytar V. Review of microparasites of mullets in the Mediterranean basin and the Sea of Japan. *Revista Română de Parazitoilogie*, 2007, vol. 17 (suppl.), pp. 142–143.

24. Özer A., Okkay S., Gürkanlı C. T., Çiftçi Y., Yurakhno V. Two novel myxosporean parasites in Black Sea fishes: *Kudoa niluferi* sp. nov. and *Kudoa anatolica* sp. nov. (Cnidaria: Myxosporea). *Diseases of Aquatic Organisms*, 2018, vol. 128, no. 3, pp. 225–233. https://doi.org/10.3354/dao03227
25. Özer A., Özkan H., Yurakhno V. New host and geographical records for *Ortholinea orientalis* (Schulman et Schulman-Albova, 1953) (Myxozoa, Myxosporea). *Acta Zoologica Bulgarica*, 2015, vol. 67, no. 4, pp. 595–597.
26. Özer A., Özkan H., Güneydağ S., Yurakhno V. First report of several myxosporean (Myxozoa) and monogenean parasites from fish species collected from Sinop coasts of the Black Sea. *Turkish Journal of Fisheries and Aquatic Sciences*, 2015, vol. 15, pp. 741–749. https://doi.org/10.4194/1303-2712-v15_3_18
27. Özer A., Özkan H., Gürkanlı C. T., Yurakhno V., Çiftçi Y. Morphology, histology and phylogeny of *Henneguya sinova* sp. nov. (Myxobolidae: Myxozoa) infecting gills of *Parablennius tentacularis* in the Black Sea, Turkey. *Diseases of Aquatic Organisms*, 2016, vol. 118, no. 3, pp. 207–215. https://doi.org/10.3354/dao02968
28. Özer A., Öztürk T., Özkan H., Çam A. First report of *Enteromyxum leei* (Myxozoa) in the Black Sea in a potential reservoir host *Chromis chromis*. *Fish Pathology*, 2014, vol. 49, iss. 2, pp. 57–60. https://doi.org/10.3147/jsfp.49.57
29. Özer A., Yurakhno V. Parasite fauna of garfish *Belone belone* collected from Sinop coasts of the Black Sea, Turkey. *Bulletin of the European Association of Fish Pathology*, 2013, vol. 33, no. 6, pp. 171–180.
30. Reshetnikova A. V. *Parasitic Fauna of Some Food Fish Species of the Black Sea* : avtoref. dis. … kand. biol. nauk. Leningrad, 1954, 14 p. (in Russ.)
31. Şimşek E. First molecular data on *Myxobolus episquamalis* (Myxozoa: Myxosporea) infecting the scale of grey mullet (*Mugil cephalus*) off the Turkish Black Sea coasts. *Türkiye Parazitoloji Dergisi = Turkish Journal of Parasitology*, 2019, vol. 43, iss. 3, pp. 135–142. (in Turkish). https://doi.org/10.4274/tpd.galenos.2019.6294
32. Strakhov N. M. *Istoriya geologii.* 2nd edition, revised. Moscow : Gosuchpedizdat, 1938, 501 p. (in Russ.)
33. Strakhov N. M. *Osnovy istoricheskoi geologii.* In 2 parts. Moscow : Gosgeolizdat, 1948, pt. 1, 253 p. ; pt. 2, 396 p. (in Russ.)
34. Yurakhno V. M. New data of the fauna of myxosporidians from fishes of the Black Sea. *Parazitologiya*, 1993, vol. 27, no. 4, pp. 320–326. (in Russ.)
35. Yurakhno V. M. *Myxosporeans of the Black Sea Fish: Systematics, Fauna, Ecology, Zoogeography.* [dissertation]. Sevastopol, 1994, 297 p. (in Russ.)
36. Yurakhno V. M. To fish myxosporean fauna (Myxozoa, Myxosporea) in Taganrog Gulf (Sea of Azov). *Vestnik zoologii*, 2005, suppl. 19, pt. 2, pp. 369–370. (in Russ.)
37. Yurakhno V. M. The origin of the Black Sea fish myxosporean (Myxozoa, Myxosporea) fauna. *Vestnik zoologii*, 2009, suppl. 23, pp. 199–207. (in Russ.)
38. Yurakhno V. M., Naidenova N. N. *Davisia cornuta* sp. n. (Myxosporea: Sinuolineidae), the parasite of *Neogobius fluviatilis* Pallas in the Azov Sea. *Ekologiya morya*, 2000, iss. 51, pp. 78–80. (in Russ.)
39. Yurakhno V. M., Ovcharenko N. A. Myxosporeans of the World Ocean mullets. In: *Parazitologiya v XXI veke – problemy, metody, resheniya* : materialy IV Vseros. kongr. Parazitologicheskogo obshchestva Rossiiskoi akademii nauk, 20–25 Oct., 2008. Saint Petersburg : "Lema", 2008, pp. 231–234. (in Russ.)
40. Yurakhno V. M., Ovcharenko M. O. Study of Myxosporea (Myxozoa), infecting worldwide mullets with description of a new species. *Parasitology Research*, 2014, vol. 113, iss. 10, pp. 3661–3674. https://doi.org/10.1007/s00436-014-4031-5
41. Yurakhno V. M., Özer A. N. Fauna of myxosporeans of the Ponto-Caspian basin fishes (origin, comparative analysis). In: *Sovremennye problemy parazitologii i ekologii. Chteniya, posvyaschennye pamyati S. S. Shulmana* : sbornik trudov Vserossiiskoi nauchnoi konferentsii s mezhdunarodnym uchastiem, Tolyatti, 15–17 May, 2018. Tolyatti : Poliar, 2018, pp. 334–345. (in Russ.)
42. Zenkevich L. A. *Fauna i biologicheskaya produktivnost' morya.* Moscow : Sovetskaya nauka, 1947, 588 p. (Morya SSSR ; vol. 2). (in Russ.)
43. Zenkevich L. A. *Biologiya morei SSSR.* Moscow : Izd-vo AN SSSR, 1963, 740 p. (in Russ.)
44. *Zhizn' zhivotnykh* : in 7 vols / Polyanskiy Yu. I. (Ed.). Moscow : Prosveshchenie, 1987, vol. 1, 448 p. (in Russ.)

ИСТОРИЯ ФОРМИРОВАНИЯ И ОСОБЕННОСТИ ФАУНЫ МИКСОСПОРИДИЙ РЫБ ПОНТО-КАСПИЙСКОГО БАССЕЙНА

В. М. Юрахно[1], А. Н. Озер[2]

[1]Федеральный исследовательский центр «Институт биологии южных морей имени А. О. Ковалевского РАН», Севастополь, Крым

[2]Синопский университет, Синоп, Турция

E-mail: *viola_taurica@mail.ru*

Рассмотрена история становления фауны миксоспоридий рыб Понто-Каспийского бассейна. Работа основана на оригинальном материале по миксоспоридиям рыб Чёрного моря (собран в 1987–2018 гг.) и Азовского моря (1997–2016). Всего исследованы 15 368 экз. рыб 87 видов (14 297 экз. рыб 80 видов в Чёрном море и 1071 экз. рыб 19 видов в Азовском). Материал собран методом неполных паразитологических вскрытий и обработан по общепринятым методикам. Также проанализированы все доступные литературные источники по миксоспоридиям черноморских, азовских и каспийских рыб (в библиографическом списке указаны только наиболее значимые публикации). Проведён сравнительный анализ фауны миксоспоридий рыб Чёрного, Азовского и Каспийского морей. Указано, что всего в Чёрном море известно 108 видов этих паразитов, в Азовском море — 42, в Каспийском море — 68. Общими для фауны миксоспоридий рыб Азовского и Чёрного морей являются 32 вида, Каспийского и Чёрного — 32, Азовского и Каспийского — 20. Во всех трёх морях встречаются 16 видов миксоспоридий. К настоящему времени из 108 видов миксоспоридий в Чёрном море 29 обнаружены исключительно в пресноводных рыбах, обитающих в устьях рек и лиманах со значительным опреснением. Для 79 видов хозяевами служат морские виды рыб, встречающиеся в основном в полносолёной части моря. Из них 17 имеют пресноводное происхождение: 7 видов встречаются в пресноводных рыбах и эвригалинных кефалях, 1 является паразитом пресноводных и морских лососевых рыб, а 9 имеют хозяевами только кефалей или других видов морских рыб. Морские формы представлены эндемиками: понтическими (22 вида), понто-азовскими (3) и понто-каспийскими (2), а также средиземноморскими вселенцами (35 видов). Среди пресноводных миксоспоридий только 1 вид эндемичен для Чёрного моря и 1 является понто-азовским эндемиком; большинство остальных видов широко представлено в пресных водоёмах. Среди средиземноморских вселенцев следует отметить 23 вида, найденных в Средиземном море; 12 видов пока не встречены в Средиземном море (вероятно, главным образом из-за слабой изученности в нём этой группы паразитов). Фауна миксоспоридий рыб Азовского моря насчитывает 42 вида миксоспоридий, 32 из которых найдены в Чёрном море, 20 — в Каспийском. К пресноводным видам, паразитирующим исключительно в пресноводных видах рыб, относятся 19. Ещё 10 видов имеют пресноводное происхождение, но встречаются и в морских видах рыб (преимущественно в кефалевых, а один вид — в бычковых). Из пресноводных видов 1 является понто-азовским эндемиком. К морским относятся 13 видов миксоспоридий: 2 азовских эндемика, 3 понто-азовских эндемика, 8 средиземноморских вселенцев. Из 68 видов миксоспоридий рыб Каспийского моря 8 являются морскими (1 древнеморской вид, 1 понто-каспийский эндемик, 6 солоноватоводных миксоспоридий), 60 — пресноводными. Эндемиков Каспийского моря известно 5 (2 вида морского происхождения и 3 — пресноводного). Установлено, что при продвижении с запада на восток (от Чёрного моря к Каспийскому) наблюдается постепенное обеднение фауны морских миксоспоридий и замещение её фауной пресноводных видов. Отмечено также обеднение видового состава миксоспоридий рыб Азовского и Каспийского морей по сравнению с таковым Чёрного моря.

Ключевые слова: фауна, миксоспоридии, рыбы, Чёрное море, Азовское море, Каспийское море