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THE INFLUENCE OF WATER SALINITY ON THE DISTRIBUTION OF MYXOSPOREANS OF THE GENUS *KUDOA* (CNIDARIA, MYXOZOA) AMONG FISH OF THE WORLD FAUNA

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The occurrence of myxosporeans of the genus *Kudoa* in fish inhabiting waters of different salinity was studied. The work is based on own materials on fish myxosporeans sampled in 1987–2021: more than 12,000 specimens of about 100 fish species in the basins of the Atlantic Ocean [the Sea of Azov (Russia and Ukraine), Black Sea (Russia, Ukraine, and Turkey), and Mediterranean Sea (Italy and Spain); the Central Eastern Atlantic (abeam Mauritania) and southern latitudes off the coast of Africa (abeam Namibia); waters of the northern (near Norway) and southern (abeam Argentina) parts of the ocean; and off the southeastern coast of the USA], the Indian Ocean [the coast of Yemen], and the Pacific Ocean [South China Sea (Vietnam)]. In total, 27 representatives of myxosporeans of the genus *Kudoa* were analyzed using original material; out of them, 19 were identified down to the species level. Also, all available literature sources and a global database of fish species FishBase were investigated. As established, out of 291 species of fish hosting *Kudoa*, 169 species are exclusively marine, 76 species can inhabit marine- and brackish-water environments, 42 species are euryhaline and can occur both in marine and brackish waters and in freshwater, and only 4 species are exclusively freshwater ones. Out of 128 *Kudoa* species, 117 (91.4%) were found in the marine zone of the World Ocean; 8 (6.3%), in its estuaries (7, in marine fish; 1, in a freshwater host); and 3 (2.3%), in freshwater reservoirs. In 2008–2019, *Kudoa nova* Naidenova, 1975 was studied in estuarine-type ecosystems off the coast of the Crimea at the Chernaya River mouth and Karkinitsky Bay (the Black Sea), as well as in Eastern Sivash (the Sea of Azov). A total of 2,232 specimens of 11 goby species were examined. As established, the periodic desalination of some areas by waters of paddy fields and the constant occurrence of freshwater in a surface layer of the Chernaya River mouth did not cause a noticeable change in salinity (except for the northern area of Eastern Sivash) which would be destructive for this parasitic species. However, there were no *K. nova* in gobies caught in 1998 in the Taganrog Bay (the Sea of Azov) significantly desalinated by the Don River water. Also, this species was not recorded in 2011 in the Bug and Vistula rivers when studying microparasites of gobies that spread from the northwestern Black Sea along the central invasive corridor. Our experiment testified to the negative influence of freshwater on spores of this parasite: under its effect, spores were deformed and darkened, and the function of the polar filament extrusion was disrupted.

Keywords: myxosporeans, *Kudoa*, water salinity, world fauna

One of the key ecological factors of the external environment (second-order environment) significantly affecting fish infestation by certain myxosporeans is salinity of water where fish and, periodically, their parasites occur. This is evidenced by the clear division of all myxosporean species into marine and freshwater ones [Shulman et al., 1997]. This monograph thoroughly examines the issue on examples of both freshwater and marine species not belonging to the genus *Kudoa* Meglitsch, 1947. An exception is *K. nova* Naidenova, 1975 reported as a marine species found in desalinated waters of the Sea of Azov. The researchers emphasize the qualitative and quantitative depletion of myxosporean fauna in marine basins within their brackish spots and adverse effects of increased salinity on diversity and abundance of exclusively freshwater species in freshwater habitats (it is entirely expected). A group of euryhaline fish hosts is highlighted whose myxosporeans typically originate from both marine and freshwater environments. They can inhabit zones of various salinity and should be classified as brackish-water species. According to S. Shulman [1966], such hosts act as a sort of 'artificial climate compartment' for parasites. The relative ease with which certain myxosporeans shift between marine and freshwater environments and backwards is associated not only with the presence of euryhaline hosts, but also with protective properties of spore valves in Myxosporea that shield an amoeboid embryo from harmful effect of environment.

In earlier work, we explored the effect of salinity on infestation of the Black Sea fish by myxosporeans of other genera [Yurakhno, 1994]. We also reported a gradual depletion of marine myxosporean fauna and replacement by freshwater elements when moving from west to east, from the Black Sea to the Caspian Sea. This trend is accompanied by a significant reduction in myxosporean species diversity in fish of the Sea of Azov and Caspian Sea as compared to that for the Black Sea [Yurakhno, 1994; Yurakhno, Özer, 2018, 2020].

Analyzing the world fauna of *Kudoa* myxosporeans comprehensively outlined in the latest synopsis of species [Eiras et al., 2014], we confirmed this pattern on the example of representatives of this genus. Thus, five *Kudoa* species are registered in the Black Sea [*K. anatolica* Özer, Okkay, Gurkanlı, Çiftci & Yurakhno, 2018, *K. niluferi* Özer, Okkay, Gurkanlı, Çiftci & Yurakhno, 2018, *K. nova*, *K. stellula* V. Yurakhno, 1991, and *K. quadratum* (Thélohan, 1895)], while only two are recorded in the Sea of Azov [*K. nova* and *K. dicentrarchi* Sitjà-Bobadilla & Alvarez-Pellitero, 1992]. Notably, there are no *Kudoa* species in the Caspian Sea. At first glance, the negative effect of desalination seems evident supporting the earlier opinion that the entire order Multivalvulida to which *Kudoa* belongs covers exclusively marine forms [Shulman et al., 1997]. However, recent investigations have revealed rare facts of *Kudoa* infecting freshwater fish not only in lagoons [Fomena, Bouix, 1997; Siau, 1971] or estuaries [Sarkar, Chaudhury, 1996], but also in a river connected to the Atlantic Ocean [Azevedo et al., 2016; Casal et al., 2008; Velasco et al., 2015]. The effect of salinity on *Kudoa* infestation of fish has not been systematically analyzed in literature, aside from carrying out experiments on survival of *K. nova* spores [Yurakhno, 2015b, 2016a, 2018] and *Kudoa septempunctata* Matsukane, Sato, Tanaka, Kamata & Sugita-Konishi, 2010 spores [Yokoyama et al., 2016] in freshwater and saline water, as well as our own studies on myxosporean fauna in Crimean estuarine zones. Results on the latter ones are published only in conference abstracts and proceedings [Dmitrieva et al., 2015; Korniichuk et al., 2016; Yurakhno, 2012, 2013, 2014, 2015a, 2016b; Yurakhno, Tokarev, 2017]. To fill this gap, we aimed at providing comprehensive insights into the issue.

MATERIAL AND METHODS

This study is based on our own original data on fish myxosporeans sampled in 1987–2021. Over 12,000 specimens of approximately 100 fish species were examined in the basins of the Atlantic Ocea [the Sea of Azov (Russia and Ukraine), Black Sea (Russia, Ukraine, and Turkey), and Mediterranean Sea (Italy and Spain); the Central Eastern Atlantic (abeam Mauritania) and southern latitudes off the coast of Africa (abeam Namibia); waters of the northern (near Norway) and southern (abeam Argentina) parts of the ocean; and off the southeastern coast of the USA], the Indian Ocean [the coast of Yemen], and the Pacific Ocean [South China Sea (Vietnam)]. In total, 27 *Kudoa* representatives were identified based on original material; this covers 19 ones identified down to the species level [*K. alliaria* Kovaleva, Shulman & Yakovlev, 1979, *K. anatolica*, *K. borimiri* Yurakhno, Slynko, Nguyen, Vo & Whipps, 2022, *K. clupeidae* (Hahn, 1917), *K. dicentrarchi*, *K. histolytica* (Pérard, 1928) Meglitsch, 1947, *K. igori* Yurakhno, Slynko, Nguyen, Vo & Whipps, 2022, *K. inornata*, *K. mirabilis* Naidenova & Gaevskaya, 1991, *K. monodactyli* Gunter, Cribb, Whipps & Adlard, 2006, *K. niluferi*, *K. nova*, *K. paniformis* Kabata & Whitaker, 1981, *K. rosenbuschi* (Gelormini, 1943), *K. stellula*, *K. thyrsites* (Gilchrist, 1924) Meglitsch, 1947, *K. trifolia* Holzer, Blasco-Costa, Sarabeev, Ovcharenko & Balbuena, 2006, *K. unicapsula* Yurakhno, Ovcharenko, Holzer, Sarabeev & Balbuena, 2007, and *K. whippsi* Burger & Adlard, 2010] and 8 *Kudoa* spp. Additionally, descriptions of 128 *Kudoa* species documented in global scientific literature up to 2021 were analyzed. To assess *Kudoa* occurrence in fish inhabiting waters of various salinity, we referenced FishBase (https://www.fishbase.se/search.php) verifying data in available sources [Debelius, 2009; Fadeev, 2005; Svetovidov, 1964; The Living Marine Resources, 2016].

For the salinity-dependent infestation analysis of gobies by *K. nova*, we examined 2,232 specimens of 11 fish species in 1998 and 2008–2019. Sampling sites included estuarine biotopes of the Black Sea and Sea of Azov and the central invasive corridor connected to the Black Sea (Bug, Narew, and Vistula rivers in Poland).

For water samples from the Karkinitsky Bay (2014–2016), salinity was measured *via* argentometry (the guiding document RD 52.10.243-92, Manual of Chemical Analysis of Marine Waters, 01.07.1993) by T. Bogdanova (IBSS). Salinity data for 2008–2013 in this region were provided orally by N. Shadrin (IBSS). Sivash Lagoon salinity was sourced from oral report by A. Boltachev (IBSS) (measurements were carried out by T. Bogdanova) and from the paper [Shadrin et al., 2018]. Data on the Taganrog Bay salinity in 1998 were provided by AzNIIRKh researchers. Salinity values for the Vistula and Bug rivers were derived from literature [Kasprzak et al., 2016] and from an online source (https://en.wikipedia.org/wiki/Bug_(river)), respectively, with lower water salinity thresholds for the Bug River provided by N. Ovcharenko (the W. Stefański Institute of Parasitology of the PAS, Warsaw, Poland). Data on salinity in the Dnieper–Bug estuary were sourced from literature [Grinevetsky et al., 2015].

RESULTS AND DISCUSSION

When analyzing all *Kudoa* hosts by their ability to survive in water of various salinity (Table 1), it becomes evident that the overwhelming majority of *Kudoa* myxosporeans parasitize marine fish inhabiting seas and oceans. Out of 294 fish hosts for *Kudoa*, habitat preferences were determined for 291 species. Out of them, 169 species are exclusively marine, 76 can inhabit marine- and brackish-water environments, 42 are euryhaline and can occur both in marine and brackish waters and in freshwater, and only 4 are exclusively freshwater ones. For 3 fish hosts with unresolved taxonomic status, habitat preferences could not be established.

Most *Kudoa* species were registered in marine zones of the World Ocean confirming the marine origin of this genus. Exceptions cover four *Kudoa* found in freshwater fish from freshwater basins adjacent to the Atlantic Ocean. Out of them, three were reported from fish of the order Cichliformes –

from *Aequidens plagiozonatus* Kullander, 1984 (*Kudoa aequidens* Casal, Matos E., Matos P. & Azevedo, 2008) [Casal et al., 2008] and *Chaetobranchopsis orbicularis* (Steindachner, 1875) (*Kudoa orbicularis* Azevedo, Rocha, Matos, Oliveira, Matos, Al-Quraishy & Casal, 2016) [Azevedo et al., 2016] – and from fish of the order Siluriformes – from *Hypophthalmus marginatus* Valenciennes, 1840 (*Kudoa* sp.) [Velasco et al., 2015] – in the lower Amazon River basin (Brazil). Interestingly, *K. orbicularis* was found in the Arari River, 135 km from the Amazon River mouth. And the fourth species (*Kudoa eleotrisi* Siau, 1971) was noted in a sleeper goby *Kribia kribensis* (Boulenger, 1907) in the Porto-Novo Lagoon (Benin, coast of Africa) [Fomena, Bouix, 1997; Siau, 1971]. *Kudoa cascasia* Sarkar & Chaudhury, 1996 was recorded in the freshwater yellowtail mullet *Minimugil cascasia* (Hamilton, 1822) in the Hooghly estuary (the Indian Ocean, Western Bengal, India) [Sarkar, Chaudhury, 1996].

Table 1. Occurrence of myxosporeans of the genus *Kudoa* in fish of various taxa of the world fauna, with indication of the affiliation of hosts to waters of different salinity*

Fish species with taxonomic classification	Fish habitat in waters of different salinity**	Myxosporean species of the genus *Kudoa*
Class Chondrichthyes **Subclass Elasmobranchii** **Superorder Selachomorpha**		
Order Carcharhiniformes		
Family Carcharhinidae		
Carcharhinus amboinensis	M, B	*K. carcharhini*
C. cautus	M	*K. carcharhini*
C. limbatus	M, B	*K. carcharhini*
Order Orectolobiformes		
Family Hemiscylliidae		
Hemiscyllium ocellatum	M	*K. hemiscylli*
Family Orectolobidae		
Orectolobus hutchinsi	M	*K. hemiscylli*
O. maculatus	M	*K. hemiscylli*
O. ornatus	M	*K. hemiscylli*
Suborder Batomorpha		
Order Myliobatiformes		
Family Dasyatidae		
Hemitrygon fluviorum	M, B	*K. hemiscylli*
Neotrygon kuhlii	M	*K. hemiscylli*
Taeniura lymma	M	*K. hemiscylli*
Order Rhinopristiformes		
Family Rhinobatidae		
Aptychotrema rostrata	M, B	*K. hemiscylli*
Glaucostegus typus	M, B, Fr	*K. hemiscylli*
Class Actinopterygii **Infraclass Teleostei**		
Order Carangaria incertae sedis		
Family Sphyraenidae		
Sphyraena jello	M, B	*K. sphyraeni*

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Fish species with taxonomic classification	Fish habitat in waters of different salinity**	Myxosporean species of the genus *Kudoa*
S. pinguis	M	*K. megacapsula*
S. putnamae	M	*K. barracudai*
Order Eupercaria incertae sedis		
Family Gerreidae		
Eugerres brasilianus	M	*K. eugerres*
Family Labridae		
Coris julis	M	*K. quadratum*
Halichoeres bivittatus	M	*K. ovivora*
H. garnoti	M	*K. ovivora*
H. poeyi	M	*K. ovivora*
Tautogolabrus adspersus	M	*K. clupeidae*
Thalassoma bifasciatum	M	*K. ovivora*
Th. lunare	M	*K. thalassomi*
Th. lutescens	M	*K. thalassomi*
Family Lethrinidae		
Gymnocranius audleyi	M	*K. lethrini*
Lethrinus harak	M, B	*K. lethrini*
L. nebulosus	M, B	*K. iwatai*
L. variegatus	M	*K. iwatai*
Family Lutjanidae		
Caesio cuning	M	*K. chaetodoni*
Lutjanus campechanus	M	*K. hypoepicardialis*
L. carponotatus	M	*K. chaetodoni*
L. ehrenbergii	M, B, Fr	*K. lethrini*, *K. yasunagai*
L. erythropterus	M	*K. iwatai*, *K. lutjanus*
L. fulviflamma	M	*K. lethrini*
L. lemniscatus	M	*K. lemniscati*
Family Monodactylidae		
Monodactylus argenteus	M, B, Fr	*K. monodactyli*
Family Moronidae		
Dicentrarchus labrax	M, B, Fr	*K. dicentrarchi*, *K. iwatai*
D. punctatus	M, B	*K. dicentrarchi*
Family Nemipteridae		
Nemipterus japonicus	M	*K. schulmani*
Scolopsis monogramma	M	*K. yasunagai*
Family Priacanthidae		
Priacanthus hamrur	M	*K. iwatai*
Family Scaridae		
Calotomus japonicus	M	*K. igami*, *K. lateolabracis*, *K. thalassomi*, *K. yasunagai*
Scarus flavipectoralis	M	*K. thalassomi*
Sparisoma aurofrenatum	M	*K. ovivora*
S. radians	M	*K. ovivora*
S. rubripinne	M	*K. ovivora*

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Fish species with taxonomic classification	Fish habitat in waters of different salinity**	Myxosporean species of the genus *Kudoa*
Family Sciaenidae		
Cheilotrema fasciatum	M	*K. sciaenae*
Cynoscion nebulosus	M, B	*K. inornata*
Leiostomus xanthurus	M, B	*K. branchiata*, *K. leiostomi*
Nibea coibor	M, B	*K. coibori*
Paralonchurus peruanus	M	*K. sciaenae*
Pogonias cromis	M, B	*K. hypoepicardialis*
Sciaena deliciosa	M	*K. sciaenae*
Stellifer minor	M	*K. sciaenae*
Family Sillaginidae		
Sillago analis	M, B	*K. ciliatae*
S. ciliata	M, B	*K. ciliatae*, *K. yasunagai*
S. maculata	M, B	*K. ciliatae*, *K. yasunagai*
S. sihama	M, B	*K. petala*
Family Sparidae		
Acanthopagrus latus	M, B, Fr	*K. lutjanus*
A. schlegelii	M, B	*K. iwatai*
Argyrops filamentosus	M	*K. iwatai*
Boops boops	M	*K. boopsi*
Dentex macrophthalmus	M	*K. nova*
Pagellus acarne	M	*K. nova*
Pagrus major	M	*K. iwatai*, *K. yasunagai*
P. pagrus	M	*K. pagrusi*
Rhabdosargus haffara	M	*K. aegyptia*
Sparus aurata	M, B	*K. dicentrarchi*, *K. iwatai*
Stenotomus chrysops	M	*K. clupeidae*
Order Ovalentaria incertae sedis		
Family Pomacentridae		
Abudefduf bengalensis	M	*K. amamiensis*, *K. thalassomi*, *K. whippsi*
A. septemfasciatus	M	*K. gunterae*
A. sexfasciatus	M	*K. amamiensis*, *K. gunterae*
A. sordidus	M, B	*K. gunterae*
A. vaigiensis	M	*K. amamiensis*, *K. whippsi*
A. whitleyi	M	*K. amamiensis*, *K. thalassomi*, *K. whippsi*
Acanthochromis polyacanthus	M	*K. whippsi*
Amblyglyphidodon curacao	M	*K. thalassomi*
Amphiprion akindynos	M	*K. kenti*, *K. thalassomi*, *K. whippsi*
A. melanopus	M	*K. kenti*, *K. thalassomi*, *K. whippsi*
Chromis chrysura	M	*K. amamiensis*
Ch. notata	M	*K. amamiensis*
Ch. viridis	M	*K. gunterae*, *K. whippsi*
Chrysiptera assimilis	M	*K. amamiensis*
C. cyanea	M	*K. gunterae*, *K. thalassomi*
Dascyllus aruanus	M	*K. gunterae*, *K. thalassomi*

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Fish species with taxonomic classification	Fish habitat in waters of different salinity**	Myxosporean species of the genus *Kudoa*
D. trimaculatus	M	*K. iwatai*
Dischistodus perspicillatus	M, B	*K. kenti*
D. pseudochrysopoecilus	M	*K. gunterae*
Neoglyphidodon melas	M	*K. gunterae*, *K. thalassomi*, *K. whippsi*
Neopomacentrus miryae	M	*K. iwatai*
Plectroglyphidodon leucozonus	M	*K. gunterae*, *K. kenti*
Pomacentrus chrysurus	M	*K. gunterae*, *K. whippsi*
Order Acanthuriformes		
Family Chaetodontidae		
Chaetodon baronessa	M	*K. thalassomi*
C. collare	M	*K. muscularis*
C. paucifasciatus	M	*K. iwatai*
C. unimaculatus	M	*K. chaetodoni*, *K. thalassomi*
C. vagabundus	M	*K. thalassomi*
Chelmon rostratus	M, B	*K. thalassomi*
Heniochus monoceros	M	*K. thalassomi*
Family Leiognathidae		
Leiognathus brevirostris	M, B	*K. uncinata*
Nuchequula nuchalis	M, B	*K. uncinata*
Family Lobotidae		
Lobotes surinamensis	M, B	*K. hypoepicardialis*
Family Siganidae		
Siganus rivulatus	M, B	*K. iwatai*
Order Acropomatiformes		
Family Lateolabracidae		
Lateolabrax japonicus	M, B, Fr	*K. cruciformum*, *K. iwatai*, *K. yasunagai*
Lateolabrax sp.	?	*K. lateolabracis*
Family Pempheridae		
Pempheris ypsilychnus	M	*K. amamiensis*, *K. minithyrsites*
Order Atheriniformes		
Family Atherinidae		
Atherina hepsetus	M, B, Fr	*K. anatolica*, *K. stellula*
Order Batrachoidiformes		
Family Batrachoididae		
Batrachoides surinamensis	M, B	*K. viseuensis*
Order Beloniformes		
Family Belonidae		
Strongylura strongylura	M, B	*K. chilkaensis*
Family Exocoetidae		
Cypsilurus ago	M	*K. thyrsites*
Cypsilurus sp.	M	*K. thyrsites*
Family Hemiramphidae		
Hyporhamphus gamberur	M	*K. iwatai*

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Fish species with taxonomic classification	Fish habitat in waters of different salinity**	Myxosporean species of the genus *Kudoa*
Order Beryciformes		
Family Berycidae		
Beryx splendens	M	*K. thyrsites*
Order Blenniiformes		
Family Blenniidae		
Parablennius gattorugine	M	*K. quadratum*
P. zvonimiri	M	*K. quadratum*
Order Callionymiformes		
Family Callionymidae		
Callionymus lyra	M	*K. quadratum*
Order Carangiformes		
Family Carangidae		
Alepes djedaba	M	*K. javaensis*, *K. pyramidalis*
Atropus atropus	M	*K. atropi*
Carangoides fulvoguttatus	M	*K. quadricornis*
C. plagiotaenia	M	*K. paraquadricornis*
Caranx crysos	M, B	*K. hypoepicardialis*
C. ignobilis	M, B	*K. paraquadricornis*
C. papuensis	M, B	*K. paraquadricornis*
C. sexfasciatus	M, B, Fr	*K. amamiensis*, *K. paraquadricornis*
Decapterus maruadsi	M	*K. decaptera*
D. russeli	M	*K. thyrsites*
Seriola dumerili	M	*K. amamiensis*, *K. insolita*
S. lalandi	M	*K. neurophila*, *K. thyrsites*
S. quinqueradiata	M	*K. amamiensis*, *K. iwatai*, *K. yasunagai*, *K. megacapsula*, *K. pericardialis*
Trachurus capensis	M	*K. nova*
T. mediterraneus	M, B	*K. quadratum*
T. picturatus	M	*K. nova*
T. trachurus	M	*K. azevedoi*, *K. nova*, *K. quadratum*, *K. thyrsites*
T. trecae	M	*K. nova*
T. japonicus	M	*K. trachuri*
Family Coryphaenidae		
Coryphaena hippurus	M, B	*K. thyrsites*
Family Istiophoridae		
Istiophorus platypterus	M	*K. musculoliquefaciens*
Family Xiphiidae		
Xiphias gladius	M	*K. musculoliquefaciens*
Order Centrarchiformes		
Family Latridae		
Latris lineata	M	*K. neurophila*
Family Oplegnathidae		
Oplegnathus fasciatus	M	*K. iwatai*, *K. yasunagai*
O. punctatus	M	*K. iwatai*

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Fish species with taxonomic classification	Fish habitat in waters of different salinity**	Myxosporean species of the genus *Kudoa*
Order Cichliformes		
Family Cichlidae		
Aequidens plagiozonatus	Fr	*K. aequidens*
Chaetobranchopsis orbicularis	Fr	*K. orbicularis*
Order Clupeiformes		
Family Clupeidae		
Alosa aestivalis	M, B, Fr	*K. clupeidae*
A. mediocris	M, B, Fr	*K. clupeidae*
A. pseudoharengus	M, B, Fr	*K. clupeidae*
Brevoortia tyrannus	M, B	*K. clupeidae*
Clupea harengus	M, B	*K. clupeidae*
Konosirus punctatus	M, B	*K. guangdongensis*
Sardinella lemuru	M	*K. thyrsites*
Sardinops sagax	M	*K. thyrsites*
Family Engraulidae		
Engraulis australis	M, B	*K. thyrsites*
E. encrasicolus	M, B	*K. histolytica*
E. japonicus	M	*K. thyrsites*
Family Spratelloididae		
Spratelloides delicatulus	M	*K. thyrsites*
S. robustus	M, B	*K. thyrsites*
Order Cyprinodontiformes		
Family Fundulidae		
Fundulus heteroclitus	M, B, Fr	*K. funduli*
F. majalis	M, B	*K. funduli*
Order Gadiformes		
Family Gadidae		
Gadus chalcogrammus	M, B	*K. thyrsites*
Macruronus magellanicus	M	*K. alliaria*
Micromesistius australis	M	*K. alliaria*
M. poutassou	M	*K. thyrsites*
Pollachius pollachius	M	*K. thyrsites*
Family Merlucciidae		
Merluccius australis	M	*K. alliaria*
M. capensis	M	*K. thyrsites*
M. gayi	M	*K. hallado*, *K. peruvianus*
M. hubbsi	M	*K. alliaria*, *K. rosenbuschi*
M. productus	M, B	*K. paniformis*, *K. thyrsites*
Order Gobiiformes		
Family Butidae		
Kribia kribensis	Fr	*K. eleotrisi*
Family Gobiidae		
Acanthogobius hasta	M, B, Fr	*K. akihitoi*, *K. empressmichikoae*
Acentrogobius chlorostigmatoides	M, B, Fr	*K. acentrogobia*

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Fish species with taxonomic classification	Fish habitat in waters of different salinity**	Myxosporean species of the genus *Kudoa*
Gobius cobitis	M, B	*K. nova*
G. cruentatus	M	*K. niluferi*
G. niger	M, B	*K. nova*
G. ophiocephalus	M, B	*K. nova*
Knipowitschia longicaudata	M, B, Fr	*K. nova*
Mesogobius batrachocephalus	M, B, Fr	*K. nova*
Neogobius melanostomus	M, B, Fr	*K. niluferi*, *K. nova*
N. fluviatilis	M, B, Fr	*K. nova*
Pomatoschistus microps	M, B, Fr	*K. camarguensis*, *K. nova*
P. minutus	M, B	*K. camarguensis*, *K. nova*
Ponticola cephalargoides	M	*K. nova*
P. eurycephalus	M, B	*K. nova*
P. platyrostris	M, B	*K. nova*
P. ratan	M, B	*K. nova*
P. syrman	M, B	*K. nova*
Proterorhinus marmoratus	M, B, Fr	*K. nova*
Tridentiger trigonocephalus	M, B, Fr	*K. nova*
Order Kurtiformes		
Family Apogonidae		
Cheilodipterus macrodon	M	*K. thalassomi*
Ch. quinquelineatus	M	*K. cheilodipteri*
Ostorhinchus aureus	M	*K. cheilodipteri*, *K. whippsi*, *K. iwatai*
O. cookii	M	*K. cookii*
O. cyanosoma	M	*K. cheilodipteri*, *K. whippsi*
O. doederleini	M	*K. whippsi*
O. fleurieu	M, B	*K. iwatai*
O. properuptus	M	*K. gunterae*, *K. whippsi*
Zoramia leptacantha	M	*K. leptacanthae*
Z. viridiventer	M	*K. leptacanthae*
Order Mugiliformes		
Family Mugilidae		
Chelon auratus	M, B, Fr	*K. dicentrarchi*, *K. trifolia*, *K. unicapsula*
Ch. labrosus	M, B, Fr	*K. dicentrarchi*
Ch. ramada	M, B, Fr	*K. dicentrarchi*, *K. trifolia*, *K. unicapsula*
Ch. saliens	M, B	*K. dicentrarchi*
Crenimugil crenilabis	M, B	*K. crenimugilis*
C. seheli	M, B, Fr	*K. dicentrarchi*
Ellochelon vaigiensis	M, B, Fr	*K. yasunagai*
Minimugil cascasia	Fr	*K. cascasia*
Mugil cephalus	M, B, Fr	*K. bora*, *K. dicentrarchi*, *K. tetraspora*, *K. intestinalis*, *K. iwatai*, *K. quadratum*, *K. surabayaensis*
M. japonica	M, B	*K. bora*
Osteomugil cunnesius	M, B, Fr	*K. borimiri*, *K. dicentrarchi*, *K. igori*, *K. valamugili*

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Fish species with taxonomic classification	Fish habitat in waters of different salinity**	Myxosporean species of the genus *Kudoa*
O. perusii	M, B	*K. bora*, *K. borimiri*, *K. dicentrarchi*, *K. fujitai*
Planiliza carinata	M, B	*K. bora*
P. melinoptera	M, B, Fr	*K. dicentrarchi*
P. parsia	M, B, Fr	*K. haridasae*, *K. sagarica*
Planiliza sp. D sensu	M, B, Fr	*K. borimiri*, *K. dicentrarchi*
Order Ophidiiformes		
Family Carapidae		
Echiodon sp.	?	*K. cutanea*
Order Perciformes		
Family Aulorhynchida		
Aulorhynchus flavidus	M	*K. thyrsites*
Family Cheilodactylidae		
Cheilodactylus zonatus	M	*K. whippsi*
Family Cottidae		
Icelinus filamentosus	M	*K. thyrsites*
Leptocottus armatus	M, B	*K. thyrsites*
Myoxocephalus brandtii	M	*K. nova*
M. scorpius	M, B	*K. quadratum*
Family Cyclopteridae		
Cyclopterus lumpus	M	*K. islandica*
Family Hexagrammidae		
Hexagrammos octogrammus	M	*K. azoni*
Ophiodon elongatus	M	*K. thyrsites*
Pleurogrammus azonus	M	*K. azoni*, *K. pleurogrammi*
P. monopterygius	M	*K. pleurogrammi*
Family Nototheniidae		
Patagonotothen canina	M	*K. alliaria*
P. ramsayi	M	*K. alliaria*, *K. ramsayi*
Family Pholidae		
Pholis ornata	M	*K. thyrsites*
Family Platycephalidae		
Platycephalus sp.	?	*K. iwatai*
Family Polynemidae		
Pentanemus quinquarius	M, B	*K. iidae*
Family Sebastidae		
Sebastes elongatus	M	*K. miniauriculata*
S. minor	M	*K. sebastea*
S. paucispinis	M	*K. clupeidae*, *K. miniauriculata*
Family Serranida		
Cephalopholis boenak	M	*K. thalassomi*
Hyporthodus nigritus	M	*K. hypoepicardialis*
Morone saxatilis	M, B, Fr	*K. cerebralis*
Family Zoarcidae		
Zoarces americanus	M, B	*K. clupeidae*

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Fish species with taxonomic classification	Fish habitat in waters of different salinity**	Myxosporean species of the genus *Kudoa*
Order Pleuronectiformes		
Family Bothidae		
Arnoglossus imperialis	M	*K. lunata*
A. laterna	M	*K. lunata*
A. thori	M	*K. lunata*
Family Cynoglossidae		
Cynoglossus senegalensis	M, B, Fr	*K. cynoglossi*
Family Paralichthyidae		
Paralichthys adspersus	M	*K. thyrsites*
P. olivaceus	M	*K. lateolabracis*, *K. paralichthys*, *K. septempunctata*, *K. shiomitsui*, *K. thyrsites*, *K. yasunagai*
Family Pleuronectidae		
Atheresthes stomias	M	*K. aburakarei*, *K. thyrsites*
Hippoglossus stenolepis	M	*K. thyrsites*
Lepidopsetta bilineata	M	*K. thyrsites*
Microstomus pacificus	M	*K. thyrsites*
Parophrys vetulus	M	*K. thyrsites*
Platichthys flesus	M, B, Fr	*K. clupeidae*
Family Scophthalmidae		
Zeugopterus punctatus	M	*K. kabatai*
Order Salmoniformes		
Family Salmonidae		
Oncorhynchus gorbuscha	M, B, Fr	*K. thyrsites*
O. kisutch	M, B, Fr	*K. thyrsites*
O. mykiss	M, B, Fr	*K. thyrsites*
O. tshawytscha	M, B, Fr	*K. thyrsites*
Salmo salar	M, B, Fr	*K. thyrsites*
Order Scombriformes		
Family Centrolophidae		
Hyperoglyphe japonica	M	*K. ogawai*
Icichthys australis	M	*K. vesica*
Family Gempylidae		
Thyrsites atun	M, B	*K. thyrsites*
Family Nomeidae		
Nomeus gronovii	M	*K. hypoepicardialis*
Family Pomatomidae		
Pomatomus saltatrix	M, B	*K. clupeidae*, *K. hypoepicardialis*, *K. nova*
Family Scombridae		
Auxis thazard	M	*K. histolytica*
Euthynnus alletteratus	M, B	*K. nova*
Grammatorcynus bicarinatus	M	*K. grammatorcyni*
Rastrelliger kanagurta	M	*K. quraishii*, *K. saudiensis*
Sarda sarda	M, B	*K. histolytica*

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Fish species with taxonomic classification	Fish habitat in waters of different salinity**	Myxosporean species of the genus *Kudoa*
Scomber japonicus	M	*K. caudata*, *K. histolytica*, *K. scomberi*, *K. thyrsites*
S. scombrus	M, B	*K. histolytica*, *K. thyrsites*
Scomberomorus commerson	M	*K. crumena*, *K. permulticapsula*, *K. scomberomori*
S. maculatus	M	*K. crumena*
S. niphonius	M	*K. konishiae*
S. sierra	M	*K. rayformis*
Thunnus albacares	M, B	*K. crumena*, *K. hexapunctata*, *K. neothunni*
T. alalunga	M	*K. thunni*
T. obesus	M	*K. nova*
T. orientalis	M, B	*K. hexapunctata*, *K. prunusi*, *K. yasunagai*
T. thynnus	M, B	*K. clupeidae*, *K. nova*
Family Trichiuridae		
Lepidopus caudatus	M	*K. thyrsites*
Trichiurus lepturus	M, B	*K. mirabilis*
Order Scorpaeniformes		
Family Anarhichadidae		
Anarhichas lupus	M	*K. islandica*
A. minor	M	*K. islandica*
Order Siluriformes		
Family Ariidae		
Ariopsis felis	M, B	*K. shkae*
Plicofollis layardi	M, B	*K. tachysurae*
P. platystomus	M, B	*K. bengalensis*
P. polystaphylodon	M, B, Fr	*K. quadratum*
Family Plotosidae		
Plotosus lineatus	M, B	*K. yasunagai*
Order Syngnathiformes		
Family Syngnathidae		
Entelurus aequoreus	M, B	*K. quadratum*
Syngnathus abaster	M, B, Fr	*K. quadratum*
S. acus	M, B	*K. quadratum*
S. tenuirostris	M	*K. quadratum*
Order Tetraodontiformes		
Family Tetraodontidae		
Sphoeroides annulatus	M, B	*K. dianae*
Takifugu rubripes	M, B, Fr	*K. shiomitsui*, *K. yasunagai*
Order Zeiformes		
Family Zeidae		
Zeus capensis	M	*K. thyrsites*
Z. faber	M, B	*K. thyrsites*

Note: *, all systematic groups and species are alphabetized, starting from cartilaginous fishes and ending with bony fishes; **, habitation in waters of different salinity (M, marine water; B, brackish water; Fr, freshwater environment).

Given the hypothesis that myxosporeans originated from marine fish [Shulman et al., 1997] and considering the overwhelming prevalence of *Kudoa* findings in saline water basins, it can be concluded as follows: the transition to parasitizing in some freshwater hosts occurred evolutionally later and likely involved euryhaline hosts.

Also, seven *Kudoa* species have been documented in marine fish inhabiting estuarine zones. In particular, they were found in euryhaline mullets. Thus, *Kudoa haridasae* Sarkar & Ghosh, 1991 and *Kudoa sagarica* Das, 1996 were reported from the goldspot mullet *Planiliza parsia* (Hamilton, 1822) (the Indian Ocean, the Hooghly estuary, Western Bengal, India) [Das, 1996; Sarkar, Chaudhury, 1996]. *K. unicapsula* was registered in the thinlip mullet *Chelon ramada* (Risso, 1827) and golden grey mullet *Ch. auratus* (Risso, 1810) (the Mediterranean Sea, Santa Pola, Ebro River delta, Spain) [Yurakhno et al., 2007]. Besides, myxosporeans were found in brackish-water gobies: *Kudoa camarguensis* Pampoulie, Marques, Rosecchi, Crivelli & Bouchereau, 1999 was recorded from the sand goby *Pomatoschistus minutus* (Pallas, 1770) and common goby *P. microps* (Krøyer, 1838) (the Mediterranean Sea, Rhône River delta, France) [Pampoulie et al., 1999]. *Kudoa cerebralis* Paperna & Zwerner, 1974 was noted in the striped bass *Roccus saxatilis* (Walbaum, 1792) from the Atlantic Ocean, where this species chiefly occurs in estuaries (North American Coast, mouths of Rappahannock and York rivers) and occasionally in marine waters (the Chesapeake Bay coast, the USA) [Paperna, Zwerner, 1974]. This host species is anadromous, migrating between freshwater and marine basins. Its spawning commonly occurs in freshwater. *K. inornata* was found in an estuarine fish, *Cynoscion nebulosus* (Cuvier, 1830) (the Atlantic Ocean, South Carolina coast, the USA, Romaine Harbor, Ashley River, Ashepoo, Combahee, and Edisto basin) [Dykova et al., 2009]. *Kudoa viseuensis* Monteiro, Da Silva, Hamoy, Sanches & Matos, 2019 was noted in a marine host, *Batrachoides surinamensis* (Bloch & Schneider, 1801), near the spot of the Amazon River inflow into the Atlantic Ocean (Viseu municipality, state of Pará, northern Brazil) [Monteiro et al., 2019]. Another *Kudoa* sp. was reported from a brackish-water host, the white perch *Morone americana* (Gmelin, 1789), in the Atlantic Ocean basin, in the Choptank River, Chesapeake Bay (Maryland, the USA) [Bunton, Poynton, 1991].

Only one ocean myxosporean species, *K. thyrsites*, is known to infect five anadromous salmonids: four Pacific species [the pink salmon *Oncorhynchus gorbuscha* (Walbaum, 1792), coho salmon *O. kisutch* (Walbaum, 1792), rainbow trout *O. mykiss* (Walbaum, 1792), and Chinook salmon *O. tshawytscha* (Walbaum, 1792)] and one inhabitant of the Atlantic and Arctic oceans [the Atlantic salmon *Salmo salar* Linnaeus, 1758] [Eiras et al., 2014]. This evidences for the likelihood that host infestation by this parasite occurs exclusively in marine habitats.

Thus, out of 128 *Kudoa* species, 117 (91.4%) were found in marine zones of the World Ocean, 8 (6.3%) were recorded in its estuaries (7 species in marine fish, and 1 in a freshwater host), and 3 (2.3%) were registered in freshwater bodies.

To assess the effect of desalination on myxosporean fauna in fish of the Black Sea and Sea of Azov, we conducted long-term studies in Crimean estuarine ecosystems focusing, among other issues, on *Kudoa* in gobies. In 2008–2019, we examined myxosporeans in 308 gobies in the Chernaya River mouth, 807 specimens in the Karkinitsky Bay (the Black Sea), and 757 Gobiidae specimens in Eastern Sivash (the Sea of Azov) (Table 2).

Table 2. Number of fish infected with *Kudoa nova* / number of fish studied (average prevalence, %) of the family Gobiidae, with indication of hosts prevalence in areas of various water salinity

Area	The Black Sea				The Sea of Azov						The Bug River	Narew and Vistula rivers
	The Chernaya River mouth	The Karkinitsky Bay		The Dnieper River mouth	Eastern Sivash					The Tagan-rog Bay		
					Northern area	Central area		Southern, inner area				
Research period	2010–2019	2008–2013	2014–2017	2012	2010, 2013	2010, 2013	2014–2016	2013	2014–2015	1998	2011	2011
Water salinity, ‰	12–16 (at the bottom)	10–15	18.6–27.6	0.05–16	1–11.5	10–40	22.7–65	10–40	22.7–75	1–3	0.25–0.5	0.2–0.573
Fish species												
Gobius niger	2 / 17 (11.8)	–	–	–	–	–	–	–	–	–	–	–
G. ophiocephalus	4 / 82 (4.9)	0 / 61 (0)	0 / 209 (0)	–	0 / 105 (0)	0 / 30 (0)	0 / 58 (0)	–	0 / 3	–	–	–
Mesogobius batrachocephalus	–	–	0 / 2	–	–	–	–	0 / 1	–	–	–	–
Neogobius fluviatilis	–	13 / 35 (37.1)	35 / 98 (35.8)	–	1 / 7	–	12 / 16 (75)	–	4 / 18 (22.2)	0 / 14 (0)	0 / 24 (0)	0 / 118 (0)
N. gymnotrachelus	–	–	–	–	–	–	–	–	–	–	0 / 35 (0)	0 / 85 (0)
N. melanostomus	40 / 79 (50.6)	27 / 80 (33.8)	48 / 271 (17.7)	1 / 37 (2.7)	11 / 74 (14.9)	–	53 / 127 (41.7)	54 / 230 (23.5)	41 / 88 (46.6)	0 / 2	–	0 / 21 (0)
Pomatoschistus microps	–	–	0 / 3	–	–	–	–	–	–	–	–	–
Ponticola eurycephalus	13 / 75 (17.3)	–	–	–	–	–	–	–	–	–	–	–
Proterorhinus marmoratus	22 / 43 (51.2)	–	28 / 48 (58.3)	–	–	–	–	–	–	–	–	–
P. semilunaris	–	–	–	–	–	–	–	–	–	–	–	0 / 24 (0)
Tridentiger trigonocephalus	2 / 12 (16.7)	–	–	–	–	–	–	–	–	–	–	–
Fish in total, ind.	308	176	631	37	186	30	201	231	109	16	59	248

We analyzed species composition and abundance of fish parasites in two estuarine biotopes in the area of the Chernaya River inflow to the Sevastopol Bay (the Black Sea): in the river mouth with increased bottom salinity and in 1,5 km upstream, in a biotope with salinity of 4–5‰ [Yurakhno, 2012, 2014, 2015a]. In investigated hydrobionts, along with eight predominantly marine myxosporeans, one *Kudoa* representative – *K. nova* – was found from the chameleon goby *Tridentiger trigonocephalus* (Gill, 1859), grass goby *Gobius ophiocephalus* Pallas, 1814, black goby *G. niger* Linnaeus, 1758, tubenose goby *Proterorhinus marmoratus* (Pallas, 1814), mushroom goby *Neogobius eurycephalus* (Kessler, 1874), and round goby *N. melanostomus* (Pallas, 1814). Infestation prevalence by this parasite varied 5 to 92% for different hosts in different seasons. In our study, *K. nova* was noted in a biotope with bottom salinity of 12–16‰. This species was absent in freshwater area of the Chernaya River we surveyed owing to the lack of hosts (gobies) in catches.

K. nova was analyzed in gobies of the Karkinitsky Bay in 2008–2018. It was recorded in three gobies: in the round goby, monkey goby *Neogobius fluviatilis* (Pallas, 1814), and tubenose goby, while the grass goby and knout goby *Mesogobius batrachocephalus* (Pallas, 1814) were free of this parasite. Fish were caught from areas with various hydrological conditions. Some sampling sites were located 8–13 km from our base, the Portovoye village (the Andreevka, Avrora, Steregushchee, and Risovoe villages). Thus, in 2008–2013, gobies were sampled in open sea zones periodically affected by freshwater inflow from paddy fields near the Portovoye and Risovoe and in more distant spots near the Avrora and Steregushchee. In different seasons, prevalence of *K. nova* infestation in the monkey goby from slightly desalinated zones was significantly high (31–56%). Infestation rates in the round goby were also high and comparable across different salinity gradients (40–47%), except for the site in the Risovoe vicinity, where it was only 12%. In subsequent years, after rice cultivation ceased in the Crimea, *K. nova* persisted in gobies, with infestation prevalence dropping noticeably in the round goby (down to 4–30%), but remaining sometimes rather elevated in the monkey goby (up to 47–63%).

In 2014 and 2015, fish was sampled near the former Andreevka village (opposite the Ogni settlement) and in the Avrora southward to the Portovoye, closer to the Bakalskaya Spit. Sampling depth was slightly more than 1 m; interestingly, by fishermen evidences, such depths stretch only along 200 m from the coast and are characterized by sandy substrates (clay-mixed sediments in the Avrora vicinity). Here, only 10% of the round goby individuals were infected with *K. nova*. In 2014, the monkey goby was sampled once from a shallow brackish lagoon (salinity of 27.60‰) in the Portovoye vicinity, on the Sary-Bulat Spit, with silty substrate; 18% of fish were infected with *K. nova*. The highest infestation rates of gobies by this parasite were recorded in 2015 in a shallow Sary-Bulat Lagoon near the Portovoye. There, depths of 10–60 cm extend over 2 km toward islands, and bottom is a black silt. Salinity gradients differed as well: areas near the Andreevka and Avrora experienced minimal freshwater effect, while shallow waters in the Portovoye vicinity were affected by six Dnieper River discharge channels until 2014. Subsequent data obtained for the open sea and adjacent Sary-Bulat Lagoon confirmed higher infection rates in the lagoon. For example, prevalence of *K. nova* infestation in the round goby from the Sary-Bulat Lagoon was 4 times higher in 2016 and 2.6 times higher in 2017 than in fish from the open sea. The monkey goby in the lagoon showed the prevalence of 63%, and the tubenose goby, 50–65%. Accordingly, higher infection rates of fish with myxosporeans were recorded in shallower and highly silty areas of the Karkinitsky Bay that seems to reflect intensified accumulation of infective stages there [Dmitrieva et al., 2015; Korniichuk et al., 2016; Yurakhno, 2013, 2015a, 2016b; Yurakhno, Tokarev, 2017].

In general, in the Swan Islands nature reserve, *Kudoa* representatives and other myxosporeans form a typical marine fauna, and it is consistent with salinity dynamics in the area. According to data provided by N. Shadrin (IBSS), salinity in periodically desalinated open sea in the Risovoe and Portovoye vicinity fluctuated between 10 and 15‰ within 2008–2013. After the cessation of freshwater discharge from paddy fields, salinity near Portovoye increased. In the open sea, we recorded the values of 19.30‰ in 2014, 21.08‰ in 2015, and 17.90–18.59‰ in 2016. In the Sary-Bulat Lagoon, salinity reached 20.87‰ in 2015 and 18.14–21.35‰ in 2016. Apparently, periodic freshwater inflow from paddy fields into the Karkinitsky Bay did not reduce salinity to levels critical for *K. nova* survival, unlike in other areas analyzed (see below).

Another estuarine biotope we examined for *Kudoa* was Eastern Sivash. The round, grass, and monkey gobies were sampled in November–December 2010 in its northern area, near the Mysovoe, Chaikino, and Chongar villages [Yurakhno, 2015a; Yurakhno, Gorchanok, 2011]. Fish were sampled with fixed nets at depths of 2–4 m; water temperature was of +10…+14 °C; and areas were characterized by various salinity. In the Mysovoe and Chaikino vicinity, salinity during sampling was 11.5‰. As known according to data provided by A. Boltachev (IBSS), the value could drop down to 1‰ due to occasional freshwater discharge from paddy fields to Sivash. In the Chongar vicinity, salinity was 17‰. In 2010, *K. nova* was absent in 47 round gobies sampled from desalinated zones of the Mysovoe and Chaikino, but it was registered in 1 out of 5 monkey gobies. In the Chongar area, 43% of round gobies were infected, and there were no *K. nova* in 1 monkey goby caught. In 2013, prevalence in the round goby near Mysovoe rose to 47% suggesting the lack of strong freshwater effect in this spot in previous years.

From December 2012 to June 2015, we carried out further studies on myxosporeans in gobies in Eastern Sivash, with the focus on its hypersaline inner zone (the Semisotka and Kamenskoe villages) and central area (the Dmitrovka village). The round, sand, grass, and knout gobies were surveyed [Yurakhno, 2015a]. One species of parasite – *K. nova* – was registered in muscles of the round and sand gobies.

Infestation prevalence of examined fish varied seasonally and annually: it was 22% in the monkey goby and 16–69% in the round goby. Neither inner zone of Eastern Sivash, nor its central area was highly desalinated; values of host infestation by *K. nova* were rather noticeable and comparable to those in marine waters, the same as in 2013 in the northern lagoon. This fact was proved by data of other researchers [Shadrin et al., 2018]. Thus, in 2013, water salinity in the central and inner areas varied within 10.0–40.0‰ (mean of 25.2‰). In 2014, it was 25.9–26.7‰ in summer and 22.7–42.2‰ in autumn; at several spots, salinity reached 50.0–65.0‰. In 2015, it was 55.0–65.0‰ in the central area and 70.0–75.0‰ in the southern one.

The cessation of freshwater inflow from paddy fields in 2014 to Eastern Sivash likely improved conditions for *K. nova* proliferation in local populations of gobies. This is evidenced by higher infection rates in the round goby (up to 53–69% in various seasons) in recent years of the study in the hypersaline inner zone of Sivash – in the Kamenskoe vicinity. It is the southernmost area, the furthest from paddy fields, and the one with maximum salinity [Yurakhno, 2015a].

K. nova was a common species in the parasite fauna of gobies for all three estuarine ecosystems surveyed.

Our data for periodically desalinated marine areas in the Crimea evidence for a negative effect of strong desalination (down to 1‰ or lower values) on infection rates of gobies by *K. nova*. Conversely, higher infection rates were observed in areas with elevated salinity (Table 2). When analyzing changes in mean infestation prevalence by this parasite in gobies up to 2013 (a period of discharge from paddy fields into the Karkinitsky Bay and Sivash, including designated spots within the latter one) and in later periods, we observed shifts in the round goby alone. Interestingly, these changes are contradictory between the areas compared. Thus, since 2014, mean infestation prevalence of the goby by *K. nova* in the Karkinitsky Bay decreased by nearly twofold, whereas in the inner Sivash zone, it doubled. This suggests that factors other than salinity may affect these dynamics.

The absence or sporadic occurrence of *K. nova* in highly desalinated areas of the Ponto–Azov region is corroborated by both literature data and our own information. According to N. Naidenova [1974] and our expeditionary research, this parasite was absent in summer 1998 in gobies sampled in the highly desalinated Taganrog Bay (the Sea of Azov) into which the Don River flows [Yurakhno, Gorchanok, 2011]. According to data of AzNIIRKh researches, the mean salinity in the area was 1–3‰. Similarly, during summer 2011, no myxosporeans were noted in the parasite fauna of invasive gobies that spread from the northwestern Black Sea along the central invasive corridor: the round goby *N. melanostomus*, racer goby *N. gymnotrachelus* (Kessler, 1857), monkey goby *N. fluviatilis*, and western tubenose goby *Proterorhinus semilunaris* (Heckel, 1837). These fish were sampled in the Bug and Vistula rivers. In 2012, the prevalence of *K. nova* infestation in the Dnieper River estuarine zone, near Ochakiv city, was only 2.7% [Kvach et al., 2014] (Table 2).

A near-complete absence of this species or its significantly low occurrence in hosts from highly desalinated areas evidence for the following. The first, *K. nova* spores which spend most time after the host death in the water column, in sediment, or substrate may not survive low salinity. The second, the species composition of oligochaetes and polychaetes – potential definitive hosts for myxosporeans – is notably scarce in regions with the pronounced desalination and salinity fluctuations. However, a two-host life cycle of myxosporeans has only been confirmed for 36 out of more than 2,000 species [Dykova, Lom, 2007]. Most of them are freshwater inhabitants, and none of them belong to the genus *Kudoa*. Thus, we just hypothesize that not only fish, but also invertebrates may participate in *K. nova* life cycle.

To assess spore survival under different salinities, an experiment was carried out in summer 2014 [Yurakhno, 2015b, 2016a, 2018]. Cysts isolated from host muscle tissue were stored in spring water (freshwater) in refrigerator. After 3 days, nearly half of spores in freshwater featured structural abnormalities, including deformities. By the 34^{th} day, 87% of spores in freshwater were degraded, and the function of the polar filament extrusion was disrupted in alkaline solutions indicating loss of viability of darkened spores. In contrast, the most comfortable conditions were formed in cysts immersed in seawater in refrigerator; there, the share of normal spores was 94–98% throughout month-long experiments. As for cysts in muscles, the key role in spore preservation was played by their occurrence in host tissues in biochemical environment. In this case, shares of abnormal spores in freshwater and marine water at ambient temperature were comparable and relatively low: in freshwater, 9 to 17%, and in seawater, 4 to 20%.

The rapid detrimental effect of freshwater on *K. nova* spores is surprising given their presumed resilience and theoretical ability to persist longer in unsuitable environment. This parasite is known to tolerate slight desalination; it occurs in significantly higher abundance in mesohaline shallows of the Sea of Azov than in the Black Sea, especially in estuaries. However, pure freshwater directly disrupts structure and viability of these spores when exposed to unsuitable environment. When *K. nova* spores remain within muscle tissue of the host, its biochemical environment mitigates adverse effects of freshwater. In contrast, spores of oceanic species are often more affected by freshwater, and this effect can be detrimental. Thus, a proven method to inactivate spores of *K. septempunctata* – a parasite causing diarrhea and vomiting in consumers of raw meat of *Paralichthys olivaceus* (Temminck & Schlegel, 1846) – is to immerse it in freshwater (0‰) or a hypersaline solution (160‰) for five minutes [Yokoyama et al., 2016].

We registered *K. nova* in both fully saline Black Sea waters and mesohaline Sea of Azov ones (there, infestation prevalence often reached 100% in host fish inhabiting shallow estuaries). However, we recorded no specimens of this parasite in oligohaline and freshwater habitats. *K. nova* spores exhibit negative buoyancy, and this is regarded as an adaptation for infecting benthic hosts. In lower-salinity environments, spores settle more rapidly onto a substrate mixing with surface silt layer and thereby optimizing the contact with potential hosts. *K. nova* proliferation into oligohaline and freshwater systems seems to reflect the limited occurrence of its putative definitive hosts: in these habitats, possibly oligochaetes or polychaetes. Moreover, as demonstrated by our experiments, *K. nova* spores cannot survive prolonged exposure to freshwater after the host death. Accordingly, this parasite is likely of marine origin; it occurs in water basins of various salinity (including oceanic one) and is widely distributed in Gobiidae representatives in the Black Sea and Sea of Azov [Yurakhno, 2014; Yurakhno, Gorchanok, 2011].

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REFERENCES

1. Grinevetsky S. R., Zonn I. S., Zhil'tsov S. S. *Chernoe more. Entsiklopediya.* Moscow : Mezhdunarodnye otnosheniya, 2015, 664 p. (Seriya: "Morya Rossii"). (in Russ.)
2. Debelius Kh. *Ryby Atlantiki, Sredizemnogo i Chernogo morei.* [Moscow] : IKAN, 2009, 308 p. (in Russ.)
3. Dmitrieva E. V., Yurakhno V. M., Kornyychuk Yu. M., Pronkina N. V., Polyakova T. A., Popyuk M. P. Characterization of species diversity and structure of fish parasite communities from Karkinitsky Bay (Black Sea). In: *Voprosy sokhraneniya bioraznoobraziya vodnykh ob"ektov* : materialy Mezhdunarodnoi nauchnoi konferentsii, Rostov-on-Don, 27 November, 2015. Rostov-on-Don : AzNIIRKh, 2015, pp. 92–98. (in Russ.). https://elibrary.ru/xvxcgt
4. Korniichuk Yu. M., Dmitrieva E. V., Yurakhno V. M., Polyakova T. A., Pron'kina N. V., Popyuk M. P., Tarina N. A., Rudenko M. I. Fauna parazitov v biotsenozakh zapovednoi akvatorii u Lebyazh'ikh ostrovov // *The Nature Reserves of the Crimea – 2016. Biological and Landscape Diversity, Conservation and Management* : the abstracts of the VIII International Scientific-Practical Conference, Simferopol, 28–30 April, 2016. Simferopol : El'in'o, 2016, pp. 305–307. (in Russ.). https://repository.marine-research.ru/handle/299011/5142
5. Naidenova N. N. *Parazitofauna ryb semeistva bychkovykh Chernogo i Azovskogo morei* / AN USSR ; Institut biologii yuzhnykh morei imeni A. O. Kovalevskogo. Kyiv : Naukova dumka, 1974, 182 p. (in Russ.). https://repository.marine-research.ru/handle/299011/5657
6. Svetovidov A. N. *Ryby Chernogo morya.* Moscow ; Leningrad : Nauka, 1964, 551 p. (in Russ.). https://repository.marine-research.ru/handle/299011/8655
7. Fadeev N. S. *Spravochnik po biologii i promyslu ryb severnoi chasti Tikhogo okeana.* Vladivostok : TINRO-Tsentr, 2005, 366 p. (in Russ.). https://elibrary.ru/qkxhkn

8. Shulman S. S. *Miksosporidii fauny SSSR*. Moscow ; Leningrad : Nauka, 1966, 507 p. (in Russ.)
9. Shulman S. S., Donets Z. S., Kovaleva A. A. *Klass miksosporidii mirovoi fauny*. Vol. 1. *Obshchaya chast'*. Saint Petersburg : Nauka, 1997, 578 p. (in Russ.)
10. Yurakhno V. M. *Miksosporidii ryb Chernogo morya: sistematika, fauna, ekologiya, zoogeografiya* : avtoref. dis. … kand. biol. nauk : 03.00.18, 03.00.19. Sevastopol, 1994, 23 p. (in Russ.). https://repository.marine-research.ru/handle/299011/9666
11. Yurakhno V. M. Miksosporidii chernomorskikh ryb v estuarii reki Chernaya (Sevastopol', Krym). In: *Materialy V Vserossiiskoi konferentsii s mezhdunarodnym uchastiem po teoreticheskoi i morskoi parazitologii, Svetlogorsk, 23–27 April, 2012* / Ch. M. Nigmatullin (Ed.). Kaliningrad : AtlantNIRO, 2012, pp. 229–231. (in Russ.)
12. Yurakhno V. M. Vidovoi sostav i sezonnaya vstrechaemost' miksosporidii ryb v nizov'yakh r. Chernaya (Sevastopol', Rossiya). In: *Trudy Tsentra parazitologii* / Tsentr parazitologii Instituta problem ekologii i evolyutsii imeni A. N. Severtsova RAN. Vol. 48: *Sistematika i ekologiya parazitov* / S. O. Movsesyan (Ed.). Moscow : Tovarishchestvo nauchnykh izdanii KMK, 2014, pp. 346–348. (in Russ.)
13. Yurakhno V. M. Miksosporidii morskikh ryb, obitayushchikh v ekosistemakh estuarnogo tipa pribrezhnoi zony Kryma In: *Biologicheskoe raznoobrazie Kavkaza i yuga Rossii* : materialy XVII Mezhdunarodnoi konferentsii, Nalchik, 5–6 November, 2015. Makhachkala : Izd-vo "Nauka-Dagestan", 2015a, pp. 499–502. (in Russ.). https://elibrary.ru/zeapev
14. Yurakhno V. M. Influence of water different salinity on the morphology of *Kudoa nova* (Myxosporea, Kudoidae) spores: Experimental study. In: *Morskie biologicheskie issledovaniya: dostizheniya i perspektivy* : v 3 t. : sb. materialov Vseros. nauch.-prakt. konf. s mezhdunar. uchastiem, priuroch. k 145-letiyu Sevastopol'skoi biologicheskoi stantsii, Sevastopol, 19–24 September, 2016. Sevastopol, 2016a, vol. 1, pp. 354–357. (in Russ.). https://repository.marine-research.ru/handle/299011/3058
15. Yurakhno V. M. Miksosporidii i mikrosporidii ryb Karkinitskogo zaliva (Krym, Chernoe more). In: *Trudy Tsentra parazitologii* / Tsentr parazitologii Instituta problem ekologii i evolyutsii imeni A. N. Severtsova RAN. Vol. 49: *Fauna i ekologiya parazitov* / S. O. Movsesyan (Ed.). Moscow : Tovarishchestvo nauchnykh izdanii KMK, 2016b, pp. 215–217. (in Russ.)
16. Yurakhno V. M., Gorchanok N. V. Myxosporea *Kudoa nova* (Myxosporea: Kudoidae) – parasite of the Black Sea and the Sea of Azov fish. *Morskoj ekologicheskij zhurnal*, 2011, vol. 10, no. 2, pp. 68–77. (in Russ.). https://repository.marine-research.ru/handle/299011/1157
17. Yurakhno V. M., Özer A. N. Myxosporean fauna of the Ponto-Caspian basin fish (origin, comparative analysis). In: *Sovremennye problemy parazitologii i ekologii. Chteniya, posvyashchennye pamyati S. S. Shul'mana* : sbornik trudov Vserossiiskoi nauchnoi konferentsii s mezhdunarodnym uchastiem, Tolyatti, 15–17 May, 2018. Tolyatti : Poliar, 2018, pp. 334–345. (in Russ.). https://elibrary.ru/otlfol
18. Yurakhno V. M., Tokarev Y. S. Fish microparasites of Karkinitsky Gulf of the Black Sea according to the data of spring and autumn of 2016. In: *Biological Diversity and Conservation Problems of the Fauna – 3* : proceedings of the international conference, 27–29 September, 2017, Yerevan, Armenia. Yerevan : LLC "TASK", 2017, pp. 337–339. (in Russ.)
19. Azevedo C., Rocha S., Matos E., Oliveira E., Matos P., Al-Quraishy S., Casal G. Ultrastructural and phylogenetic description of *Kudoa orbicularis* n. sp. (Myxosporea: Multivalvulida): A parasite infecting the muscle of the fish *Chaetobranchopsis orbicularis* (Teleostei: Cichlidae) in the Amazon region. *Journal of Eukaryotic Microbiology*, 2016, vol. 63, iss. 1, pp. 27–36. https://doi.org/10.1111/jeu.12244
20. Bunton T. E., Poynton S. L. *Kudoa* sp. (Myxosporea, Multivalvulida) infection in juvenile white perch, *Morone americana* (Gmelin): Histopathology and spore morphology. *Journal*

of Fish Diseases, 1991, vol. 14, iss. 5, pp. 589–594. https://doi.org/10.1111/j.1365-2761.1991.tb00615.x

21. Casal G., Matos E., Matos P., Azevedo C. Ultrastructural description of a new myxosporean parasite *Kudoa aequidens* sp. n. (Myxozoa, Myxosporea), found in the sub-opercular musculature of *Aequidens plagiozonatus* (Teleostei) from the Amazon River. *Acta Protozoologica*, 2008, vol. 47, iss. 2, pp. 135–141.
22. Das M. K. Myxozoan and urceolarid ciliate parasites of wild and cultured *Liza parsia* in deltaic West Bengal. *Journal of the Inland Fisheries Society of India*, 1996, vol. 28, no. 2, pp. 46–56.
23. Dykova I., Lom J. Comments on the recent knowledge and some of the topics to be solved in the research on Myxozoa. *Parassitologia*, 2007, vol. 49, suppl. 2, pp. 146. (The 7th International Symposium on Fish Parasites, 24–28 September, 2007, Viterbo, Italy).
24. Dykova I., de Buron I., Fiala I., Roumillat W. R. *Kudoa inornata* sp. n. (Myxosporea: Multivalvulida) from the skeletal muscles of *Cynoscion nebulosus* (Teleostei: Sciaenidae). *Folia Parasitologica*, 2009, vol. 56, iss. 2, pp. 91–98. https://doi.org/10.14411/fp.2009.014
25. Eiras J. C., Saraiva A., Cruz C. Synopsis of the species of *Kudoa* Meglitsch, 1947 (Myxozoa: Myxosporea: Multivalvulida). *Systematic Parasitology*, 2014, vol. 87, iss. 2, pp. 153–180. https://doi.org/10.1007/s11230-013-9461-4
26. Fomena A., Bouix G. Myxosporea (Protozoa: Myxozoa) of fresh-water fishes in Africa: Keys to genera and species. *Systematic Parasitology*, 1997, vol. 37, iss. 3, pp. 161–178. https://doi.org/10.1023/A:1005839220014
27. Kasprzak A., Juśko K., Motyka J. Zmienność jonu chlorkowego i siarczanowego w Wiśle między zbiornikiem Goczałkowickim a ujściem Skawy. *Zeszyty Naukowe Instytutu Gospodarki Surowcami Mineralnymi i Energią Polskiej Akademii Nauk*, 2016, no. 94, pp. 197–204.
28. Kvach Yu., Kornyychuk Y., Mierzejewska K., Rubtsova N., Yurakhno V., Grabowska J., Ovcharenko M. Parasitization of invasive gobiids in the eastern part of the central trans-European corridor of invasion of Ponto-Caspian hydrobionts. *Parasitology Research*, 2014, vol. 113, iss. 5, pp. 1605–1624. https://doi.org/10.1007/s00436-014-3791-2
29. Monteiro E. P., Da Silva D. T., Hamoy I., Sanches O., Matos E. R. Morphological and molecular characteristics of *Kudoa viseuensis* n. sp. (Myxosporea: Multivalvulida), found in the muscle of *Batrachoides surinamensis* (Teleostei: Batrachoididae) in the Brazilian Amazon region. *Acta Protozoologica*, 2019, vol. 58, iss. 1, pp. 7–16. https://doi.org/10.4467/16890027AP.19.002.10833
30. Pampoulie C., Marques A., Rosecchi E., Crivelli A. J., Bouchereau J. L. A new myxosporean parasite, *Kudoa camarguensis* n. sp., recorded on two goby species (Teleostei: Pisces) in the Rhône delta (Mediterranean Sea, France). *Journal of Eukaryotic Microbiology*, 1999, vol. 46, iss. 3, pp. 304–310. https://doi.org/10.1111/j.1550-7408.1999.tb05129.x
31. Paperna I., Zwerner D. E. *Kudoa cerebralis* sp. n. (Myxosporidea, Chloromyxidae) from the striped bass, *Morone saxatilis* (Walbaum). *The Journal of Protozoology*, 1974, vol. 21, iss. 1, pp. 15–19. https://doi.org/10.1111/j.1550-7408.1974.tb03610.x
32. Sarkar N. K., Chaudhury S. R. *Kudoa cascasia* sp. n. (Myxosporea: Kudoidae) parasitic in the mesentery of *Sicamugil cascasia* (Ham.) from Hooghly estuary of West Bengal, India. *Acta Protozoologica*, 1996, vol. 35, no. 4, pp. 335–338.
33. Sarkar N. K., Ghosh S. Two new coelozoic myxosporida (Myxozoa: Myxosporea) from estuarine teleost fishes (Mugilidae) of West Bengal, India. *Proceeding of the Zoological Society, Calcutta*, 1991, vol. 44, pp. 131–135.
34. Shadrin N. V., Anufriieva E. V., Kipriyanova L. M., Kolesnikova E. A., Latushkin A. A., Romanov R. E., Sergeeva N. G. The political decision caused the drastic ecosystem shift of the Sivash Bay (the Sea of Azov). *Quaternary International*, 2018, vol. 475, pp. 4–10. https://doi.org/10.1016/j.quaint.2017.12.009
35. Siau Y. Myxosporidies de *Synodontis ansorgii*

Bouleng. Ann. et Mag. N. H., 1911 et de *Eleotris (Kribia) kribensis* Boulenger 1964, poissons des eaux saumâtres de la lagune de Porto-Novo (Dahomey). *Bulletin de la Société zoologique de France*, 1971, vol. 96, pp. 563–570.
36. *The Living Marine Resources of the Eastern Central Atlantic.* Vol. 3. *Bony Fishes pt 1 (Elopiformes to Scorpaeniformes)* / K. E. Carpenter, N. De Angelis (Eds). Rome : FAO, 2016, pp. 1511–2342. (FAO Species Identification Guide for Fishery Purposes).
37. Velasco M., Videira M., Viana da Silva J. M., Sanches O., Matos P. S., Carmona de São Clemente S., Matos E. Esophageal infection due to *Kudoa* sp. (Myxozoa) in mapará catfish, *Hypophthalmus marginatus*. *Aquaculture Reports*, 2015, vol. 2, pp. 22–25. https://doi.org/10.1016/j.aqrep.2015.05.001
38. Yokoyama H., Funaguma N., Kobayashi S. *In vitro* inactivation of *Kudoa septempunctata* spores infecting the muscle of olive flounder *Paralichthys olivaceus*. *Foodborne Pathogens and Disease*, 2016, vol. 13, no. 1, pp. 21–27. https://doi.org/10.1089/fpd.2015.2003
39. Yurakhno V. M. The nature protection aspect of the Black Sea fish myxosporean studies. *Vestnik zoologii*, 2013, vol. 47, iss. 6, pp. 537–545. https://repository.marine-research.ru/handle/299011/11600
40. Yurakhno V. Experimental research of *Kudoa nova* (Myxosporea: Kudoidae) spores in saline and fresh water. In: *The 9th International Symposium on Fish Parasites*, 31 August – 4 September, 2015, Valencia, Spain : book of abstracts. [Valencia], 2015b, pp. 138. https://doi.org/10.13140/RG.2.1.4227.8482
41. Yurakhno V. Effect of water different salinity on the morphology of *Kudoa nova* (Myxosporea: Kudoidae) spores: Experimental study. In: *Diversity in the Coastal Marine Sciences: Historical Perspectives and Contemporary Research of Geology, Physics, Chemistry, Biology and Remote Sensing* / C. W. Finkl, C. Makowski (Eds). Dordrecht, the Netherlands : Springer, 2018, chap. 29, pp. 495–503. (Coastal Research Library ; vol. 23). https://doi.org/10.1007/978-3-319-57577-3_29
42. Yurakhno V. M., Ovcharenko M. O., Holzer A. S., Sarabeev V. L., Balbuena J. A. *Kudoa unicapsula* n. sp. (Myxosporea: Kudoidae), a parasite of the Mediterranean mullets *Liza ramada* and *L. aurata* (Teleostei: Mugilidae). *Parasitology Research*, 2007, vol. 101, iss. 6, pp. 1671–1680. https://doi.org/10.1007/s00436-007-0711-8
43. Yurakhno V. M., Özer A. N. History of formation and peculiarities of Ponto-Caspian fish myxosporean fauna. *Morskoj biologicheskij zhurnal*, 2020, vol. 5, no. 1, pp. 99–110. https://doi.org/10.21072/mbj.2020.05.1.10

ВЛИЯНИЕ ФАКТОРА СОЛЁНОСТИ ВОДЫ НА РАСПРОСТРАНЕНИЕ МИКСОСПОРИДИЙ РОДА *KUDOA* (CNIDARIA, MYXOZOA) СРЕДИ РЫБ МИРОВОЙ ФАУНЫ

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Изучена встречаемость миксоспоридий рода *Kudoa* в рыбах, обитающих в водах разной солёности. Работа основана на собственных материалах по миксоспоридиям рыб, собранных в 1987–2021 гг. Это более чем 12 000 экз. около 100 видов рыб в бассейнах Атлантического океана [Азовское (Россия, Украина), Чёрное (Россия, Украина, Турция) и Средиземное (Италия, Испания) моря; регионы Центрально-Восточной Атлантики (на траверзе Мавритании) и южные широты у берегов Африки (на траверзе Намибии); вóды северной (недалеко от Норвегии) и южной (на траверзе Аргентины) частей океана; юго-восточные берега США], Индийского океана [побережье Йемена] и Тихого океана [Южно-Китайское море (Вьетнам)]. Всего на оригинальном материале исследовано 27 представителей миксоспоридий рода *Kudoa*, из которых 19 определены до вида. Также проанализированы все доступные литературные источники и электронная база FishBase. Установлено, что из 291 представителя рыб — хозяев *Kudoa* 169 видов являются чисто морскими, 76 видов могут обитать в морской и солоноватоводной среде, 42 вида эвригалинны и могут быть встречены как в морских и солоноватых, так и в пресных водах, и лишь 4 вида являются чисто пресноводными. Из 128 видов *Kudoa* 117 (91,4 %) были найдены в морской зоне Мирового океана, 8 (6,3 %) — в его эстуариях (7 видов — в морских рыбах, 1 вид — в пресноводном хозяине), 3 (2,3 %) — в пресноводных водоёмах. В 2008–2019 гг. проведены исследования *Kudoa nova* Naidenova, 1975 в экосистемах эстуарного типа у берегов Крыма в устье реки Чёрная и в Каркинитском заливе (Чёрное море), а также в Восточном Сиваше (Азовское море). Всего вскрыто 2232 экз. 11 видов бычковых рыб. Установлено, что периодическое опреснение этих районов водами рисовых чеков, а также постоянное присутствие пресной воды в поверхностном слое устья реки Чёрная не вызывали сильного изменения солёности (за исключением мелководной северной части Восточного Сиваша), которое было бы губительным для данного вида паразитов. При этом *K. nova* полностью отсутствовала в бычках, выловленных в 1998 г. в значительно опреснённом водами реки Дон Таганрогском заливе Азовского моря. Не обнаружена она и в 2011 г. в реках Буг и Висла при исследовании микропаразитов бычков, распространившихся из северо-западной части Чёрного моря по центральному инвазивному коридору. Поставленный нами опыт засвидетельствовал негативное влияние пресной воды на споры данного паразита: под её воздействием они деформировались и темнели; также нарушалась функция выстреливания полярной нити.

Ключевые слова: миксоспоридии, *Kudoa*, солёность воды, мировая фауна