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MYCOLOGY AND ALGOLOGY

Fifty Years of Mycological Studies at the White Sea Biological Station of Moscow State University: Challenges, Results, and Outlook

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Abstract—This review covers the history of the mycological studies performed at Pertsov White Sea Biological Station, Moscow State University (WSBS MSU). The WSBS was established more than 70 years ago; presently, it is one of the main divisions of the university, where numerous educational and research marine programs are fulfilled. Mycological studies have been performed here for more than half a century, focusing on biodiversity and ecology of marine, littoral, and soil fungi and fungi-like protists. Various research projects resulted as a number of scientific publications, diploma (MSc) theses, and dissertations. Presently, WSBS MSU and its vicinity is the northernmost area researching the best in regard to mycobiota. However, a number of blind spots still exist; thus, the future studies in this region should focus on diversity and biology of epiphyte fungi, ecology of fungi and fungi-like protists, and on fungi phylogeny.

Keywords: White Sea, WSBS MSU, fungi, fungi-like protists, biodiversity.

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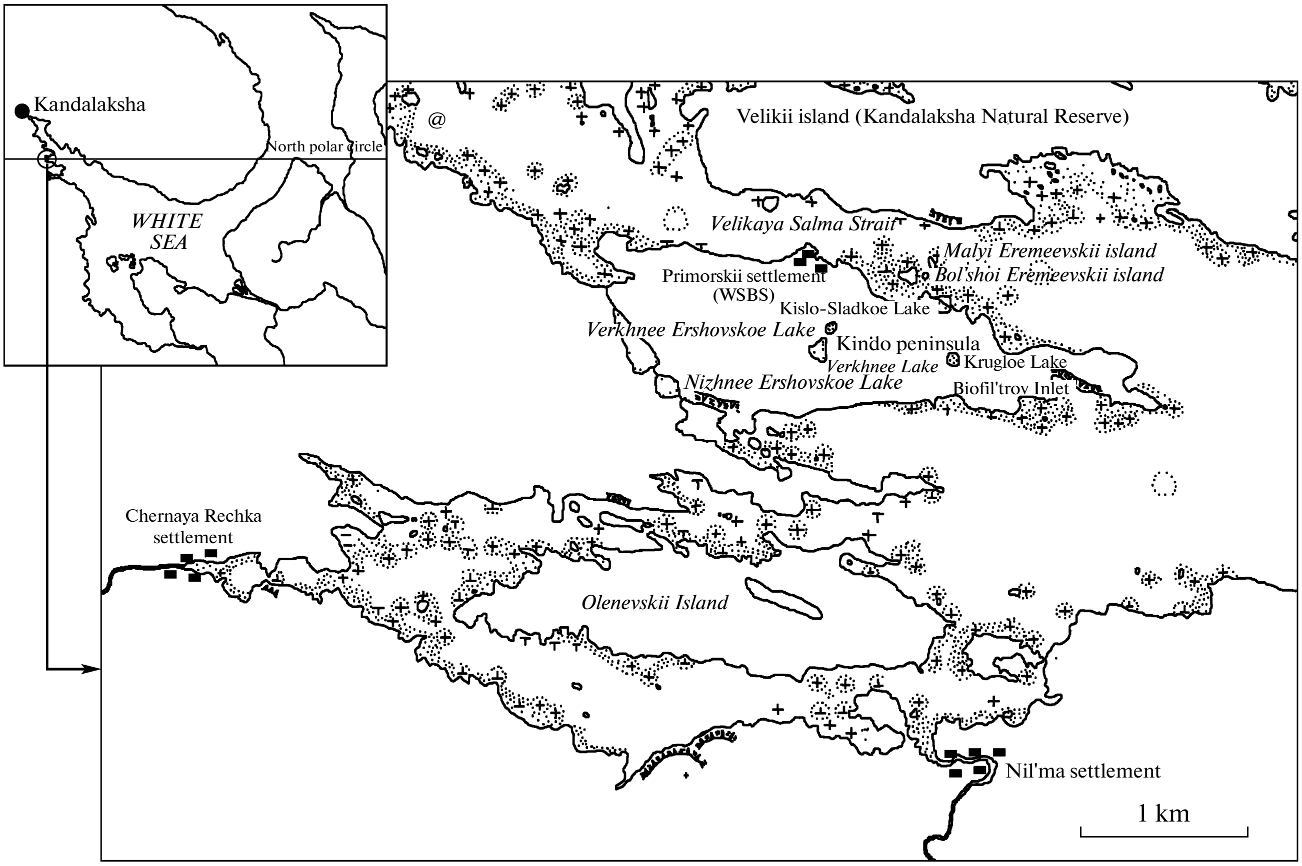
Pertsov White Sea Biological Station, Moscow State University, (WSBS MSU) is an educational and research center established in 1938 for performing marine scientific studies and conducting field summer practice for the students in northern areas. The station is located on the Karelian coast of the White Sea, on Kindo Peninsula (66°34′ N, 33°08′ E) (Fig. 1). The weather conditions [1], oceanographic peculiarities [2, 3], geomorphology [5], soils [5–8], algae [9–11] and vascular plants [10–13] are well studied for this area. Most of the cited studies, as well as many of zoological research, were performed directly here [10, 11]. The mycological studies also received much attention.

The first study of fungi in the vicinity of WSBS MSU was in 1961, when Egyptian scientist, Anvar Abdel Alim, one of the world-known researchers in oceanology, algology, and marine mycology [14], visited the station. His publication [15] was the first study of fungi at the White Sea area. Later, the station became the center of mycological studies in the region. The students' summer field practices on non-vascular plant ecology have been performed here for several dozens of years, including the studies of lichens [16]. Fifteen BSc and MSc theses, four candidate theses [17–20], and one doctoral dissertation [21] in the field of mycology, as well as numerous scientific publications, were the result of the studies performed at the station. In addition, some results were also included in other student and candidate theses and monographs [22–27]. The findings were reported on numerous regional and international scientific conferences and were published in a series of books "Proceedings of WSBS MSU" ("Trudy BBS MGU") [28–32].

The first review on long-term studies of mycobiota appeared as a chapter in the book "Catalogue of Biota of MSU White Sea Biological Station" [10]. The annotated list of the catalogue includes the ecological data referring to each fungi species and describing such parameters as the location of finding (marine, freshwater, or terrestrial species), trophic group, substrate, and frequency of occurrence. The species characteristics include the list of the authors and publications (where possible). The list is presented in regard to the taxonomy; it comprises the representatives of most of the orders of fungi and fungi-like protists (Table 1). After the catalogue was published, some more studies appeared [19, 20, 46, 47, 54]. This allowed expanding the species list, mostly by including deuteromycetes found in marine environment and swamplands (Table 2).

The biodiversity and ecology of fungi inhabiting marine, soil, and swampland ecosystems are the major scientific topics of mycological studies at WSBS MSU.

As was noted above, the first mycological study at WSBS MSU belongs to A.A. Alim [15]. This research



Map of the White Sea Biological Station of Moscow State University (WSBS MSU) and its vicinity.

made a start for the whole spectrum of mycological research in the marine environment in the vicinity of the station. The algae thalli were sampled in August 1961 at littoral and sublittoral zones, down to 20–25-m depth. Most of the common algae species were examined. In total, nine fungi-like species and two representatives of genera *Ectrogella* and *Labyrinthula* were found. In addition, the author noted on mycelium of one of saprophyte ascomycete species observed on thalli of red sublittoral algae *Rhodomela*. All the species were illustrated and described in detail, including the algae species (substrate), morphological and ecological peculiarities, and geographic characteristics. The author concluded the wide distribution of fungi-like protists inhabiting the marine algae in the sublittoral zone. Most of the species belonged to eurytherm and euryhaline forms, characterized by a wide geographic range. Regard must be paid to this work as the first one for the White Sea region and one of the first in the studies of marine fungi in Arctic and Subarctic areas [22].

In late 1960s–early 1970s, much interest was paid to the studies of fungi and fungi-like protists inhabiting marine environment in different areas of the ocean [22]. During this period, Nina Ya. Artemchuk and Evgenii A. Kuznetsov led the studies of biodiversity and biology of marine mycobiota at the station.

In 1972, the publication by N.Ya. Artemchuk [31] appeared in "Berichte zür Polar- und Meeresforschung" ("Reports on Polar and Marine Research"), where the description of two new genera and four new species of fungi-like protists found in Velikaya Salma Strait was given. The new genus of Thraustochytriales, *Elina* (two new species, *E. marisalba* and *E. sinorifica*) and new species, *Thraustochytrium arudimentale*, and new genus and species of oomycetes, *Lagenidicopsis arctica*, were described[1] We do not provide modern synonyms if teleomorph name refers to anamorph name. Since only conidial stages were found in all the cases, we suppose such an approach to be trustworthy. We do not provide here the species names for marine genus *Dendryphiella* ("Dictionary of the Fungi"), because the last studies [62] do not support their reference to *Scolecobastidium* genus.) The publication

[1] All the species names in this publication are given in accordance with the original citation by the author. If the recent name (according to Ainsworth & Bisby's "Dictionary of the Fungi," http://www.indexfungorum.org/Names/fungic.asp) does not refer to the historical one, we place the most recent species name in brackets as (recent:).

Table 1. Total number of genera and species of fungi and fungi-like protists found in the vicinity of WSBS MSU. The names are given in accordance with [10]

Order	Number of genera	Number of species	References
FUNGI-LIKE PROTISTS			
Acrasiomycota	5	6	Kuznetsov, 2003 Tarasov and Kuznetsov, 2003
Dictyosteliomycota	2	5	Kuznetsov, 2003 Tarasov and Kuznetsov, 2003
Myxogasteromycota	19	28	Kuznetsov, 2003
Plasmodiophoromycota	7	14	Kuznetsov and Vekhov, 2001 Kuznetsov, 2003
Labyrinthulomycota	8	27	Artemchuk, 1974 Kuznetsov, 1979 Kuznetsov and Vekhov, 2001 Kuznetsov, 2003 Kuznetsov, 2003
Oomycota	49	135	Alim, 1962 Artemchuk, 1972 Artemchuk, 1974 Kuznetsov, 1979 Kuznetsov and Vekhov, 2001 Kuznetsov, 2003
Hyphochytriomycota	4	5	Kuznetsov, 2003
FUNGI-LIKE PROTISTS, TOTAL	94	220	
FUNGI			
Blastocladiomycota	5	9	Kuznetsov, 2003
Chytridiomycota	36	127	Alim, 1962 Artemchuk, 1974 Kuznetsov, 1979 Kuznetsov, 2003
Zygomycota	22	42	Lisina and Maksimova, 1967 Tolpysheva, 1979a, b, c Sogonov and Marfenina, 1999 Kuznetsov and Vekhov, 2001 Bubnova et al., 2002 Kuznetsov, 2003 Bubnova and Kuznetsov, 2003 Bubnova and Velikanov, 2004 Bubnova, 2005 Kireev and Bubnova, 2006 Marfenina and Kislova, 2006
Ascomycota	31	51	Lisina and Maksimova, 1967 Kuznetsov and Vekhov, 2001 Kuznetsov, 2003 Bubnova et al., 2006 Kireev and Bubnova, 2006 Marfenina and Kislova, 2006
Basidiomycota	64	139	Vishnevskii and Bubnova, 2003 E.A. Kuznetsov and K.L. Tarasov, personal communication
Deuteromycota	72	219	Lisina and Maksimova, 1967 Tolpysheva, 1979a, b, c, d Sogonov and Marfenina, 1999 Kuznetsov and Vekhov, 2001 Bubnova et al., 2002 Kuznetsov, 2003 Bubnova and Velikanov, 2004 Bubnova, 2005 Bubnova et al., 2006 Kireev and Bubnova, 2006 Marfenina and Kislova, 2006

Table 1. (Contd.)

Order	Number of genera	Number of species	References
Incertae sedis Fungi	1	1	Artemchuk, 1974
Lichens	52	174	Piyn, 1967 T.Yu. Tolpysheva, personal communication
FUNGI, TOTAL	283	762	
FUNGI AND FUNGI-LIKE PROTISTS, TOTAL	377	982	

included the species description and drawings. All the species are saprotrophic fungi and are found on the *Pinus* pollen sampled from the seawater, they were also found at lower littoral and supralittoral areas in July 1969.

Two years later, the next publication of N.Ya. Artemchuk [50] was devoted to saprotrophic phycomycetes of Velikaya Salma Strait. That time, the group of phycomycetes included the organisms we now call “fungi-like protists,” i.e. Oomycetes, Labyrinthulomycetes, Thraustochytriales, and Chytridiales. The samples were obtained in July 1968 and July–August 1969 on the littoral transects on Kindo Peninsula, opposite to Eremeevskie Islands (Fig. 1). The littoral at this site is typically sandy-silty with boulder intrusions, and a minor freshwater discharge is observed here. Water, bottom sediments, and algae were sampled. In addition, three samples of water, bottom sediments, and marine foam (pleuston) were obtained from Chernorechenskaya Inlet. Water, bottom sediments, algae, and invertebrates (sponges and mussels) were also sampled in the sublittoral zone of Rugozerskaya Inlet, Velikaya Salma Strait, and Biofil’trov Inlet (figure). In total, 37 littoral and 72 sublittoral samples were obtained. The publication includes the detailed table containing the characteristics of each species found. The same table also includes the information on each sample about the finding the organisms from the groups of Chytridiomycetes, Thraustochytriaceae, Oomycetes, and Fungi imperfecti (Deuteromycetes). The fungi were reared at standard media (pine-tree pollen and germinated boiled linen seeds). In total, sixteen species representing ten genera were found: *Olpidium, Rhizophidium, Chytridium, Elina, Thraustochytrium, Schizochytrium, Saprolegnia, Lagenidicopsis, Pythium, Coulterella.* Detailed taxonomical list of species is given in the publication, including the data on the sporulation period, ecotopes of organisms' findings, and biogeographical characteristics. The publication is illustrated by the sampling site map and the drawings of the species, nine of them were found in the Soviet Union for the first time.

The next publication of the same author [50] covers the ecological analysis of the distribution of the species studied before. The author concludes that water salinity is the major factor affecting the distribution of fungi-like organisms in the studied biotopes. The publication also comprises the data on the geographic range of the studied taxa and its reference to the salinity of the environment. Particularly, Chytridiomycetes were found in the littoral at salinity of 4–25%; they comprised both marine and freshwater species; some of these freshwater species were found in a true marine environment. The species of *Elina* genus described previously [31] were also typically marine, since they were found only in the water samples of 18.3–26.5 psu. Thraustochytriaceae are also true marine organisms. They are found in sublittoral (depths down to 75 m), although they may also be registered in the mesohaline environment (15–16 psu). *Saprolegnia* can survive such salinity, but it cannot grow and reproduce; its salinity optimum range is 0.0–5.0 psu. *Pythium* species are euryhaline, and they may perform and finish the whole life cycle at 0–25 psu. The author concludes that the composition of mycobiota is preconditioned by the salinity of the environment.

In 1969, Evgenii A. Kuznetsov began studies of marine fungi-like protists in the vicinity of WSBS MSU. Ten years later, his first publication appeared [52]. This article describes the biodiversity of marine fungi of Velikaya Salma Strait. The samples were taken during summer periods of 1969–1971. The study was aimed at the analysis of the species diversity of saprotrophic and parasitic marine fungi in the vicinity of the station. Different types of samples were analyzed, including marine and brackish water, littoral sediments, algae, and some common invertebrate species. The whole organisms of invertebrate or algae were scanned visually under the microscope to find parasitic fungi. When the parasitic fungi were found, they were transferred together with the host organism into the Petri dish with sterile seawater to track the life cycle. Saprotrophic fungi were “caught” on the “drag” (pollen of vascular plants, human hair, dragonfly wings, dead crustaceans, and sterilized thalli of different algae species). In total, 132 samples were examined; seven fungi genera were found in 94 of them. The species of *Thraustochytrium* genus were found most frequently (61.2% of the total number of samples). It was also noted that these species preferred pine tree pollen as a substrate for development. The publication also comprised the data on the frequency of occurrence of different saprotrophic fungi in various

Table 2. Fungi species found in the vicinity of WSBS MSU after 2008

Fungi species	References					
	1	2	3	4	5	6
ZYGOMYCOTA						
Mortierella elongata Linnem.						+
M. lignicola (G.W. Martin) W. Gams & R. Moreau						+
M. longicollis Dixon-Stew.						+
Mucor circinelloides Tiegh.						+
Umbelopsis isabellina (Oudem.) W. Gams						+
ZYGOMYCETES, TOTAL	5					
ASCOMYCOTA						
Emericellopsis minima Stolk	+					+
Chaethomium difforme W. Gams						
C. murorum Corda					+	
Cordyceps militaris (L.) Link						+
Debariomyces hansenii (Zopf) Lodder & Kreger			+			
Gelasinospora tetrasperma Dowding			+			
Monodictys levis (Wiltshire) S. Hughes					+	
Nectria mauritiicola (Henn.) Seifert & Samuels					+	
Pseudeurotium zonatum J.F.H. Beyma	+					
Sydowia polyspora (Bref. et Tavel.) E. Müll.						+
ASCOMYCETES, TOTAL	10					
BASIDIOMYCOTA						
Amylosterium areolatum (Chaillet ex Fr.) Boidin						+
Antrodia xantha (Fr.) Ryvarden						+
Antrodiella romellii (Donk) Niemelä						+
Ceriporiopsis subvermispora (Pilát) Gilb. & Ryvarden						+
Cylindrobasidium laeve (Pers.) Chamuris						+
Gloephyllum sepiarium (Wulfen) P. Karst.						+
Peniophora piceae (Pers.) J. Erikss.						+
Phlebiopsis gigantea (Fr.) Jülich						+
Piptoporus betulinus (Bull.) P. Karst.						+
Resinicium bicolor (Alb. & Schwein.) Parmasto						+
Sistotrema brinkmannii (Bres.) J. Erikss.						+
Strobilurus tenacellus (Pers.) Singer						+
Tilletiopsis albescens Gokhale			+			
BASIDIOMYCETES, TOTAL	13					
DEUTEROMYCETES						
HYPHOMYCETES						
Acremonium dichromosporum W. Gams & Sivasith					+	
A. furcatum (Moreau & V. Moreau) W. Gams	+					
A. implicatum (J.C. Gilman & E.V. Abbott) W. Gams						+
A. potronii Vuill.			+		+	+
A. roseolum (G. Sm.) W. Gams					+	
A. salmoneum de Hoog			+			
Acrodontium album Kushwaha & S.C. Agarwal					+	
A. crateriforme (J.F.H. Beyma) de Hoog				+		+

Table 2. (Contd.)

Fungi species	References					
	1	2	3	4	5	6
A. hydnicola (Peck) de Hoog			+			
Arthrinium algicola (N.J. Artemczuk) E.B.G. Jones, Sakay., Suetrong, Somrith. & K.L. Pang					+	
Aspergillus proliferans G. Sm.						+
A. repens (Corda) Sacc.						+
A. tubingensis Mosseray						+
Beauveria brongniartii (Sacc.) Petch						+
Broomella acuta Shoemaker & E. Mull.			+			
Cadophora fastigiata Lagerb. & Melin	+				+	+
C. luteo-olivacea (J.F.H. Beyma) T.C. Harr. & McNew					+	+
C. malorum (Kidd & Beaumont) W. Gams					+	+
C. melinii Nannf.						+
Cephalotrichum nanum (Ehrenb.) S. Hughes					+	
Chrysosporium carmichaelii Oorschot					+	
Cladophialophora humicola Crous et U. Braun						+
Cladosporium antarcticum K. Schub., Crous et U. Braun						+
C. bruhnei Linder						+
C. halotolerans Zalar, de Hoog & Cunde-Cim.					+	
C. langeronii (Fonseca, Leão & Nogueira) Vuill.						+
Cryptococcus albidus (Saito) C.E. Skinner			+			
Cylindrocarpon cylindroides Wollenw.			+			
C. destructans (Zinssm.) Scholten					+	
C. lucidum C. Booth					+	
Cylinrocarpon sp. c.f. anam. *Nectria coccinea* Desm.			+			
Embellisia phragmospora (Emden) E.G. Simmons					+	
Epicoccum nigrum Link			+			
Exophiala dermatitidis (Kano) de Hoog			+			
E. heteromorpha (Nannf.) de Hoog & Haase					+	
Fusarium acuminatum Ellis & Everh.					+	
F. graminearum Schwabe						+
F. sporotrichioides Sherb.					+	
F. tricinctum (Corda) Sacc.					+	
Humicola fuscoatra Traaen						+
Isaria alba J.F.H. Beyma					+	
Lecanicillium evansii Zare & W. Gams						+
L. muscarium (Petch) Zare & W. Gams					+	+
Lecythiophora mutabilis (J.F.H. Beyma) W. Gams & McGinnis						+
Memnoniella echinata (Rivolta) Galloway						+
Oedocephalum glomerulosum (Bull.) Sacc.					+	
Oidiodendron ambiguum Peyronel et Malan						+
O. griseum Robak				+		+
O. maius var. *citrinum* (Barron) Rice a. Currah.						+
O. periconiodes Morrall				+		+
Penicillium aculeatum Raper & Fennell						+

Table 2. (Contd.)

Fungi species	References					
	1	2	3	4	5	6
P. atrovenetum G. Sm.					+	
P. citreoviride Biourge				+		
P. dierckxii Biourge						+
P. duclauxii Delacr.						+
P. italicum Wehmer	+					
P. multicolor G.–M. & Porad.		+				+
P. restrictum J.C. Gilman & Abbott	+			+		+
P. rolfsii Thom				+		+
P. solitum Westling						+
P. verruculosum Peyronel				+		+
Phialophora europaea de Hoog, Mayser & Haase						+
P. lagerbergii (Melin & Nannf.) Conant						+
P. verrucosa Medlar						+
Pochonia suchlasporium (W. Gams & Dackman) Zare & W. Gams	+					
Polyscytalum fecundissimum Riess						+
Stachybotrys dichroa Grove						+
Stachybotrys anam. *Melanopsamma pomiformis* (Pers.) Sacc.					+	
Stephanosporium atrum Dal Vesco						+
Teberdinia hygrophila Sogonov, W. Gams, Summerb. et Schroers						+
Tolypocladium geodes W. Gams				+	+	+
T. nubicola Bissett						+
T. tundrense Bissett						+
Trichoderma asperellum Samuels, Lieckf. & Nirenberg						+
T. piluliferum J. Webster & Rifai						+
Trixosporon lignicola (Diddens) Fell & Scorzetti						+
Wardomyces anomalus F.T. Brooks & Hausford	+					
Verticillium albo-atrum Reinke & Berthold					+	
Ulocladium chartarum (Preuss) E.G. Simmons			+			
U. consortiale (Thum) Simmons		+	+		+	
U. septosporum (Preuss) E.G. Simmons					+	
Zythiostroma pinastri (P. Karst.) Höhn				+		+
HYPHOMYCETES, TOTAL	82					
COELOMYCETES						
Coniothyrium cerealis E. Mull			+			
Paraconiothyrium sporulosum (W. Gams & Domsch) Verkley					+	
Phoma herbarum Westendorp	+		+			
Ph. leveillei Boerema & G.J. Bollen			+			
Ph. poolensis var. *verbascicola* (Ellis & Kellerm.) Aa & Boerema						+
COELOMYCETES, TOTAL	5					
TOTAL NUMBER OF NEW SPECIES FOUND IN VICINITY OF WSBS MSU AFTER 2008	115					

Cited under: (1) Bubnova, 2009, (2) Bubnova and Kireev, 2009, (3) Konovalova and Bubnova, 2011, (4) Grum-Grzhimaylo and Bilanenko, 2012, (5) Konovalova, 2012, (6) Grum-Grzhimaylo, 2012.

biotopes. The highest biodiversity was observed in the estuarine waters, brackish lagoons, and rock pools. The author concludes that high concentration of organic matter and micronutrients preconditioned by the terrigenous income, good heating, and high primary production of phytoplankton and phytobenthos as the major reasons promoting such biodiversity in these biotopes. Only *Olpidium maritimum* Höhnk et Aleem and Thraustochytriaceae were found in the marine biotopes located far from the shoreline, at the depths of 70–75 m. The author suggested that all the other species found in the marine environment were transported here; they were euryhaline organisms inhabiting mostly brackish waters along the seashore. However, the publication is lacking the full list of the species found. Only description and distributional patterns of three Thraustochytriaceae species were presented (*Thraustochytrium pachydermum* Scholz, *T. aggregatum* Ulken, and *T. striatum* Schneider); these species were not cited in [34]. The author concluded the presence of both parasitic and saprotrophic fungi species found on algae and crustaceans, but the exact species definition was not performed for all the specimens, since it was impossible to track the life cycle for some of them.

The next publication of E.A. Kuznetsov [53] was devoted to the dormancy in fungi-like protists. The introduction chapter gives an overview on the ability of these organisms to stay alive and resist drying/freezing. Different species of Thraustochytriaceae and Chytridiomycetes were used for the experiments; these species originated from the White Sea (vicinity of WSBS) and from other seas. In addition, the fungi were sampled from the algae herbaria from different seas (including the White Sea). The article gives a detailed description of methods used, including original modifications. It was found that all the studied Thraustochytriaceae and most Chytridiomycetes might withstand drying and stayed alive for at least 10 years after. It was also found that strains sampled in the northern areas had a better chance. However, heating them up to +40°C during 10 min killed these organisms. *Saprolegnia* fungi withstood the drying with less success, and they remained alive for only 1 month. If the fungi were reared from the herbarium algae, the best germination rates were found for those that spent less than 8 years dried; the fungi from herbaria sampled more than 20 years ago were characterized by less success. Some isolates of Thraustochytriaceae and Chytridiomycetes from the White Sea stayed alive for at least one month of freezing, as was found experimentally. *Saprolegnia* fungi did not withstand freezing. The author concluded that the ability for dormancy at drying/freezing promoted a wide geographical range of the studied organisms. The original methods of preserving of Thraustochytriaceae and Chytridiomycetes were also described; these approaches are based on the ability of these fungi to withstand drying successfully.

Later, E.A. Kuznetsov continued studying the biodiversity and ecology of marine fungi-like protists. He defended a doctoral dissertation (Dr. habil.) [21], and became a coauthor of the catalogue [10] where the material of several dozens of years of his studies was generalized.

In the early 2000s, the studies of marine fungi were continued using state-of-the-art methods and approaches. The fungi inhabiting different marine ecotopes were the main objects of the study. Biodiversity was studied using rearing on the media, and the imperfect hyphomycetes, pycnidial fungi, zygomycetes, and ascomycetes were the focus group.

In 2009, the first publication [46] described these results. The publication covers the biodiversity of the fungi in the bottom sediments of Velikaya Salma Strait (figure). Ten samples were obtained in July 2006 from the depths of 54–108 m and reared on the agar media. The abundance of the fungi, as well as the number of the fungi propagules, was assessed; their concentration and frequency of occurrence were calculated. The number of the fungi propagules in the studied bottom sediments varied from dozens ($n \times 10$) to hundreds ($n \times 10^2$) per one cubic cm of the sediment and did not refer to any environmental characteristics (depth, bottom geomorphology, type of sediment, etc.). The mycobiota was quite diverse, and the distributional pattern was quite patchy. In total, 65 species of 24 genera were registered. Eight morphotypes were defined down to the genus level, most of the species were found only once and in certain samples. Several species dominated, *Geomyces pannorum* (together with isolate *Pseudogymnoascus roseus* that had sexual reproduction on the media; frequency of occurrence was 80%), *Penicillium chrysogenium, P. expansum, P. nalgiovense, Tolypocladium inflatum*, and *Trichoderma viride*. *P. chrysogenium* were the most abundant (15%). The author discussed the peculiarities of the fungi species composition in the studied biotopes, compared them to the similar environment in other geographic areas and to the soil mycobiota of the studied region. Particularly, it was found that the mycobiota of the studied bottom sediments was presented mostly by the eurybiont species (*Penicillium* spp.); high ratio of common or key species of soil phytocenoses was also registered (*Tolypocladium* spp., *Pseudogymnoascus roseus + Geomyces pannorum, Trichoderma* spp.). Only three obligate marine species were found, *Acremonium fuci, Dendryphiella arenaria*, and *D. salina*), and all the others were common for terrestrial biotopes. High abundance and diversity of *Acremonium* species was a feature of the studied bottom sediments.

The next publication [47] referred to the studies of the fungi communities on thalli of brown algae (*Fucus* spp.) from the coastal area of the White Sea, and the factors affecting the mycobiota structure and distribution. The research was performed in early August 2005 in the vicinity of WSBS. Six catenae were studied at three different types of the costal areas (open to the sea, semi-closed, and closed). The thalli of live *Fucus* were sampled in their typical biotopes, *F. vesiculosus* was sampled at the middle littoral zone, *F. distichus* was sampled at the lower littoral zone, and *F. serratus* was sampled in sublittoral (0.5-m depth). In addition, dead thalli of *F. vesiculosus* from the shore bar were analyzed. In total, more than 20 samples were taken for the analysis. The seeding of the seawater sampled at the same sites was also performed. The algae thalli were incubated on agar media. The abundance and frequency of occurrence was assessed; Sorensen-Chekanovsky index, hierarchical cluster analysis, and principal component analysis (PCA) were applied. In total, 21 species of zygomycetes, ascomycetes, and deuteromycetes were identified; 39 morphotypes were identified down to the species level, and four morphotypes were identified by the genus level. The maximal diversity was found on the dead thalli (25 species), and the minimal was found in the seawater (13). *Penicillium* genus comprised nine species, and it was also the most abundant (51% on average), followed by marine species of *Dendryphiella* genus (11%) and *Acremonium* (9%). It was also found that the mycobiota on thalli of live algae were relatively similar despite the algae species. The mycobiota of the dead thalli differed significantly from those observed for live specimens; the most pronounced differences were found for the seawater communities. The samples collected on the closed bays did not differ much; the fungi communities in the areas open to the sea differed among themselves and with the communities of the closed areas. The authors concluded that hydrodynamic regime (shore type and littoral zone) and algae type had the most pronounced effect on the structure of fungi communities inhabiting thalli of the brown algae.

In 2011, another publication [48] appeared; it was also performed at WSBS. The diversity of the fungi inhabiting the brown algae thalli on the surface and inside was studied for *Ascophyllum nodosum, A. nodosum* ecad *muscoides*, and *Pelvetia canalicula*. The sampling was performed in August 2006 and 2007 at three sites on Kindo Peninsula and one on Kokoikha Island. The thalli were incubated on agar media. The number of colonies of different morphotypes was counted; the correspondence analysis and PCA were applied. Thirty-three genera of zygomycetes, ascomycetes, basidiomycetes, and deuteromycetes were found; fifty morphotypes were identified at the species level, seven were identified at the genus level, and a significant number of different sterile mycelia were found. The mycobiota on the surface and inside thalli differed significantly. The mycobiota inhabiting the surface of thalli was presented by a common species of soil or marine saprotrophic fungi (*Penicillium, Dendryphiella*, and *Cladosporium*), but the "inner" mycobiota comprised specific species that were not found before in other biotopes. The numbers of the isolates of these species were relatively low; sterile isolates, *Cephalosporium*-like and *Cladosporium* genus, attracted much interest. The localization (thallus surface or inner part) had the most pronounced effect on the composition of mycobiota. The ecotope characteristics were also the limiting factors; the species of the algae had a minor effect on mycobiota composition.

In 2012, the most recent publication [54] on fungi studies in marine biotopes appeared. The study described the biology of *Stigmidium ascophylli* and the symbiotic fungi of brown algae *Ascophyllum nodosum* and *Pelvetia canalicula* found in the vicinity of WSBS. The life cycle of this symbiosis was tracked; it differed greatly from those observed in the warmer environments and was affected by the ice period present in the White Sea. For the first time, the differences in the strategies of forming de novo associations were found for *A. nodosum* and *P. canaliculata*. The life cycles were described and illustrated in detail. For the first time, the mycobionts were found in thalli of ecads (ecological forms), *A. nodosum* ecad *scorpioides*, and *A. nodosum* ecad *muscoides*. The taxonomical analysis of these endotrophic fungi comprised sequencing of ITS1-5.8S-ITS2 genes of fungi extracted from the algae thalli. Similar sequences were found for the fragments extracted from *A. nodosum* and *P. canaliculata*. It was supposed that this sequence belonged to *S. ascophylli*; it was obtained for the first time, and phylogenetic analysis was applied. The sequences extracted from *A. nodosum* ecad *muscoides* sampled at various sites differed from each other and belonged to two biotrophic species, *Neonectria fuckeliana* and *Plectosphaerella cucumerina*. The authors concluded that common symbiont, *S. ascophylli,* might disappear in uncommon biotopes for *A. nodosum* and might be replaced by aggressive eurybiont terrestrial species.

In 2012, O.P. Konovalova defended her Cand. Sci. (Biol.) thesis [19]. She gave an overview on mycobiota of *A. nodosum* and *P. canaliculata*, as well as the description of *S. ascophylli* biology referring to the earlier publications [48, 54]. In addition, physiological studies were performed to track the peculiarities of the growth of different isolated belonging to different taxonomical groups. A significant number of the colonies that could not be identified by standard methods were reared. For these colonies, molecular genetic analysis was performed, including phylogenetic analysis of ITS1-5.8S-ITS2 sequence performed for 15 *Cadophora*-like isolates, 13 *Alternaria*-like, and 37 *Acremonum*-like isolates. It was found that some of them could not be identified as any of recently known species. The author argued that a significant number of the new species existed in marine anamorphic fungi; these species did not have strong morphological differences due to the secondary simplification of the condial structures in the aquatic environment. New halophilic species, *Emericellopsis* sp.1, was reared and studied.

Presently, the studies of the fungi in marine biotopes continue.

The study of micromycete complexes at ecotone “sea-shore” is another topic of the research on fungi on WSBS. The first results obtained by M.V. Sogonov and O.E. Marfenina [37] referred to the mycobiota of salt marsh of the White Sea. The sediments and soil from different littoral zones were sampled at five catenae located at the seashore of different geomorphological types (accumulative, abrasive, and abrasive-accumulative) in Kiv Inlet and in the vicinity of WSBS in 1995–1996. The mycobiota was also studied for Al-Fe-humus ashen-grey soil in fruticulose-green moss pinewood. The succession of micromycete community was studied for the shore bar of lower supralittoral zone. Medium-rearing methods were applied. The abundance of mycelia in the soils was assessed on membrane filters (mg per 1 g of soil). In total, 47 fungi species belonging to 15 genera of zygomycetes and deuteromycetes were identified, and some isolates were identified at the genus level; sterile isolates were also found. The authors concluded that a specific type of mycobiota communities existed in salt marsh ecotopes; these communities differed significantly from those existing in the soils, both by taxonomic composition and by the abundance of mycelia belonging to different biomorphological groups. It was found that the species diversity and frequency of occurrence of genera *Penicillium* and *Mortierella* decreased in the row “zonal soil—salt march of the grasslands of the upper, middle, and lower levels,” the opposite pattern was observed for genera *Fusarium* and *Acremonium*. The species of the last genus (*A. persicinum* and *A. charticola*) dominated in the soils of the grasslands of the lower level; here *Embellisis annulata* and *Dactylella aquatica* were registered, and these two species were not found anywhere else. The soils belonging to different types of the shore were characterized by the diversity of the mycobiota structure and composition. The roots of the vascular plants had a great effect on the mycobiota community in the upper zone of littoral; the fungi were presented by a high number of micromycetes when cultivating the samples obtained from the near-root space. The fungi were totally absent in the soil samples taken between the weed beds. When studying the succession of the fungi community from the shore bars, it was observed that *Aspergillum* and *Fusarium* dominated at the beginning but they were replaced by *Penicillium* and *Acremonium* in the end. Dark-colored mycelia prevailed in all the types of the studied soils. The total abundance and biomorphological structure of mycelia changed greatly when moving seawards. The highest abundance and diversity of mycelia was usual for the zonal soils, while both parameters decreased significantly in the near-shore areas.

M.A. Shcheglov, O.E. Marfenina, and E.N. Bubnova continued these studies. M.A. Shcheglov found that the life activity of littoral invertebrates had a pronounced effect on the mycelia abundance in the studied soils. The middle littoral zone of the White Sea is inhabited by the lobworms *Arenicola marina*; these polychaetes process the sediments actively, and their population density may reach dozens of specimens per square meter. The sediments processed by these worms contain less mycelia, fungi spores, and bacteria. Probably, this is the consumption of the microbial biomass [38].

The Cand. Sci. (Biol.) thesis of E.N. Bubnova was devoted to tracking the changes of the complexes of micromycetes at the landscape gradient (from the terrestrial soils through the littoral ecotone to the marine ecosystems). In total, 132 species of fungi were found; most of them were hyphomycetes imperfecti. In the zonal ashen-grey soils, *Micromucor ramannianus* var. *ramannianus* (recent: *Umbelopsis ramanniana* (Müller W. Gams), *Pseudogymnoascus roseus* (and its conidial stage *Geomyces pannorum*), *Trichoderma* spp., and *Penicillium* spp. dominated. Species of *Fusarium* and *Acremonium*, dark-colored hyphomycetes, and sterile mycelia dominated in the soils of the seashore area. Species of *Penicillum, Cladosporium*, and *Mucor hiemalis* (and some others) dominated in the bottom sediments and the seawater. The freshwater influx increased the biodiversity of the littoral mycobiota by the transport of typical soil species; this promoted similarity of the species composition of fungi in the sediments of different types of littoral. A large number of different soil fungi were transported to the littoral area, but they did not survive there. The domination of particular species and genera of the soil fungi in the marine ecotopes was preconditioned by their resistance to the marine environment. The deuteromycetes were the most ecologically flexible, especially ascomycete-like species of the orders Pleosporales and Hypocreales.

The studies of mycobiota of terrestrial ecosystems have a long history at WSBS together with the studies of marine and littoral fungi and fungi-like protists.

The first study of terrestrial mycobiota was published in 1967 by E.S. Lisina and R.A. Maksimova [32]. The species composition and antagonistic features of the soil fungi were described for the mycobiota of the rhizosphere of some mosses, lichens, and vascular plants (legumes, gramineous, solanaceous, and orpine plants) usual for the White Sea coast. The sampling was performed in the vicinity of WSBS; the upper soil layer was analyzed. The soil suspension was reared in Petri dishes on Chapek medium (pH = 6). The fungi antagonism was studied by the method of agar blocks to several test objects, *Staphylococcus aureus* 209, *Escherichia coli, Neurospora sitophila,* and *Saccharomycetes cerevesiae*. Unfortunately, the plant species were not indicated in this publication but only the plant families, so it is hard to conclude now about the real environment of studied rhizosphere. For example, high biodiversity of legumes and gramineous plants is usual for the studied area, all of them inhabit different biotopes, including salt marshes, forests, etc. Three species of Crassulaceae are known for this area; two of them (*Sedum acre* and *S. rosea*) inhabit the sea rocks, and the third species, *S. decumbens*, is usual for kitchen gardens and in the settlement, i.e., they represent a different environment. Only one solanaceous species grows here, potato *Solanum tuberosum* [12]. The CFU (colony-forming units) number in the rhizosphere of mosses and lichens (8.3×10^3 CFU per 1 g of soil, for mosses) is ten times lower than in the rhizosphere of vascular plants. Generally, CFU increases accordingly to the concentration of organic matter and is maximal for agriculture soil, in potato rhizosphere (910×10^3 CFU per 1 g of soil). The authors defined several groups of fungi that corresponded to the rhizosphere of specific plants: fungi of *Penicillium* genus (section *Monoverticillata*) were the most abundant under the mosses, lichens, and orpine plants; *P. frequentans* (current: *P. glabrum* (Wehmer) Westling) and *P. thomii* were the key species. The species belonging to the section *Asymmetrica divaricata* were usually found in the rhizosphere of legumes. The species of *Fusarium* genus were typical for the rhizosphere of vascular plants (mostly gramineous plants); they were rarely found for mosses and lichens. After analyzing all the data presented in the publication, *Fusarium* species appeared to be most common for the soils under the lichens (7% by abundance) than under the legumes (3.5%), although they were the most abundant under the gramineous plants (22%); these species were not found at all under the mosses, solanaceous and orpine plants. Regard must be paid to the lowest number of fungi species (7) found under solanaceous plants, although CFU was the highest here. The most common species was *Hormodendrum hordei* Bruhne (recent: *Cladosporium hordei* (Bruhne) Hordei); this species is also abundant in the rhizosphere of gramineous plants. This species was not common in each soil type, as was *Isaria* sp. that was also found for gramineous plants. The maximal fungi diversity was found for the rhizosphere of mosses (17 species) and lichens (15 species); the lowest fungi diversity was found for vascular plants, when maximal number of species (9) was found for gramineous plants. The studies of the antagonistic characteristics revealed the minimal number of active forms for mosses and lichens and maximal (wide spectra of antibiotic activity), for rhizosphere of legumes. The authors concluded that high frequency of occurrence of the fungi of *Penicillium* genus (section *Monoverticillata*), under orpine plants (63.2%), mosses (44.7%) and lichens (25.3%), as well as low number of antagonistic fungi in this region, might be explained by the harsh temperature regime and low activity of microbiological processes. We would like to pay attention also to significant differences in species composition of soil fungi under particulate plants. Although the microenvironment for each studied plant was different and unknown (not described in the paper), it is hard to conclude now if this variability was preconditioned mostly by the environmental or other factors.

In 1976, the studies of soil fungi were continued at WSBS by T.Yu. Tolpysheva. She studied the effect of lichens (mostly *Cladina stellaris* and *Cladina mitis*) on the mycobiota of the soils in white moss pinewood, resulting as a number of publications [33–36] and candidate thesis [17]. The soils were sampled in Kandalaksha Nature Reserve (Velikii Island, opposite to WSBS) and at WSBS (Fig. 1).

In July 1973 and 1976, soil samples were obtained without regard to the lichen presence on Velikii Island and at WSBS [34]. Fifty-one fungi species belonging to 13 genera were found: three species of zygomycetes (two genera), one species (one genus) of imperfect coelomycetes, and all the others belonged to hyphomycetes. The most variability was found for genus *Penicillium* (29 species, 19 of them belonged to *Asymmetrica* section, nine belonged to *Monoverticillata* section). A large number of species belonging to *Monoverticillata* section (*Penicillum* genus) and to subsections *Velutina* and *Fasciculata* (section *Asymmetrica*) and a low number of *Mucor* species were preconditioned by the barren soil and harsh temperature regime. The most typical species (frequency of occurrence more than 60%) are *Penicillium fuscum* (recent: *P. velutinum* J.F.H. Beyma), *P. frequentans* (recent: *P. glabrum*), and *Trichoderma viride*. The common species (frequency of occurrence 40–60%) are *Trichoderma harzianum, P. raistrickii, P. purpurogenum, Aspergillus niger*, and *Mortierella* sp. The article provided, in table form, the full list of the species found, where the presence/absence (+/–) of the species in the soils of the studied sites were indicated, as well as the total frequency of occurrence. The author concluded that the species compositions of fungi at both sites were quite similar. The differences were explained by the presence of the rare species (frequency of occurrence less than 10%).

The next publication of the same author described the effect of the lichen on the species composition of fungi in the primitive soils [34]. The soil was sampled at four experimental sites with 100% coverage by the lichens (*Cladina stellaris* and *C. rangiferina* up to 70–80%; lingonberry, blueberry, foxberry, black crowberry, and erica up to 10–15%; other lichens, less than 10%) and at three control sites almost without lichen presence (fruticulose plants: 10–15%; lichens: less than 1%; other soil without plant coverage at all). The mixed soil samples were obtained from 8–10 sites under the lichens (*Cladina stellaris* and *C. rangiferina*), fruticulose plants (without reference to the species), and at plant-free soil. Forty species (or nonidentified morphotypes) of fungi belonging to eight genera were identified. *Penicillium* genus was the most diverse (20 species and eight nonidentified morphotypes). The total number of fungi species found under *Cladina* *stellaris* was 18, that under *C. rangiferina* was 21, that under fruticulose plants was 22, and that without any plants/lichens was 18 species. Differences were found for the fungi composition in the soils covered by the lichens, by the fruticulose plants, and without plant coverage. This was the most pronounced in *Penicillium* genus as the most diverse and common one in the studied soils. Particularly, the species representing the section *Biverticillata–Symmetrica* were not found for the soils covered by lichens. The ratios of the species representing the sections *Monoverticillata* and *Asymmetrica* in the soils sampled at control sites (under the fruticulose plants and without plan coverage) were nearly the same; but the number of species belonging to *Asymmetrica* section was 1.5 times higher than the species number in *Monoverticillata* section in the soils covered by lichens. The total number of *Penicillium* species in the soils covered by lichens exceeded the species number obtained for control sites by 30%. All the identified fungi species were grouped as: (1) absent under the lichens, but found at control sites (12 *Penicillium* species and *Rhinocladiella elatior*); (2) species found exclusively under the lichens (*Aspergillus fumigatus, Mucor racemosus*, and ten species of *Penicillium* genus); and (3) fungi species common for both experimental and control sites (*Aspergillus niger, Humicola* sp., *Mortierella ramanniana* (recent: *Umbelopsis ramanniana*), *Mortierella* sp., *Oidiodendron tenuissimum, Trichoderma harzanium, T. viride*, and six species of *Penicillium* genus). Sterile mycelia were indicated for group nos. 1 and 2. The corollary of the article was "the lichens have a significant effect on soil micromycetes and their species composition in the pine-woods, but the way of this differentiation is still unknown."

The third publication is entirely experimental, and the effect of lichens on the soil colonization by fungi is studied [35]. The experiments were performed in natural conditions (lichen-covered pinewood) on Velikii Island. The soil was sampled at the sites without plant/lichen coverage at 0–2-cm depth; the plant remains were removed, and the soil was screened and triple sterilized. The sterile soil was placed onto flat sterile boxes with small holes in the bottom and put at the soil level in the lichen-covered pinewood. Some of the boxes were covered by the lichens. The experiment took one year, starting from late July. After a year passed, the soil was taken out from the box and studied for mycobiota. In total, 15 boxes were analyzed: five were covered by *Cladina stellaris*, five by *C. rangiferina*, and the last five were control (without coverage). The total fungi CFU per 1 g of soil was 72.1×10^3 under *C. stellaris,* 56.1×10^3 under *C. rangiferina*, and significantly lower, 7.7×10^3, at the control sites. The species of *Penicillium* were the least presented in the last type (approximately 60%), the soil covered by lichens was characterized by a higher number of species (90% under *C. stellaris* and >80% under *C. rangiferina*). In total, 33 species of fungi were defined; 19 of them belong to *Penicillium* genus. The number of the species that appeared under *C. stellaris* was 15, that under *C. rangiferina* was 22, and 21 species were found in the control boxes. Eight species were common for all three treatments, *Cladosporium herbarum, Mortierella ramanniana* (recent: *Umbelopsis ramanniana*), *Penicillium frequentans* (recent: *P. glabrum*), *P. fuscum* (recent: *P. velutinum*), *P. raistrickii, Penicillium* sp. 9, and *Trichoderma harzianum, T. viride*. The similarity between the soils covered by *C. rangiferina* and the control sites was assessed by the ratio of *Penicillium* species, when the number of the common species was 11; the ratios between the species of the sections *Monorticillata* and *Asymmetrica* were equal in both cases, and the representatives of the section *Biverticillata–Symmetrica* were found in both treatments. The soil under *C. stellaris* contained less species of *Penicillium* (nine), and the ratio between *Monorticillata* and *Asymmetrica* was 2 : 1, and total absence of the species belonging to *Biverticillata–Symmetrica* was observed. Two experimental (lichen) treatments differed from each other more than compared to the control sites. For example, the abundance of *Penicillium frequentans* (recent: *P. glabrum*) was 40–50% in both experimental treatments and twice less in the control. Similar pattern was observed for the species *P. fuscum* (recent: *P. velutinum*) and *P. raistrickii*, when both species were more abundant in the experiment than in the control. Such a difference in the fungi species composition was explained by different competition ability of the fungi species and by the lichen metabolites that might affect the mycobiota (or the absence of such effect in the control). The author concluded that "Probably, the lichen metabolites may support the microenvironment, which is favorable for some fungi species that appear to be more competitive." However, no analysis on lichen metabolites was presented.

The last publication from this series [36] described the study of effect of the lichens *Cladina stellaris* and *C. rangiferina* on the abundance of the soil mycobiota in the natural sites. The sampling was performed under the lichens, the fruticulose plants, and at the sites free of plants. The total CFU per 1 g of air-dry soil was assessed, as well as CFU of certain species and genera. The total CFU range fell to $n \times 10^3$. It was maximal under the fruticulose plants and minimal under the lichens (1.5–2.0 times difference). *Penicillium* genus was the most abundant: from 57% at plant-free sites to 75% under *C. stellaris*. High abundance was registered for *P. fuscum* (recent: *P. velutinum*): from 12% under *C. stellaris* to 30% under fruticulose plants; as well as for *Trichoderma viride*: from 4% under *C. stellaris* to 26% under fruticulose plants. The author concluded that there was a significant effect of the lichen/plant coverage on the number of fungi diaspores in soils, both on total CFU and on CFU of particular species and genera.

After a long gap, the next publication by E.N. Bubnova and L.L. Velikanov appeared [40]; it described the mycobiota in different soil types in the vicinity of WSBS. The sampling was performed in August 1998 and 1999 in the upper under-soil layer (A0, A0/A2). The study focused on marsh turf under marine herbpoaceous meadow and zonal Al-Fe-humus ashen-gray soil in four plant associations. The method of serial dilution and rearing on agarose media was used. The abundance (CFU) and frequency of occurrence of different fungi species were assessed; these data were then used to calculate the Shannon index and similarity coefficient of Sorensen–Chekanovsky. The abundance of light- and dark-colored mycelia (m) was assessed per 1 g of air-dry soil. The mycelia abundance was 180–220 m/g in fruticulose-green moss pinewood up to 600–730 m/g in lichen pinewood. The ratio of dark-colored mycelium was 20–52% of total biomass. Total CFU was $27.5–72.5 \times 10^3$ per 1 g of air-dry soil. In total, 65 fungi species belonging to 20 genera of zygomycetes and fungi imperfecti were identified; some isolates were identified only at genus level, and a significant number of sterile isolates was found. *Penicillium* genus was the most abundant and diverse (abundance ratio of 21.0–68.5%; frequency of occurrence of 90–100%). It was found that the representatives of *Monoverticillata* section prevailed under the lichens in pinewoods; in the other ashen-gray soils, they were replaced by *Asymmertica* section. The soils of marine meadows contained less *Penicillium* species than ashen-gray soil did. In the meadow soils, the species of several genera—*Acremonium, Paecilomyces, Verticulum*, and *Fusarium*—dominated. The representatives of genera *Paecilomyces, Verticulum,* and *Fusarium* were also found in the herb-covered soils of the secondary birch-tree wood. The most similar fungi complexes belonged to the soils of fruticulose-green moss pinewood and lichen pinewood; the complex of micromycetes of the meadow soil differed significantly from these two.

Presently, the studies on the soil mycobiota are not performed at WSBS MSU.

During several years, the studies of deep soils and sediments were performed at WSBS together with research of the covering soils [42]. The presence of viable microfungi in the deposited marine sediments of approximately 10000 years old was searched. These sediments lay deeper than 2 m, and they are covered by an interlayer of sand, gravel, and marine silt. These deposited organogenic silty sediments contain the shells of the marine bivalves *Tridonta borealis* (Schumacher, 1817), *Hiatella arctica* (L., 1767), *Elliptica elliptica* (Brown, 1827), and brachiopod *Rhynchonella psittacea* (Gmelin, 1792). These ancient deposited sediments contain the complex of viable fungi. However, their abundance is quite low (single spores, direct counting). When rearing on the medium, the number of CFU per 1 g of sediment was $24.1 \pm 3.2 \times 10^3$ in the upper sediment layer, and only $0.8 \pm 0.3 \times 10^3$ in the deposited sediments. However, despite low abundance, this deposited sediment and upper layers contained a variety of micromycetes. The presence of dark-colored fungi, especially *Cladosporium* (*C. cladosporoides, C. sphaerospermum*) and *Aureobasidium*, was a feature of this ancient deposit, which lacked a number of *Penicillium* species (typical for modern coniferous biogeocenoces) up to the layer that contained the remains of invertebrates. Many fungi species typical for the forest soils of the studied region and for the freshwater runoff and littoral deposits were present in the ancient layer, which might be linked to the transport of these fungi though the layers. For example, we have found the edificator of the ashen-grey soils, *Umbellopsis ramanniana* and *Pseudogymnoascus roseus* and *Trichoderma* species, as well as various *Penicillium* species (*P. janczewskii, P. thomii, P. implicatum*, et al.).

The other type of the soil profile was studied for the areas where the surface soil layer was deposited relatively recently. This profile was studied in the vicinity of a power transmission line, which was built after the WSBS was founded. The ex-upper layer is located now at a 1-m depth, and it is covered by the sands; the upper layer is a newly formed thin layer of illuvial-iron ashen-grey soil. Opposite to the covering layers, the mycelia of different types were present here in the buried deposit, particularly, dark-colored, thick light-colored, thin light-colored with nodules, thin dark-colored (probably, of porosporous fungi), and *Fusarium* spores. In addition, when rearing on the media, the composition of dominant species was different for the buried sediments (*Mucor hiemalis* and dark-colored *Cladosporium* spp. and *Alternaria* spp., usually common for the substrates rich by organic matter) and for the sand interlayer (*Penicillium simplicissimum, P. expansum, P. chrysogenum*, and *Peacilomyces lilacinus* (recent: *Purpureocilium lilacinum* (Thom) Luangsa-ard, Hywel-Jones & Samson)). In the buried deposits, the *Penicillium* genus was present by the other species, *P. brevicompactum, P. viridicatum* (recent: *P. aurantiogriseum* Dierckx), *P. janczewskii* and some others, psychrotolerant *Geomyces pannorum*, and atypical for the northern areas *Aspergillus versicolor*. These data evidenced to viability of active fungi complexes at significant depth for a long time period.

In 2007, a new study of micromycetes of the peat of the acid bogs was launched by O.A. Grum-Grzhimaylo. After the first year of study, thirty-two anamorphous fungi (Ascomycetes) and eight types of sterile mycelia were identified. Most of the anamorphous ascomycetes belong to *Penicillium* genus, sections *Monoverticillata* and *Biverticillata–Symmetrica* (*P. funiculosum, P. glabrum, P. spinulosum, P. thomii*, etc.). The species belonging to the genera *Oidiodendrum, Tolypocladidum*, and *Geomyces pannorum* were found quite frequently, as well as sterile mycelia. Generally, the species diversity and abundance of the viable forms in the peat was relatively low; however, the peat of the acid bogs was characterized by a specific structure of the micromycete complexes, as was observed both for the species diversity and for abundance [49].

The candidate of science thesis of O.A. Grum-Grzhimaylo [20] describes the mycobiota of bogging waterbodies of Kindo Peninsula; these waterbodies are at different stages of separation from the sea. For the first time, the complex study of the fungi was performed for the peat and silts of the nearshore bogs of different stages of bogging and freshening. The sampling was performed in five distinct lakes (Fig. 1): Verkhnee Lake (87 m above sea level), Krugloe Lake (27.5 m), Verkhnee Ershovskoe Lake (4 m), Nizhnee Ershovskoe Lake (3 m), and Kislo-Sladkoe Lake (1–2 m). Molecular-genetic methods (ITS and LSU sequencing) were used together with rearing on the media. This allowed identification of many uncertain colonies and finding totally new fungi species. In total, 328 species were identified, and fungi imperfecti dominated. In the sphagnum peat of all the studied lakes, the dominant species belonged to the genera *Penicillium, Cladosporium, Thichoderma, Oidiodendron*, and anamorphous fungi of *Cordyceps* genus. However, the species composition differs for the bottom silts of each studied lake. The common species were *Tolypocladium inflatum, Penicillium funiculosum, Tricgoderma hamatum*, and *Th. polysporum*. The prevalence of the sterile mycelia and dominance of the species common for marine habitat (*Acremonium potronii, A. strictum*, and *Emericellopsis minima*) was a feature of the silts; these forms were found in silts. The peculiarities of the structure of micromycete complexes were also described in regard to the distance from the sea and the bogging stage. The analysis of growth of several cultures at different pH was also performed, as well as in regard to different sources of organic carbon and under hypoxia.

This scientific direction is ongoing.

Therefore, presently, WSBS MSU is a small territory, where the variety of mycobiota is studied for different areas, from the soils, littoral, and bogs. Several groups are studied in details; these are medium-reared imperfect hyphomycetes, coelomycetes, zygomycetes, ascomycetes, and some groups of fungi-like protists.

The fungi of the freshwater pools and streams are not so well studied in the vicinity of WSBS. The same words may be applied to the nonsoil terrestrial fungi (parasites of vascular plants, xylotrophic fungi, on-soil macromycetes). The annotated lists of the freshwater and on-soil groups of fungi are presented in the candidate of science dissertation of E.A. Kuznetsov [21] and in the "Catalogue of Biota of White Sea Biological Station of MSU" [10] according mostly to his data.

The only publication refers to agaricoid basidiomycetes, presented in the "Proceedings of WSBS MSU" [44]. The annotated list of 110 species of agaricoid basidiomycetes belonging to 41 genera and 15 families comprises the samples obtained in July–September 1992 and July–August 1998–2000; this list is presented in the "Catalogue of Biota of White Sea Biological Station of MSU" [10]. In the vicinity of WSBS MSU, one more study was performed (Velikii Island) [55]. This publication comprises the annotated list of basidiomycetes, terrestrial ascomycetes, and fungi imperfecti.

The studies on the lichens are also lacking. In 1967, T.Kh. Piyn presented the annotated list of fruticose and foliose lichens sampled on Kindo Peninsula and Velikii Island [45]. The data on the crustose lichens were not published. These results, together with the personal data of T.Yu. Tolpysheva, were combined in the list of the lichens presented in the "Catalogue of Biota of White Sea Biological Station of MSU" [10]. In 2007, a small study on the lichen ecology was performed at WSBS, where the effect of the distance from the seashore was studied for the abundance of the epiphyte lichens [56]; this publication also comprised the species list.

The list of fungi and fungi-like protists found in the vicinity of WSBS is long and comprise different taxonomical groups (Tables 1, 2). Several studies resulted as the combined list of the soil mycobiota [18, 32–36, 38], and the dominant fungi species were identified; the effect of the plant/lichen coverage was studied for the species composition of soil fungi. The other publications [18, 37, 38] covered the issue of the fungi complexes in the soils of the meadow cenoses. In the sea, the bottom sediments [18, 29, 34–36], macrophyte algae [15, 18, 38, 47, 48, 50–52] and invertebrates [52] were analyzed.

Regard must be paid to the northernmost location of WSBS when speaking about the mycological studies in the seashore areas. This area is one of the most studied one in the world. The other marine regions where the fungi complexes were studied is situated in the Far East seas [57–59], the Black Sea [22, 60] (Soviet and post-Soviet territories), and tropical and sub-tropical seas [61, 62]. The only study describing the new species of pycnidial fungi *Septoria ascophylli* Melnic et Petrov inhabiting the marine brown macroalgae *Ascophyllum nodosum* was performed by marine mycologists in the White Sea outside WSBS [63]. However, WSBS MSU is the only laboratory in the world where the complex studies of fungi inhabiting marine, shore, and terrestrial environments is performed simultaneously.

Presently, the ability of laboratory-reared imperfect hyphomycetes to form specific complexes in the marine ecotopes and in the zonal soils is proven [18, 37, 38]. *Geomyces pannorum, Penicillium* spp., *Umbellopsis ramanniana, Trichoderma* spp. dominate in zonal Al-Fe-ashen-gray soils, which is a common feature of this soil type. *Acremonium* spp., *Fusarium* spp., dark-colored *Dendryphiella* spp., *Alternaria* spp., and *Phoma* spp., and sterile mycelia prevail in marine habitats. Among the marine fungi, many species reared in the laboratory are still unidentified [19, 20, 48]. That is why the next step in the mycological studies belongs to the finding and identification of hardly laboratory-reared species, inhabiting different environments, by the molecular-genetic analysis, since the marine habitats are the place of the potential biodiversity of unknown mycobiota.

The future studies of marine biotopes, i.e., the vertical distributional pattern of fungi from the surface to the bottom sediments, the places of their high abundance, and their relationships with marine flora and invertebrate fauna, are of the great interest. The data on terrestrial ecosystems in regard to the fungi are also lacking, for example, the epiphyte fungi complexes, the first colonizers of rock substrates, and some functional groups of fungi are not yet studied. The unique possibility to conduct complex studies at WSBS MSU, together with the scientists exploring other fields of biology, and in the natural environment, close to the objects of the study, using state-of-the-art scientific facilities provided at the station, lead us to conclude that there is a good perspective for future studies and interesting results.

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