Arctoa (2015) **24**: *210-215*
doi: 10.15298/arctoa.24.21

THE ECOLOGICAL AND PHYTOCENOTIC PREFERENCES OF *DICHELYMA CAPILLACEUM* (FONTINALACEAE, BRYOPHYTA) IN WEST SIBERIA

ЭКОЛОГИЧЕСКИЕ И ФИТОЦЕНОТИЧЕСКИЕ ПРЕДПОЧТЕНИЯ *DICHELYMA CAPILLACEUM* (FONTINALACEAE, BRYOPHYTA) В ЗАПАДНОЙ СИБИРИ

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Abstract

Ecological conditions and phytocenotic characteristics of *Dichelyma capillaceum* habitats in the Nature Park "Kondinskie Lakes" (Khanty-Mansiysk Autonomous District, West Siberia – 60°54' N; 63°30' E) are described based on a geobotanical survey. Unlike the previous finds of *Dichelyma capillaceum* in Russia this locality is represented by several collections and multiple records of the species. Nineteen vegetation relevйs with *Dichelyma capillaceum* are analyzed. It is noted that the habitats of this species in West Siberia are similar to those in Western Europe. The habitats in both Europe and Siberia have a strongly variable water level (amplitude up to 1.0 m). The main distinctions are the low amounts of nutrients in river and lake waters in Siberia (nitrogen: NO_3^-=0.32-0.76 mg/l, NO_2^-=0-0.06 mg/l, NH_4^+=0.6-0.8 mg/l; phosphorus: PO_4^{3-}=0.05-0.15 mg/l), the low mineral levels (total sum of ions is 32.7 – 43.7 mg/l), and the relatively acid water (pH=5.1-5.8). The collections from the study area lack sporophytes. However, the frequency and abundance of *Dichelyma capillaceum* in suitable habitats suggests that the asexual reproduction is rather efficient, which allows us to assume a wider distribution of the species in West Siberia.

Резюме

Сообщается об особенностях произрастания и экологических условиях местообитаний *Dichelyma capillaceum* в природном парке «Кондинские озера» (Ханты-Мансийский автономный округ, Западная Сибирь – 60°54' N; 63°30' E). В отличие от всех предыдущих находок *Dichelyma capillaceum* в России это местонахождение представлено многократными сборами и регистрациями вида. Приведено 19 полных геоботанических описаний растительных сообществ с участием *Dichelyma capillaceum*. Отмечено, что в целом местообитания и характер произрастания этого вида мха в Западной Сибири сходны с таковыми в Западной Европе. Общим является довольно большая амплитуда перепада уровня воды (до 1.0 м). Основное отличие заключается в крайней бедности речных и озерных вод биогенными элементами (азот: NO_3^-=0.32-0.76 mg/l, NO_2^-=0-0.06 mg/l, NH_4^+=0.6-0.8 mg/l; .фосфор: PO_4^{3-}=0.05-0.15 mg/l) и их низкой минерализации (общая сумма ионов 32.7 – 43.7 mg/l) при слабо кислой реакции среды (pH=5.1-5.8). Спорофитов мха в районе исследования не обнаружено. Однако, судя по частоте встречаемости и обилию *Dichelyma capillaceum* во всех подходящих по условиям произрастания растительных сообществах, вегетативный способ размножения является весьма эффективным, что позволяет ожидать более широкое распространение этого вида в Западной Сибири.

KEYWORDS: *Dychelyma capillaceum*, ecology, habitat, vegetation community, West Siberia, Russia.

Introduction

Until recently *Dichelyma capillaceum* was referred to the group of boreal species with a well-defined amphi-atlantic distribution (Toivonen, 1972; Hedenäs *et al.*, 1996). Further floristic explorations in the European part of Russia and West Siberia expanded the distribution of this rare European species to the East (Czernyadjeva & Ignatova, 2013).

The species is widespread in the boreal zone of eastern North America (Ireland *et al.*, 1987; Ireland, 1989). In a number of Canada's provinces, such as Nova Scotia, it is frequent, though in most of the densely populated areas of the USA and Canada it is considered to be vulnerable, endangered, or even critically endangered. *Dichelyma capillaceum* is a rare species in Europe. It is included in the Red Data Book of European Bryophytes (Schumacker *et al.*, 1995) and in the Red Data Book of East Fennoscandia (Kotiranta *et al.*, 1998). The species is distributed in southern and central Sweden where about 150 locations have been discovered (Hylander, 1998; Hallingbäck, 2010). Only scattered records are known from other areas of Western Europe (Schumacker *et al.*,

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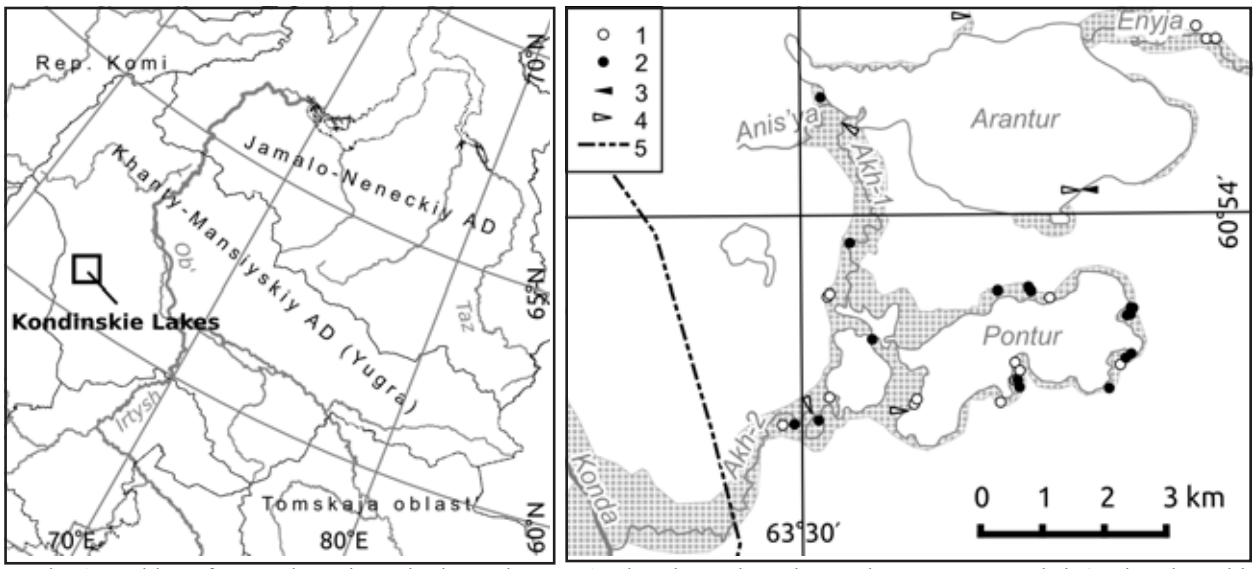

Fig. 1. Position of vegetation relevйs in the study area: 1 – locations where the species was not recorded; 2 – location with *Dichelyma capillaceum*. Location of the ecological monitoring points: 3 – measurement of water level; 4 – hydro-chemical research. 5 – Western boundary of "Kondinskie Lakes" Nature Park.

1995), and in most of these it is critically endangered (Bensettiti *et al.*, 2002; Ludwig & Weddeling, 2003).

The main factors that restrict the dispersal of the species and which threaten its occurrences are the regulation of rivers, preventing the natural flooding of river floodplains and surface water pollution (Schumacker *et al.*, 1995). The development of action plans to protect the habitats of *Dichelyma capillaceum*, and to provide the ecosystem services of wetland woods (Wetterin, 2004), requires further knowledge of its optimal ecological conditions and phytocenotic preferences (composition and structure of plant communities), that is, where this species occurs with high frequency and abundance.

The current records and moss floras provide only brief information about the ecology of the species (Schumacker *et al.*, 1995; Kotiranta *et al.*, 1998; Bensettiti *et al.*, 2002; Ludwig & Weddeling, 2003; Czernyadjeva & Ignatova, 2013); they state that the species is typically found in flood valley habitats represented by woods. It occupies rocks, the base of trees and shrubs, roots and tree branches near water courses, the banks of lakes, ponds and slow rivers with high amplitude of the water level (annual variation between 0.6-1 m) (Hedenäs *et al.*, 1996; Hylander 1998). Most localities are periodically flooded by water poor in nutrients, but it can also be found in more eutrophic conditions at relatively high pH levels, between 6.5 and 7.0 (Ludwig & Weddeling, 2003).

In terms of its phytocoenotic preference in Europe the species relates to the ***Alnion glutinosae*** alliance – alder and willow woods and carrs from submeridional (nemoral) to boreal regions and to the ***Alnion incanae*** alliance which includes submeridional (nemoral) and hemiboreal deciduous woods in the south of Europe.

In West Siberia two locations of *Dichelyma capillaceum* are known. The first was found at the Vah River which is a right tributary of the Ob River (Czernyadjeva, 2002). The second location was discovered by the author together with E. Muldiyarov and I. Filippov in 2006 on the territory of the Nature Park "Kondinskie Lakes" about 1000 km to the west of the first finding (Czernyadjeva & Ignatova, 2013). Both sites are located approximately at the same latitude in the Ob River basin in the middle taiga sub-zone. Compared with the previous findings in Russia the location of *Dichelyma capillaceum* in the Nature Park "Kondinskie Lakes" is represented by multiple records made in the course of a geobotanical investigation of the Park area. This allows a more detailed evaluation of the ecological patterns and phytocoenotic preferences of this species.

Study area

The Nature Park "Kondinskie Lakes" is located in the eastern part of the upper Konda River basin, which is a left tributary of the Ob River (Sovetskiy sub-district, Khanty-Mansiysk Autonomous District – 60°54' N; 63°30' E). The area of the park is 43900 ha.

During the quaternary period, the region was affected by several glaciations. Landforms of glacial material are therefore widespread, with altitudes varying from 70 to 170 m above the sea level. The park area includes moraine hills and ridges that rise 15-20 m above the surrounding lands (Kalinin, 2012).

After de-glaciation the main land-forming factor was streaming waters that formed the fluvial land forms connected with the activity of the Konda River and its tributaries. A distinctive feature of the study area is its large lake basins, lowlands and ancient ice marginal valleys that are now occupied by numerous peat bogs. Among the remains of the ancient hydrological network is the picturesque lakes system with flowing-through water consisting of the lakes Arantur, Pontur, Lopukhovoe and Krugloe (Fig. 1).

The area has a continental climate with cold winters and warm summers (Lapshina & Maksimov, 2014) according to measurements of the Sovetskiy town Weather Station.

The hydrological network is represented by the left-bank tributaries of the Konda River. The main sources of rivers and lakes are melt-water from snow (42% of annual flow), rainfall (25%), and ground (incl. peat bogs) water (33%) (Kalinin, 2012). The Konda River basin contains extensive peat land areas that cause a slow decline after the maximal high-water level, which can last for up to 3.5 months. Numerous lakes connected with river valleys and filled with large volumes of water at prolonged flooding periods are natural drain regulators. The biggest lakes of the system are the Arantur (11.1 km^2) and the Pontur. The small rivers – the Akh, Anisya, Eniya, and Okunevaya – are characterized by pronounced backwater from the side of high water levels in the Konda River.

The vegetation of the Nature Park is represented by forests (40.2%), bogs (51.98%) and shrub-meadows (0.1%). Most of the area is covered with Scots pine (*Pinus sylvestris*) forests, rain-fed raised bogs, and to a lesser extent with poor fens.

MATERIAL AND METHODS

In the course of the geobotanical study due consideration was given to get complete lists of mosses and liverworts, and collections of bryophytes were taken at each relevй site for identification in laboratory.

All specimens are kept in the Herbarium of the Yugra State University (Khanty-Mansiysk, Russia), duplicates of three specimens of *Dichelyma capillacea* are kept in MHA and of some liverworts in KPABG. The nomenclature of vascular plants follows Cherepanov (1995), that of mosses Ignatov, Afonina, Ignatova *et al.* (2006), and that of liverworts Konstantinova *et al.* (2009).

RESULTS

In total 530 geobotanical relevés were made, mainly of the mire vegetation; in 19 of them *Dichelyma capillaceum* was found (Table 1). All the relevés with *Dichelyma capillaceum* are from the zone of spring flooding around the lakes (Pontur, Krugloe, Lopukhovoe), the estuary part of the Anisya river where it flows into the Arantur Lake and the flood plains of the Akh river, connecting all the mentioned lakes with the Konda river (Fig. 1). The total flooding area around the lake system of Arantur – Pontur and the valley of the river Akh that connects them, including the estuary portions of small rivers valleys, comprises 800 ha.

The dominating vegetation types of the area, ordered according to increasing height above the water table, are as follows: (i) – swampy sedge and sedge-*Sphagnum* birch woods, (ii) – willow bushes (*Salix cinerea, S. pentandra*) where birch trees are sparsely distributed, (iii) – sedges (*Carex aquatilis*) and ribbon grass (*Digraphis arundinacea*) moist meadows with sparse willow shrubs. A narrow zone at the lake banks consists in some parts of *Salix lapponum* and *Frangula alnus* shrubs.

The distribution of *Dichelyma capillaceum* is limited to the two highest levels occupied by dense birch communities (ass. ***Carici aquatilis-Betuletum pubescentis*** ass. nov. prov.) and willow shrubs (ass. ***Sphagno fimbriati-Salicetum cinereae*** ass. nov. prov.), more rarely buckthorn (***Frangula alnus*** community) with sparse birch trees.

The tree layer of the flooded forests consists entirely of *Betula pubescens* of 6-8 (10) m tall. A rare shrub layer, if any, is represented by *Frangula alnus*, *Salix cinerea* and the dwarf shrub *Chamaedaphme calyculata* on hummocks. The herb layer is dominated by *Carex aquatilis* with a small admixture of *Calamagrostis purpurea, Carex chordorrhiza, Naumburgia thyrsiflora* and *Comarum palustre*. In terms of composition and structure of the moss cover the communities of flooded birch woods (ass. ***Carici aquatilis-Betuletum pubescentis)*** are divided into three subassociations (Table 1): ***sphagnetosum fimbriati***, ***sphagnetosum fallacis*** and ***typicum***.

Subassociation ***sphagnetosum fimbriati*** is widespread in the flooding area around Pontur lake and is characterized by appreciable participation in the ground layer of peat mosses – *Sphagnum fimbriatum, S. fallax* (Table 1, columns 6-13). Further away from the lake shore the percentage ratio of these species is shifting to *Sphagnum fallax*. Birch woods with absolute dominance of *Sphagnum fallax* in the ground layer (subassociation ***sphagnetosum fallacies***) occur on sites where the lake basin borders with rain fed raised bogs with pine-dwarf shrubs-*Sphagnum* vegetation (Table 1, columns 14-19). These communities develop on a shallow peat layer, 20-50 cm deep.

Both these subassociations are characterized by a similar list of additional moss and hepatic species. In the ground layer a small admixture is formed by *Polytrichastrum longisetum*, more rarely by *Sphagnum squarrosum* and *S. centrale*. On fine alluvium, as well as on humus and peaty soil, *Pohlia nutans, Oncophorus wahlenbergii, Calliergonella lindbergii, Gymnocolea inflata, Scapania irrigua,* and *Aulacomnium palustre* can be seen. In small pools and hollows *Warnstorfia fluitans, Leptodictium riparium,* and *Calliergon cordifolium* are found. At the bottom of trees, on decaying trunks and dead fallen wood pure and mixed mats are formed by *Callicladium haldanianum* and *Sanionia uncinata*. A distinctive group consists of *Dichelyma capillaceum* and accompanying epiphytes growing at the base parts of birch trunks and limited by the height of the annual flooding (30-50 cm). *Dichelyma capillaceum* grows in the form of pure mats without admixture of other bryophytes or mixed with *Myrinia pulvinata* and *Leskaea polycarpa*.

The flooded shrub communities with sparse birch trees (Table 1, columns 1-3) and swampy sedge birch woods (subass. ***typicum***) (Table 1, columns 4-5) are developed in the Akh River valley in areas affected by longer periods of flooding. They are characterized by the lack of a dense ground moss layer and hardly any mesophyte and mesohygrophyte moss species. An exception is *Dichely-*

Table 1. Phytocoenotic table of vegetation relevés with *Dichelyma capillaceum*. Vegetation communities: 1-2: Ass. ***Sphagno fimbriati-Salicetum cinereae***; 3: ***Frangula alnus*** community; 4-19: Ass. ***Carici aquatilis-Betuletum pubescentis***, 4-5: subass ***typicum,*** 6-13: subass. ***sphagnetosum fimbriati***, 14-19: subass. ***sphagnetosum fallaces***.

Relevé numbers	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
trees, %	15	15	10	65	65	55	45	55	80	80	60	75	50	65	70	80	75	70	80
shrubs, %	55	40	70		5	5		2	10										
herbaceous, %	60	30	30	20	30	30	40	30	30	25	30	40	25	15	20	5	25	15	10
mosses, %	1	5	20	30	10	40	35	45	50	60	40	70	95	70	70	95	75	100	100
Vascular plants																			
Betula pubescens	15	15	10	65	65	55	45	55	80	80	60	75	50	65	70	80	75	70	80
Salix cinerea	40	30			3			1	10										
Frangula alnus		5	70			2	10	1	1										
Chamaedaphne calyculata						+	1	+					+			+		+	+
Carex aquatilis	15	10	10	15	5	15	5	10	15	20	25	20	20	15	1	5	25	15	10
Calamagrostis purpurea		10	5	+	20	10	5	10	10	5	+	20	5	+	20	+			
Carex vesicaria	10		10		5	5	25	5	5		1						1		
Carex chordorrhiza						1	2	1			+		+		+				
Carex canescens						+	2		1										
Naumburgia thyrsiflora		5		1	1	+		1	1		+				+			+	
Comarum palustre	20	10		5	5	+					1		1		+				
Juncus filiformis			3				1		+										
Bryophytes																			
Ground cover																			
Sphagnum fimbriatum	+	5	15	30	10	25	10	40	40	20	10	10	15	5	1				
Sphagnum fallax		+				5	15	10	15	40	30	60	75	70	70	90	70	100	100
Sphagnum squarrosum		+				5		+			1								
Sphagnum centrale							5	3			+								
Polytrichastrum longisetum		+	1			1	1	+	3	+				+		+	+		+
Warnstorfia fluitans	+	1				1	+	1	+			+			+	1		+	
Calliergonella lindbergii	+		3	+	1	1								1					
Leptodictium riparium							1			+			1	+		+		+	+
Calliergon cordifolium		1					+	+	1			+		+	+		+		
Aulacomnium palustre						+		+					+						
Pohlia nutans				+		+	+	+	+	+	+	+	+		+		+	+	
Oncophorus wahlenbergii									+	+	+		+					+	+
Gymnocolea inflata						2	+	1	+	+		+	3	1		1	+	1	+
Scapania irrigua		+				+	+	+	+				1	+			+		
Schljakowia kunzeana						+							+					+	
Epiphytes																			
Dichelyma capillaceum	+	**1**	**1**	**5**	**3**	+	+	+	**1**	**1**	**1**	**10**	**1**	**3**	**1**	**1**	**5**	**1**	**1**
Callicladium haldonianum						+			+	+	1	1	1	1		1		1	1
Sanionia uncinata					1	1	+	+	+	+	1	1	1	1		1	1	+	1
Myrinia pulvinata						+	+		+	+	+	+	1	+	+	+	+		+
Leskaea polycarpa			+												+				+

Other vascular plants: *Agrostis stolonifera* (2 +), *Calla palustris* (13 +), *Carex rostrata* (11 5), *Equisetum fluviatile* (1 1; 2 +), *Galium palustre* (2 1), *G. trifidum* (2 +), *Ledum palustre* (6 +; 7 1), *Lysimachua vulgaris* (3 +), *Lythrum salicaria* (1 1), *Rumex aquatilis* (2 +), *Salix pentandra* (2 5), *Salix rosmarinifolia* (1 5), *Scutellaria galariculata* (3 1), *Stellaria palustris* (2 +), *Vaccinium uliginosum* (6 +).

Other bryophytes: *Bryum elegans* (6 +), *Calliergon giganteum* (14 +), *Cephaloziella hampeana* (6 +), *C. spinigera* (11 +), *Ceratodon purpureus* (6 1; 7 +), *Climacium dendroides* (8 +), *Dicranella cerviculata* (18 +), *Dicranum spadiceum* (6 +), *Polytrichum commune* (3 +; 6 1), *P. juniperinum* (13 +, 18 +), *Serpoleskaea subtilis* (15 +), *Sphagnum obtusum* (11 +), *S. platyphyllum* (3 1; 6 1), *Warnstorfia exannulata* (8 +).

Table 2. Chemical composition of surface and snow water, mg/l (Kalinin et al., 2012). Surface water was measured in July 2002-2011; snow water – in the last decade of April 2000-2011. Monitoring points are mapped in Fig. 1.

Location	pH	HCO_3^-	NH_4^+	NO_2^-	NO_3^-	PO_4^{3-}	Fe total	Ca^{2+}	Mg^{2+}	Cl^-	SO_4^{2-}	K^++Na^+
Arantur Lake	5.78	17.03	0.55	0.0	0.76	0.06	1.04	0.75	0.61	2.74	4.43	8.58
Pontur Lake	5.81	<10	0.70	0.06	0.52	0.13	1.14	–	0.36	2.00	<10	–
Akh River 1	6.17	21.40	–	0.0	0.32	0.15	2.00	9.65	1.66	2.14	3.81	4.61
Akh River 2	5.11	<10	0.8	0.02	0.68	0.05	1.80	–	–	<10	<2.0	–
Enyya River	5.73	20.26	0.59	0.0	0.97	0.11	1.60	1.02	0.96	2.61	7.02	9.25
Snow	5.29	–	0.29	0.042	0.96	0.06	0.22	0.52	0.36	2.64	5.72	–

ma capillaceum that forms pure mats, sometimes quite abundant, on the bases of trees and shrubs.

DISCUSSION

This study of vegetation communities with *Dichelyma capillaceum* in the Nature Park "Kondinskie Lakes" shows that the habitat and vegetation characteristics of this moss species are generally similar in West Siberia and Western Europe (Hylander, 1998; Hedenäs *et al.*, 1996). The detailed characterization of the ecological conditions of *Dichelyma capillaceum* in the Nature Park has become possible due to long-term monitoring of the water level dynamics and chemical composition of lake and river waters. The results of the long-term studies were summarized for the period 1999-2011 in the monograph "Kondinskie Lakes Nature Park" (Kalinin, 2012).

The similarity of the environmental conditions of habitats is first of all found in the high amplitude of the water level variation due to the spring high water in the Konda River, and backwater in the Arantur – Pontur lake system. The average water level during the warm period of the year (May – September) in Arantur Lake is 85.6 cm of the conventional "0" varying from 47 cm (2003) to 121 cm (2002). The average maximum levels (May – June) comprise 138.5 cm varying between 82 cm (2003) and 192 cm (2007). Flooding of the Akh River valley, low lake banks and estuary part of inflowing rivers occurs when water level reaches 120 cm. above the conventional "0". In 2006 when the vegetation relevиs took place (04-09.VII), water level in the lake system Arantur – Pontur was 117 cm (May), 160 cm (June) and 97 cm (July). In different plant communities with *Dichelyma capillaceum* the flooding marks on tree trunks were indicated at the height of 30-50 cm. The flooding period varies between 2 and 8 weeks for different years. Three times (2003, 2008, and 2010) during a decade of ecological monitoring the *Dichelyma capillaceum* habitats were not flooded at all.

There are significant differences between the *Dichelyma capillaceum* habitats in the study area and those of Western Europe in the river and lake water quality. The average values for some water chemistry parameters of surface and snow melt waters in the Nature Park "Kondinskie Lakes" are presented in Table 2.

Chemically, water in all the monitoring sites for all years is low in minerals of the hydro-carbonate class and sodium group, acidic, and rich in iron. The total concentration of ions during summer varied between 32.7 – 43.7 mg/l. The lowest mineral levels were recorded in Arantur Lake, the maximal – in the Akh River. Ions of sodium and potassium dominate in the cationic composition. The content of chlorides and sulfates is low for all the seasons. In terms of water hardness the water in the lakes and rivers is "very soft". The minimum hardness, 0.09 mmol/l was recorded in Arantur Lake; the value for the rivers is 0.12-0.15 mmol/l.

The content of nutrients (N- and P-compounds were studied) in all the water bodies under consideration is insignificant. Nitrates are the most characteristic of the nitrogen compounds; the content of ammonium was low during the whole monitoring period. Nitrites, as an intermediate product of nitrification, are often fully consumed by phytoplankton during the growing period. The content of organic matter in the water was estimated indirectly from the value of biochemical oxygen consumption. This value varied from 1.28 to 1.56 mg O_2/l. It is within the interval of 1.1 – 1.9 mg O_2/l when water is considered to be "pure".

In North America almost 25% of all the studied specimens contain sporophytes (Ireland, 1989); however both female and male plants are similarly frequent (Hedenäs *et al.*, 1996). On the contrary in Western Europe sporophytes of *Dichelyma capillaceum* are quite rare. They were recorded only from two sites in Sweden in the 19th century. The long-term intensive search by Hylander (1998) did not provide any additional plants with sporophytes, and only recently additional sporophytes were discovered by Tommy Pettersson in Sweden (Hallingbäck, 2010). In most cases this species is dispersed in Europe by parts of shoots. This way of propagation is considered to preserve small number of vegetative parts, which is one of the reasons of the species rarity. In Sweden the species seems to occur in certain river systems, which fits with mainly vegetative propagation.

Sporophytes of *Dichelyma capillaceum* have not been found in the studied biotopes in the "Kondinskie Lakes" Nature Park; thus the main reproduction and dispersal is vegetative. However, the frequency and abundance of the species' habitats in favorable conditions make us con-

clude that vegetative reproduction is rather efficient. This allows suggests that *Dichelyma capillaceum* is spread in West Siberia in a greater extent than has been known so far, and further study into potentially favorable habitats can change our knowledge regarding its distribution in Siberia.

ACKNOWLEDGEMENT

I would like to express my gratitude to T.L. Bespalova, Deputy Director of "Kondinskie Lakes" Nature Park, for her help and support in the field trip organization, to I. Filippov for preparing of the map of the studied area, to Y. Papanova and O. Hopiaynen for help with English translation. I am grateful to the reviewers L. Hedenäs and T. Hallingbäck for valuable comments and improving the English.

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