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Article

Distribution, ecology and biology of *Sparganium hyperboreum* (Typhaceae) in Western Siberia

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Abstract. Geographical analysis has shown that *Sparganium hyperboreum* is most widespread in the forest-tundra and in the subarctic tundra subzone. In Western Siberia, this species grows in low and slightly mineralized and slightly acidic/neutral/slightly alkaline cool waters with fluctuating water level. It forms both monodominant communities (**Sparganietum hyperborei purum** association), and communities in which it is an edificator. In the southern tundra, *S. hyperboreum* is often found in anthropogenically transformed water bodies and man-made reservoirs. The species is characterized by high vegetative mobility and ecological plasticity with four ecological forms, depending on the depth of growth. Along with this, *S. hyperboreum* is characterized by only one life form.

Key words: bur-reed, morphology, life form, seed productivity, area, phytocenology

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Introduction

The bur-reed *Sparganium hyperboreum* Laest. ex Beurl. is a hypoarctoalpine circumpolar species (Ito and Cota-Sánchez, 2014) with a disjunctive range; it belongs to the ecological group of short-grass helophytes. The species is interesting because of its vast range and pronounced polymorphism.

Data on the morphology and ecology of *S. hyperboreum* are fragmentary and are often discussed in comparison with *S. natans L.* (Belavskaya, 1984; Bobrov et al., 2014; Casper and Krausch, 1980; Cook and Nicholls, 1986; Takahashi et al., 2000; Timokhina, 1988) or while analyzing key morphological characters necessary for the identification of these taxa (Harms, 1973). The identification of this species of bur-reed is complicated by the presence of sterile forms, often found in the north of European Russia, Siberia, and the Far East (Bobrov et al., 2014), as well as the plasticity of shoot morphology and possible hybridization (Harms, 1973). Thus, in places where the ranges of *S. hyperboreum* and *S. natans* overlap, there are “atypical” specimens that are presumably of a hybridogenic nature (Bobrov and Mochalova, 2014; Cook and Nicholls, 1986; Harms, 1973; Mochalova, 2009; Takahashi et al., 2000).

Detailed studies on the biomorphology, ecology, and phytocenology of *S. hyperboreum* have not yet been carried out; the available data are very scattered and largely outdated. In scientific publications, there is fragmentary information on the anatomy, ecology and phytocenology of the species. Information on the seed productivity of this plant is not available; in addition, its ecological and morphological adaptations have not been studied.

The aim of the work is to study the morphological features of the vegetative and generative sphere, seed productivity of *S. hyperboreum*, as well as to summarize the data on the ecological and phytocenotic features of this species in Western Siberia.

Material and methods

The work is based on materials collected in 2016–2020 in the north of Western Siberia. For biomorphological analysis and study of seed productivity of *S. hyperboreum*, we took fixed (in 75% alcohol) and herbarium material collected in five natural habitats (Fig. 1):

1) Tyumen region, Yamalo-Nenets Autonomous Okrug, Tazovsky District, a tundra water body along the highway in the area of the village of Gaz-Sale, N 67.341° E 78.946° (N = 15);

2) same locality, Nadymskii District, village of Pangody, quarry reservoir, N 65.836° E 74.469° (N = 5);

3) same locality, Priuralsky District, drying water body, N 67.270155° E 65.758255° (N = 5);

4) Tyumen Region, Khanty-Mansi Autonomous Okrug, Beloyarskii District, shallow, backwater of an unnamed lake, N 63.853721° E 70.301057° (N = 5);

5) same locality, Nizhnevartovsk District, Novomolodezhnoye Field, 50 km from the village of Kolek’egan, N 62.154° E 79.445° (N = 6).

To clarify the biomorphological features, 50 plant specimens stored in the IBIW herbarium were additionally studied. For biomorphological analysis of plants we used previously described methods (Belyakov and Filippov, 2018). In vegetative organs of plants, we recorded the total length of the plant, the number and length of internodes of rosette sections of shoots and geophilic rhizomes, as well as the order of their branching. In generative organs of plants, we measured the length of the peduncle and its metameres, counted the number of pistillate and staminate capitate inflorescences/compound fruits, and measured their diameter. We studied seed productivity by direct counting of formed (normally developed and small, underdeveloped) fruitlets on the shoot. For a study of the morphometric characteristics of the fruitlets (N = 100), we measured the length of the fruitstem, rostellum, as well as the length of the main part of the fruitlets (containing the drupe) and its diameter.

Data on the ecology of the species were collected from 47 water bodies. In the places inhabited by *S. hyperboreum*, the type of soil was determined visually, the depth was measured with a ruler, pH was determined using a HI98130 Combo portable analyzer (Hanna instruments, USA).

For the geobotanical description of the sample plots we used traditional approaches to the study of the vegetation cover of reservoirs and watercourses (Belavskaya, 1979; Katanskaya, 1981; Papchenkov, 2001, etc.). When describing the survey sites, we recorded the type of the water body, the ecological features of the habitat (the nature of the soil, depth, flow velocity, water temperature and pH), made a list of species included in the community, the phenological phase, and abundance-coverage. When identifying associations, a dominant-determinant approach was used (Papchenkov, 2001). Analysis of ecological scales according to Tsyganov (1983) is based on the work of L.A. Zhukova et al. (2010).

To compile a detailed map of the distribution of *S. hyperboreum* in Western Siberia, we used herbarium collections of MW, MHA, IBIW, LE, TK, TMN, NS, NSK, and VLA. A total of 650 herbarium sheets were reviewed. To describe the distribution of the species in the latitudinal direction, the characteristics of geobotanical zones and subzones of the West Siberian Plain were used (Ilyina et al., 1976, 1985).

Numerical values in the text of the work and in tables are presented as $x \pm SD$.

Results

Distribution

In Russia, *S. hyperboreum* is widespread from the northern taiga to typical tundra in the European part (Murmansk and Arkhangelsk regions, the Republic of Karelia and the Republic of Komi), in the Urals and in Siberia (Western Siberia: Altai Republic, Altai Region, Yamalo-Nenets and Khanty-Mansi Autonomous Regions; Central Siberia: Krasnoyarsk Region, Republic of Sakha (Yakutia), Buryatia, Irkutsk Region; Eastern Siberia: Republic of Sakha (Yakutia), Chukotka Autonomous Region, and Magadan Region (Fig. 1). Note that in Western and Central Siberia, the species enters the northern part of the middle taiga subzone. In northeastern Siberia, *S. hyperboreum* was found in the middle taiga, but it is predominantly found in areas with altitudinal zonality. In southern Siberia (the territory of Altai-Sayan (Altai Region, Altai Republic and Tyva Republic) and Baikal regions of Siberia (Irkutsk Region, Buryatia, Transbaikalia) this species is distributed exclusively in areas with altitudinal zonality. In the North Pacific

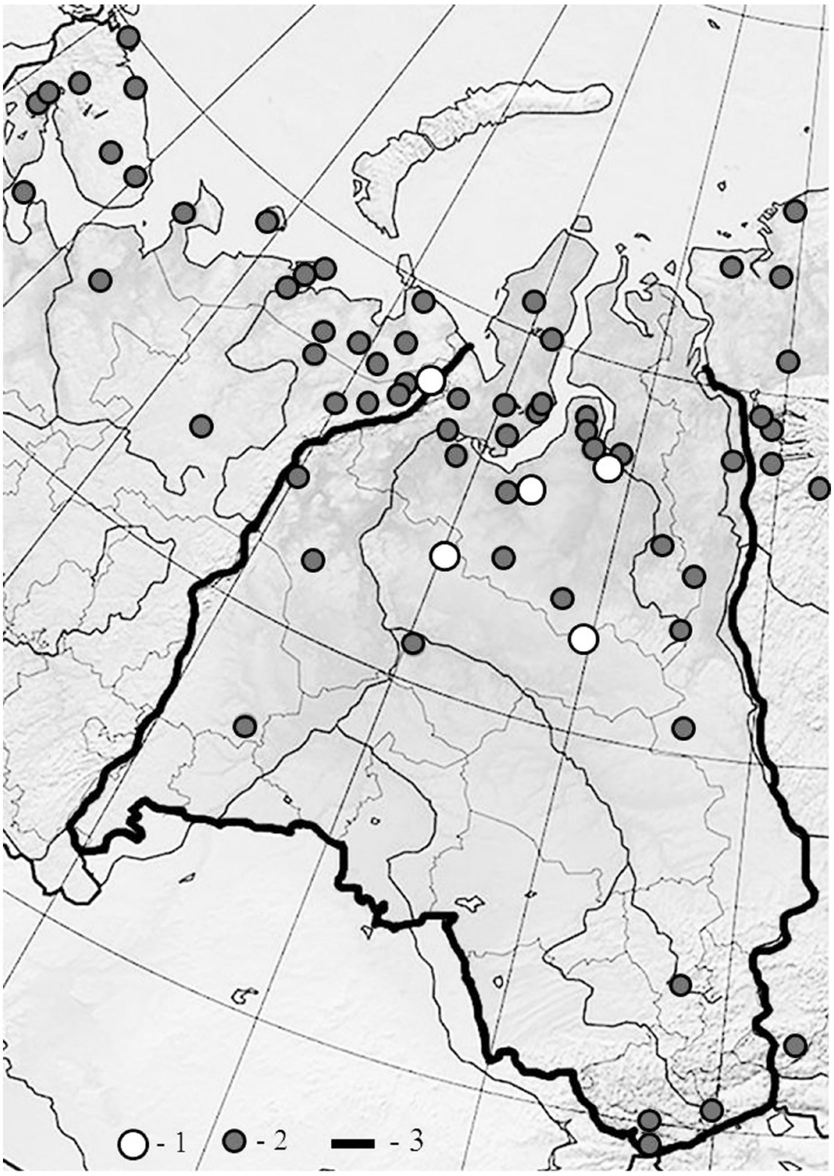

Fig. 1. General distribution and places of collection of material for biomorphological analysis of *S. hyperboreum* on the territory of Russian Western Siberia. 1 – places of collection of samples for morphological analysis, 2 – the distribution of the species, 3 – the border of Russian Western Siberia.

region (Chukotka Autonomous Okrug and Kamchatka Territory), records are confined to mountain forest tundra, in the Amur-Sakhalin region (Amur Region, Khabarovsk and Primorsky regions, northern Sakhalin Region), the species was recorded in the middle taiga zone and mountainous regions.

Ecology

S. hyperboreum in Siberia usually grows in ultra-fresh water bodies with a slightly acidic or close to neutral environment (water pH 5.9–7.5). It is found in shallow waters of lakes and small lakes, in small thermokarst lakes and baths, oxbow lakes, quarries/excavation pits, roadside ditches, hollows in swamps, slowly flowing streams and rivers. It occurs on peaty, silty, sandy and sandy soils with silt. It prefers depths from 0.2–0.5 to 0.8 m, but can also be found at greater depths.

Within the main range, there are changes associated with the nature of habitats and the abundance of occurrence. In typical plain tundras, *S. hyperboreum* is found in lacustrine-alluvial depressions and large river valleys; it was only once found in a moraine landscape. To the south, the occurrence and abundance of the species increase; in swamps in the subzone of the southern tundra, in some places it completely occupies small polygons (Ary-Mas forest, Lukunsky Grove, Taimyr Biosphere Reserve, Krasnoyarsk Region). *S. hyperboreum* exhibits the highest partial activity in the northern forest tundra and in the subarctic tundra subzone, where it grows everywhere in bog hollows, thermokarst lakes, shallow valley lakes, roadside ditches, less commonly in streams, floodplain lakes, and oxbow lakes. In the northern taiga subzone, it is observed in almost all valley water bodies, but does not rise into the mountains.

Analysis of the data obtained using Tsyganov's amplitude ecological scale (Zhukova et al., 2010) showed that the potential ecological valence (PEV) in *S. hyperboreum* varies from 0.13 to 0.73 (Table 1). This makes it possible to characterize the species as stenovalent (SV) according to the soil moisture (Hd), salt regime (Tr), and illumination/shading (Lc) scales; hemisthenovalent (HSV), according to the thermoclimatic scale (Tm), scales of moisture variability (*ƒ*H) and soil acidity (Rc); mesovalent (MV), according to the scales of aridity-humidity (Om) and soil nitrogen richness (Nt); hemi-euryvalent (HEV), according to the cryoclimatic scale (Cr) and euryvalent (EV), according to the climate continentality scale (Kn) (Table 1). The overall tolerance index (It) was determined for *S. hyperboreum* as 0.42. This indicates that the studied species (together with all factors) can be characterized as a hemistenobiont. The success in the development of the ecological space of a species is expressed by the coefficient of ecological efficiency ($K_{ec.\ eff.}$), the value of which is quite high and averages about 71.67%.

The data obtained indicate that the distribution of *S. hyperboreum* is limited to the greatest extent by the continentality of the climate, the temperature regime, the content of nitrogen in soils, and illumination.

Like most species of the genus, *S. hyperboreum* is characterized by high ecological plasticity, which manifests itself in the ability to change its ecological form. Thus, in anthropogenic reservoirs (roadside ditches) of the subzone of the southern shrub tundra of Western Siberia, especially in shallows and shallow waters, *S. hyperboreum* is more typical of an emerged form than a submerged one. For reservoirs of natural origin, which are distinguished by great depths, on the contrary, a submerged form is characteristic. In the latter case, the species behaves like a typical hydrophyte. In the northern regions, a completely submerged sterile form is sometimes found. During temporary drying of water bodies, the species is able to take on a terrestrial ecological form.

Cenotic characteristics

In Western Siberia, in tundra thermokarst and secondary intramarsh lakes, *S. hyperboreum* is characterized by the formation of monodominant communities. In floodplain well-heated lakes, the influx of allochthonous matter increases, which contributes to the development of mesotrophic and, more rarely, eutrophic species; at the same time, the structure of communities with the participation of *S. hyperboreum* becomes much more complicated, and the projective cover of the species decreases.

In the subzone of the southern tundra, *S. hyperboreum* manifests itself as an apophyte, commonly found in water bodies of artificial origin: roadside ditches, flooded depressions formed as a result of flooding along road embankments, and quarries. As a result of anthropogenic eutrophication, *Utricularia vulgaris* L., *Potamogeton pusillus* L., and, less commonly, *Lemna trisulca* L. are actively developing along with *S. hyperboreum* in such areas, which are usually protected from the wind and well warmed. Associations are multi-tiered and more complex.

Based on the described groups involving *S. hyperboreum*, we identified 10 associations:

Table 1. Characteristics of potential and realized ecological valencies, coefficient of ecological efficiency and tolerance index of *S. hyperboreum*. PEV – potential ecological valency; REV – realized ecological valency; $K_{ec.\ eff.}$ – coefficient of ecological efficiency; TI – tolerance index; groups of ecological scales: C – climatic; S – soil; I/S – scale of illumination/shading; species tolerance groups according to ecological scales: MB – mesobiont species; HSB – hemistenobiont species; SB – stenobiont species. Other designations are given in the text.

Ecological scale		Value range	PEV	REV	$K_{ec.\ eff.}$, %	TI in scales
C	Tm	1–6	0.35 (HSV)	0.30	85.71	0.55 (MB)
	Kn	3–13	0.73 (EV)	0.66	90.41	
	Om	7–14	0.53 (MV)	0.46	86.80	
	Cr	1–9	0.60 (HEV)	0.53	88.33	
S	Hd	19–21	0.13 (SV)	0.08	61.54	0.35 (HSB)
	Tr	1–5	0.26 (SV)	0.21	80.77	
	Nt	2–7	0.54 (MV)	0.45	83.33	
	Rc	5–9	0.38 (HSV)	0.31	81.58	
	*ƒ*H	1–5	0.45 (HSV)	0.36	80.00	
I/S	Lc	1–2	0.22 (SV)	0.11	50.00	0.22 (SB)

Sparganietum hyperborei purum association. Diagnostic species – *S. hyperboreum* with projective cover area (PC) up to 70% (depth up to 0.8 m, soil: all types). The association is typical of tundra thermokarst and secondary intrabog lakes. The total projective cover area (TPC) of the association is 10–70%. It is most widespread in the subzone of the southern shrub tundra (everywhere in the Tazovsky District), where it is found in all types of water bodies, except for floodplain lakes. We also recorded this association in tundra lakes in the Polar and Subpolar Urals.

Utricularieto – **Sparganietum hyperborei** association. Diagnostic species – *S. hyperboreum* with PC 20–40%. Either *Utricularia vulgaris* (PC 30%) or *Utricularia minor* L. (PC 10%) acts as a codominant (depth 0.3–0.5 m, soil: coarse detrital silt, clay, sand). The assectator is *Myriophyllum sibiricum* Kom. (PC 3%). TPC – 20–60%. The association was recorded in the subzones of the southern tundra and northern forest tundra, mostly in well-heated anthropogenically transformed areas of water bodies, in which the influx of allochthonous matter increases, which contributes to the development of mesotrophic and, less often, eutrophic plant species.

Potameto sibirici – **Sparganietum hyperborei** association. Diagnostic species – *S. hyperboreum* (PC 30%). *Potamogeton sibiricus* A. Benn. is a codominant in the lower tier of the community (PC 15–20%) (depth 0.5 m; soil: silt). TPC is 45–50%. The association was recorded in the subzone of the southern tundra in the shallow waters of floodplain lakes.

Potameto alpini – **Sparganieum hyperborei** association. Diagnostic species – *S. hyperboreum* (PC 20–30%). *Potamogeton alpinus* Hegetschw. is a codominant (PC 40%). The group also includes *Hippuris vulgaris* L. with PC 7% (depth 0.1–0.3 m; soil: sand, detritus). TPC is 40–60%. The association was recorded only once, in the subzone of the northern forest-tundra (N 66.996111° E 78.270833°) in Western Siberia.

Potameto pusilli – **Sparganietum hyperborei** association. Diagnostic species – *S. hyperboreum*, PC ~30%. *Potamogeton pusillus* is a codominant (PC 50–70) (depth 0.5–0.8 m; soil: silt). TPC is 60–90%. In the northern forest-tundra, *Lemna turionifera* Landolt is very rare (PC 5–7%). The association was recorded in the subzones of the southern tundra and northern forest tundra, mainly in anthropogenically transformed areas of water bodies and quarries.

Warnstorfieto exannulati – **Sparganietum hyperborei** association. Diagnostic species – *S. hyperboreum* with PC 20%. *Warnstorfia exannulata* (Schimp.) Loeske is a codominant with PC 40–50%. This community commonly includes species of the genus *Sphagnum* L. and occasionally *Hippuris vulgaris* (depth 0.1–0.3 m; soil: silty, silty-sandy). TPC is 20–40%. The association is widespread in the subzones of the southern tundra and northern forest tundra, found in well-heated areas of thermokarst lakes, less commonly in small floodplain water bodies. Also recorded in the mountainous part of Western Siberia (Polar Urals).

Calliergoneto cordifolii – **Sparganietum hyperborei** association. Diagnostic species – *S. hyperboreum*, PC 20–40%. *Calliergon cordifolium* Kindberg is a dominant of the second tier with PC 30–60%. *Sphagnum squarrosum* Crome is recorded community in a well-developed moss cover in the coastal zone of the reservoir and in shallow water (depth 0.1–0.3 m; bottom: silty, silty-sandy), TPC is 20–70%. The association is often found in the subzones of the southern tundra and northern forest tundra in the shallow waters of thermokarst lakes, intra-marsh depressions, floods along roads, rarely in small floodplain reservoirs of small rivers.

Sparganieto hyperborei – **Hippuridetum vulgaris** association. *Hippuris vulgaris* is an edificator and diagnostic species with PC 7–10%. *S. hyperboreum* is a dominant of the second tier of the community (PC 30–40%). *Potamogeton pusillus* is recorded at the lower tier, in roadside ditches (PC 3–5%) (depth 0.2–0.5 м; soil: coarse detrital silt). TPC is 20–40%. The association is widespread in the subzone of the southern tundra in flooded areas along roads, near drainage pipes, as well as in bays, small rivers, tundra thermokarst and secondary intramarsh lakes.

Sparganieto hyperborei – Caricetum aquatilis association. Diagnostic species – *S. hyperboreum* (PC 30–40%). *Carex aquatilis* Wahlenb. (PC 30%) and *Utricularia vulgaris* (PC 20%) are codominants in different tiers of the community (depth 0.3–0.4 m; soil: coarse detrital silt). Assectors: *Menyanthes trifoliate* L. and *Equisetum fluviatile* L. (PC 1–3%). TPC is 40–60%. The association is typical for floodplain well-heated lakes of the southern tundra subzone.

Aqui-herboso – Equisitetum fluviatilis association. Diagnostic species – *Equisetum fluviatile* with PC 10–30%. *S. hyperboreum* (PC 20–60%) and *Myriophyllum verticillatum* L. (PC 20–40%) are codominants with a significant abundance (depth 0.2–0.4 м; soil: fine-detrital silt). *Lemna trisulca* (PC 20–30%) is less common, TPC is 30–90%. The association was recorded on the northern border of the forest-tundra and in the subzone of the southern tundra in tundra thermokarst, intra-marsh and floodplain water bodies. *Arctophila fulva* (Trin.) Andersson is found occasionally in the northern forest-tundra. For example, such a community was found in the Tazovsky District, 139 km south along the highway from the village of Tazovsky, on a flooded area by a roadside near the drainage pipe (N 66.516095° E 79.350598°).

Morphology

The sympodially growing shoot system of *S. hyperboreum* is formed by shoots of different ages (taking into account the phase of the bud): di- and tricyclic monocarpic middle-rosette anisotropic, as well as mono- and dicyclic vegetative rosette, interconnected by a system of hypogeogenic rhizomes. The dicyclic monocarpic middle-rosette shoots are developed on the basis of tricyclic monocarpic shoots. The rosette part of a dicyclic monocarpic shoot (unlike the one-year monocarpic shoot) is characterized by the presence of two elementary shoots separated from each other by a section of a smaller diameter (up to 0.16 ± 0.03 cm) up to 1.50 ± 0.97 cm long. The first (lower) elementary shoot (length, 0.80 ± 0.20 cm; diameter, 0.23 ± 0.02 cm) is formed by 10–15 shortened metameres, the second, located higher (length, 1.17 ± 0.64 cm, diameter, 0.35 ± 0.08 cm), 6–10(14). Buds were found in the axils of all leaves of the rosette part of the shoots. Some of them (3–5(7)), located in the basal part of the shoot, develop into hypogeogenic rhizomes, the rest remain dormant. As a result of iterative branching, by the end of the growing season, on the basis of the primary shoot, a sympodial system of anisotropic monopodial anchoring shoots is formed up to n+3–4 branching orders.

Hypogeogenic rhizomes (length 12.14 ± 6.74 cm, diameter 0.11 ± 0.01 cm) are formed by 6–8 metameres and are located in the soil at a depth of 5–10 cm. The rhizomes, like those of all *Sparganium* species, are formed extravaginally from the axillary buds. From the nodes of the rhizomes, thin amplexicaul scale-shaped leaves (cataphylls) radiate, in the axils of which buds are formed. One part of them, usually located closer to the apical end of the rhizome of the nth order, provides branching of the renewal shoot to the next order (n+1), and the other part of the buds (located closer to the basal end of the rhizome of the nth order) remain dormant. The length of metameres of rhizomes of the n+1 branching order reaches 2.55 ± 1.33 cm, the diameter is 0.08 ± 0.01 cm.

The root system of *S. hyperboreum* is fibrous, represented by annual shoot-borne adventitious roots formed at the nodes of the shoot's rosette vegetative part. Roots branch up to n+2 orders. The number of roots developing at the base of the rosette shoot reaches 60.0 ± 20.4, and their length varies from 15 to 30 cm.

All leaves on the rosette part of the shoot are arranged alternately in two rows. They are sessile, with initially closed sheaths without ligule, linear, entire, smooth edged blade, closed at the base. The leaves are usually yellowish green, slightly translucent in freshly harvested plants, without a keel. On the underside of the leaf (especially in herbarium specimens), longitudinal and transverse veins are clearly

Table 2. The main parameters of compound fruit of *S. hyperboreum*.

No. of compound fruit (from bottom to top)	The total number of fruits in the compound fruit	Number of large fruits	Number of small fruits	Fruit diameter, cm
1	124.00 ± 32.00	41.50 ± 36.06	82.50 ± 9.20	1.25 ± 0.21
2	93.33 ± 26.10	29.00 ± 41.57	64.33 ± 16.50	1.02 ± 0.35
3	75.71 ± 18.61	36.50 ± 29.08	39.21 ± 24.25	0.96 ± 0.20
4	67.74 ± 18.13	46.88 ± 17.94	20.85 ± 17.32	1.03 ± 0.17
5	60.20 ± 19.05	48.44 ± 16.28	11.75 ± 11.02	1.03 ± 0.17

Table 3. The main parameters of compound fruit of *S. hyperboreum* in the subzones of Western Siberia.

	The total number of fruits in the compound fruit	Number of large fruits	Number of small fruits
Natural subzones of the West Siberian Plain			
Forest tundra	183.12 ± 117.10	121.40 ± 70.77	62.40 ± 58.51
Middle taiga	149.10 ± 76.55	104.82 ± 61.23	44.27 ± 42.76
Polar Urals (eastern part)			
Mountain tundra	177.00 ± 40.65	82.00 ± 21.10	95.00 ± 38.77

visible. In the terrestrial (developing in drying areas of water bodies) and emerged forms (developing at a depth of 5–10 cm), rosette leaves reach a length of 22.80 ± 8.00 cm and a width of 0.30 ± 0.10 cm. In emerged plants, the length of leaves floating on the water surface is up to 48.33 ± 14.11 cm, width – 0.21 ± 0.06 cm. In some cases, the leaf width barely exceeds 1 mm. The length of leaves in submerged sterile forms, often found in the Far East, reaches 69.50 ± 12.16 cm, while the average width of the leaf blade does not change significantly.

In winter, the entire system of geophilic rhizomes formed during the last growing season in *S. hyperboreum* remains in the ground, at a depth of up to 3–5 cm. At the same time, the terminal buds of vegetative rosette shoots with short living leaves (unfolding during the winter period) remain hidden bases last year's dead leaves.

In July, a terminal inflorescence develops on the basis of the terminal bud of last year's vegetative rosette. The inflorescence is frondose-bracteous-ebracteous, like a raceme with floral units – axillary capitate inflorescences of unisexual flowers. In different ecological forms, the length of the floriferous axis can vary greatly. For example, in the terrestrial form, the length of the inflorescence can reach 7.83 ± 1.44 cm, in the emerged one, 19.34 ± 6.47 cm. In the submerged form with leaves floating on the water surface, the length of the floriferous axis increases to 36.55 ± 8.60 cm. Note that the peduncle in the terrestrial form often turns out to be *S*-shaped, curved.

The floriferous axis (including the inflorescence) is formed by 6–8(9) metameres. The lower part of the floriferous axis is formed by 2–3 elongated metameres (0.21 ± 0.06 cm in diameter). At their nodes are typical leaves of the middle formation with axillary buds, which, as a rule, do not develop. Unrealized rudimentary pistillate capitate inflorescences are often found in the axils of the nodes of overlying metameres (1–2(3)) with leaves of the middle formation. Further along the floriferous axis are metameres with realized pistillate capitate inflorescences (2–3(4)) and one terminal staminate capitate inflorescence. Quite commonly all pistillate heads are located in the axils of assimilating bracts. However, sometimes the uppermost pistil head can be located in the axil of a scarious, almost imperceptible bract. At the base of the staminate head, the bract can be almost completely reduced. The pistillate and staminate capitate inflorescences are separated from each other by a metamere up to 0.77 ± 0.42 cm long.

The inflorescence is mostly formed from extra-axillary, unevenly spaced pistillate heads, the lower ones (1–2(3)) on pedicles (often fused with the inflorescence axis at the base). The length of the pedicle of the first (lower) inflorescence is 3.20 ± 0.92 cm, while that of the second is 2.16 ± 0.61 cm (the second pedicle partially or completely fuses with the main axis of the inflorescence). The third pistillate inflorescence is either sessile in the leaf axil or close to the one located above, as in the previous case, due to the fusion of its pedicle (0.88 ± 0.37 cm long) with the main axis of the inflorescence. Thus, there is an impression of crowding of the upper pistillate inflorescences. In the upper part, the flower-bearing axis ends with a shortened internode with a sessile staminate capitate inflorescence.

By the end of July – beginning of August, dense compound fruits ripen on the monocarpic shoots of the *S. hyperboreum* (therm. according to: Levina, 1987). Their number on the shoot ranges from 1 to 5. The most common plants are those with 2 (in 37.5% of cases) and 3 (45.8%) compound fruits. In ~4.1% of cases, 1 or 4 compound fruits are located on the shoots, and in 8.3% – 5 compound fruits. The average number of fruits in one icompound fruit reaches 68.70 ± 21.90 (of which 44.68 ± 21.67 are large, normally developed and 24.01 ± 22.34 are small, underdeveloped), the diameter is 1.01 ± 0.20 cm. The main characteristics of the compound fruits of the *S. hyperboreum* on a monocarpic shoot are given in Table 2. Evidently, the total number of fruits in the realized compound fruits decreases from bottom to top, which is due to a sharp decrease in the number of small fruits and an increase in the number of large ones.

The fruit of *S. hyperboreum* is a dry upper pseudomorphic drupe. In the lower part, the fruit has a short pedicle 0.04 ± 0.01 cm long. The middle part of the fruit is usually elongated-obovate, rarely spindle-shaped (length 0.30 ± 0.03 cm, diameter 0.14 ± 0.02 cm), with a weakly expressed constriction in the middle part, often with a few smooth longitudinal ribs. In the upper part, the fruit narrows quite sharply and passes into a short stile (0.03 ± 0.01 cm long). As they ripen, the fruits acquire a yellowish or yellowish-brown color. The tepals are transparent, light brown, 0.16–0.23 cm long.

Under the conditions of Western Siberia, the average value of the actual seed productivity of one monocarpic shoot of *S. hyperboreum* is 189.31 ± 91.81 fruitlets (of which 121.78 ± 62.81 are normally developed and 67.53 ± 51.96 are small, underdeveloped). Our observations show that in the subzone of the northern forest-tundra (Tazovsky and Nadymsky districts), middle taiga (Beloyarsky and Nizhnevartovsky districts), and in the mountains (Priuralsky District), the differences between the average seed productivity of the generative shoot of *S. hyperboreum* are statistically unreliable (Table 3).

Discussion

S. hyperboreum is considered to be one of the few species with belt-zonal confinement (Sulman et al., 2013). Its main range covers the Arctic, Subarctic, and taiga zone of the northern hemisphere (Bobrov et al., 2014; Cook and Nicholls, 1986; Harms, 1973; Takahashi et al., 2000; Timokhina, 1988). According to Cook and Nicholls (1986), the range of this species extends from Scandinavia in an easterly direction through the territory of Russia (the European part, Western, Central and Eastern Siberia) to Kamchatka and Hokkaido Island (Japan). Note that in northern Japan, *S. hyperboreum* occurs exclusively in mountainous areas (Takahashi et al., 2000). In North America, the predominantly transcontinental (Arctic-Subarctic and northern Alpine regions) range of this rare, vulnerable, endangered species (Ito and Cota-Sánchez, 2014) extends from the coastal Pacific forests of the Yukon to Alaska and on to the Atlantic coast of Canada (Newfoundland, Anticosti and Cape Breton) (Casper and Krausch, 1980; Cook and Nicholls, 1986). The species has also been found in Greenland and Iceland (Cook and Nicholls, 1986). In addition, *S. hyperboreum* is known from a small area in the southern Alps (Northern Italy), where it has been recorded at an altitude of 2250–2350 m. Alpine populations may represent genuine glacial relics (Cook and Nicholls, 1986).

As shown by our data and materials of other researchers (Secretareva, 2004), *S. hyperboreum* is widespread in all regions of the Russian Arctic. The species enters the boreal zone only insignificantly; it occurs in the mountain forest-tundra (subalpine belt) and in the subarctic tundra subzone. Thus, in the west of the European part of Russia, *S. hyperboreum* is distributed from the northern taiga subzone to the tundra zone (between 64 and 69° N), where it is common, but not very common. In the northern forest-tundra and southern tundras of Western Siberia, this species, on the contrary, is found constantly, massively in the shallow waters of lakes and small lakes, less commonly in the water of streams (Rebristaya, 2013). Here, the northern limit of its range is 71° N. (Ribristaya, 1998), which is also suggested by our studies. The southern limit of distribution of *S. hyperboreum* in Western Siberia includes localities in the high-mountain part of the Kuznetsk Alatau (N 53° E 89°) (Nekratov et al., 2002) and on the Ukok Plateau (N 49° E 87°) (Kamelin et al., 1999) at an altitude of about 2500 m above sea level. Most of the finds were made in the Tyva Republic (Ivanova et al. 2017; Shaulo et al. 2003). One record of the species was recorded in the Western Sayan (Glushchenko et al., 2009). In Central Siberia, *S. hyperboreum* is widely distributed from the middle taiga subzone (62–63° N) (Shcherbina, 2009) to the arctic tundra zone at 75° N. (in coastal lakes near the mouth of the Lenivaya River, Cape Sterlegova) (Khodachek and Sokolova, 2004). In Eastern Siberia, it occurs in the tundra reservoirs of the eastern part of Chukotka (Korobkov and Sekretareva, 2001). In Kamchatka, it was recorded in the forest, elfin forest and mountain-tundra belts (Neshatayeva, 2009). Widely distributed in Yakutia (mainly in the northeast) and in the Magadan region (Bobrov and Mochalova, 2017; Mochalova, 2009).

According to our observations, hybrid populations can be found in the zone of contact between the ranges of *S. hyperboreum* and *S. natans* in Western Siberia between 60–62° and 68–70° N. A similar latitudinal range was indicated by Takahashi et al. (2000) for Eastern Siberia.

S. hyperboreum is characterized as an ultra-freshwater, oligotrophic and mesotrophic hydrophyte whose ecological requirements are met by tundra lakes characterized by high transparency and low water temperature (Panarina and Papchenkov, 2005; Sviridenko et al., 2013; Teteryuk, 2014; Teteryuk et al., 2022; Zarubina, 2016). Consequently, the distribution of the species to the south is limited by two main factors: summer temperature and trophic conditions of water bodies (Takahashi et al., 2000). At the same time, Cook and Nicholls (1986) describe *S. hyperboreum* as a species not characteristic of either high oligotrophic or high eutrophic calcium-poor waters. The latter is confirmed by Casper and Krausch (1980). Sometimes *S. hyperboreum* is found in slightly brackish waters (Yuzepchuk, 1934). For example, this species was indicated for habitats flooded or periodically flooded by tides within brackish marshes located in the area of the Bolvanskaya Bay of the Pechora Sea (the Novaya Neruta – Yachey interfluve) (Lavrinenko and Lavrinenko, 2018).

In mountainous areas, *S. hyperboreum* is found mainly in shallow tundra thermokarst lakes. In the flat tundra, *S. hyperboreum* is associated with depressions in the valleys of large rivers (oxbow lakes) (Pospelova, 1998). This species is found in a wide range of natural and anthropogenically transformed biotopes with various soil types. So, it is recorded in shallow lakes of glacial origin, along hollows, in oxbow lakes, slowly flowing channels, backwaters (Mochalova, 2009; Rebristaya, 1998; Yuzepchuk, 1934) on peaty, mineral and silty (confined to lakes located in river valleys) soils (Mochalova, 2009; Vekhov, 1991). Prefers shallow waters from 0.1–0.3 to 0.5 m deep. At depths up to 0.8–1.0(1.5) (Cook and Nicholls, 1986; Vekhov, 1991), and sometimes up to 2 m (Razumovskaya and Petrova, 2017), forms sterile plants with floating or submerged leaves. Populations of this species are not resistant to wave events (Cook and Nicholls, 1986).

According to our observations, *S. hyperboreum* vegetates more often in the Arctic region, but in favorable years, flowering and fruiting plants can be found, when water bodies warm up relatively well. The latter is also confirmed by the data of other researchers (Pospelova, 1998; Rebristaya, 2013; Shcherbina, 2009). For example, in the tundras of the Gydan Peninsula (68–69° N) and the Yamal Peninsula (67–71° N), *S. hyperboreum* grows in the form of a completely submerged form or a form with leaves floating on the water surface (Rebristaya, 2013; Shcherbina, 2009). In the eastern part of the Bolshezemelskaya tundra (N 67° E 62°), *S. hyperboreum* is known as a helophyte, an emerged plant (Teteryuk, 2014).

In the vegetation cover of water bodies, *S. hyperboreum* can form pure thickets (**Sparganietum hyperborei purum** association), play the role of a dominant or an assectator. In the first case, the area of *S. hyperboreum* PC reaches 70%. Such communities are typical for thermokarst and secondary intra-marsh lakes of the middle and northern taiga, southern tundra subzones of Siberia and the Far East. The **Sparganietum hyperborei purum** association has also been described from the lakes of the Murmansk Region (Lakes Glubokoe and Zabolotnoe) located on the territory of the Kandalaksha Nature Reserve (growing depth 0.2–0.4 m) (Panarina and Papchenkov, 2005), as well as in the Komi Republic (Teteryuk et al., 2022). Note that we did not record the **Sparganietum hyperborei subpurum** association (Neshatayeva, 2009; Neshataev et al., 2017) in Western Siberia. This association is characterized by an insignificant (up to 5%) participation of other macrophyte species in comparison with the dominant *S. hyperboreum*.

Most frequently, *S. hyperboreum* occupies a leading position in communities where the proportion of other species is no less significant. In this case, the PC of *S. hyperboreum* is usually ⅔ higher (30–90%) than that of other species (10–60%). An example of this are the **Utricularieto – Sparganietum hyperborei** and **Potameto sibirici – Sparganietum hyperborei** associations that we described above. We and other authors (Panarina and Papchenkov, 2005) also recognize the **Potameto alpini – Sparganietum hyperborei** association. Panarina and Papchenkov (2005) recorded this association in a meso-dystrophic water body on Berezhnoy Vlasov on the territory of the Kandalaksha Reserve. The group was identified in the conditions of silt-small-stone bottom sediments and a depth of 0.4 m. The community is two-tiered: the surface layer is formed by *S. hyperboreum* (PC 16%), the lower layer is formed by leaves of *Potamogeton alpinus* (Balb.) floating on the water surface (PC 75%). There are also groupings where, despite a significant PC, *S. hyperboreum* transfers the role of an edificator to another species (occupying a higher tier in the community), albeit with a much smaller coverage. The **aqui-herboso – Equisetum fluviatilis** association, in which the PC of *Equisetum fluviatile* ranges from 10 to 30%, and the PC of *S. hyperboreum* ranges from 40 to 90% can be considered as example. A group with another edificator, *Hippuris vulgaris* (**Sparganieto hyperborei – Hippuridetum vulgaris** association), was also recorded from the water bodies of the Commander Islands (community TPC is up to 80%) (Mochalova and Yakubov, 2004).

S. hyperboreum may be found in groups as an accompanying species. So, for example, on lake Talovskoye *S. hyperboreum* is a part of the **Batrachietum trichophylli subpurum** association (**Batrachieta trichophylli** formation) along with other macrophytes, such as *Sparganium emersum* Rehmann, *Arctophila fulva* (Trin.) Andersson, *Potamogeton gramineus* L., *Subularia aquatica* L., *Callitriche palustris* L. (Neshataev et al., 2017). In the same lake, *S. hyperboreum* was recorded in the **Callitrichetum palustris subpurum** association (**Callitricheta palustris** formation), where it is one of 10 associated species (Neshataev et al., 2017). On lake Imandra Lake, *S. hyperboreum* is recorded in the **Isoetetum echinosporae** association and **Potametum praelongii** association, as well as in coastal reed beds (Razumovskaya and Petrova, 2017). In habitats flooded or periodically flooded by tides (brackish marshes in the area of Bolvanskaya Bay), *S. hyperboreum*, as a low-abundance companion species, is included in the **Eleocharietum palustris** association (Lavrinenko and Lavrinenko, 2018). A similar situation is typical for the *Batrachospermum turfosum* Bory de Saint-Vincent (PC 10–20%) + *Isoetes echinospora* Durieu (PC 5%) association, described from an unnamed lake (N 63°36'45'' E 70°57'13''), located north of lake Won-Vasinglor (Khanty-Mansi Autonomous Okrug – Yugra) (Sviridenko et al., 2019). As part of the group, *S. hyperboreum* was recorded as single shoots together with *Carex aquatilis* Wahlenb. and *C. rostrata* Stokes. Recently, a community of *S. hyperboreum* with hypnum mosses (*Warnstorfia exannulata* (Schimp.) Loeske) was described from the Nenets Autonomous District (Teteryuk et al., 2022). We also noted similar communities in Western Siberia.

Note that *S. natans*, which is ecologically and taxonomically close to *S. hyperboreum*, also often forms both monospecific associations (**Sparganietum natanti purum** association) and cenoses (**Utricularieto – Sparganietum natanti** association) (Belyakov and Philippov, 2018).

S. hyperboreum and *S. natans* have similar morphology of both vegetative and generative spheres (Belyakov and Philippov, 2018; Bobrov and Mochalova, 2014; Harms, 1973). The most pronounced difference between these two species is the nature of the leaf blade – in *S. hyperboreum* the leaves floating on the water surface are often narrower and thicker, slightly translucent when freshly harvested (Mochalova, 2009), while in *S. natans* they are thin, translucent, longitudinal and the transverse veins are more pronounced. Another main difference between the species is the individual features of the morphology of the fruitlets. Fruitlets of *S. hyperboreum*, as a rule, are smaller in diameter and often have a few smooth longitudinal ribs. However, the main taxonomically significant parameter here is style length, which is practically absent in *S. hyperboreum* (Cook and Nicholls, 1986; Harms, 1973). Note that the size characteristics of *S. hyperboreum* fruits recorded by us fully correspond to the data presented by other authors (Belavskaya, 1984; Cook and Nicholls, 1986; Harms, 1973; Timokhina, 1988).

Published data on the number of fruitlets per compound fruit of *S. hyperboreum* were contradictory. According to Belavskaya (1984), the average number of fruitlets in a compound fruit reaches 27, while we recorded considerably more fruitlets. Apparently, A.P. Belavskaya (1984) only took into account large, well-developed fruitlets.

Conclusions

S. hyperboreum – circumpolar hypoarctic species with a disjunctive range, growing exclusively in the northern hemisphere. The species is most widely distributed in the Arctic and Subarctic – in the subzones of the northern forest tundra and subarctic tundra. In the subarctic tundra subzone, it is a regionally moderately active species. Here it can be considered an indicator of the corresponding zonal-climatic boundary and used to monitor climate change in our sector of the Arctic. The expansion of the range in a southerly direction occurs exclusively at high altitudes of Eurasia and North America. Here it is found in the mountain-taiga, subalpine and alpine zones.

The available data allow us to characterize *S. hyperboreum* as an ultrafreshwater, oligotrophic, and mesotrophic species that prefers cool waters with fluctuating water levels. It also occurs in brackish waters. It is common in shallow mountain-tundra thermokarst lakes, shallow lakes of glacial origin, in swamp hollows, oxbow lakes, slowly flowing channels, and backwaters. It grows on various types of soil at depths from 0 to 0.8–1.5(2) m. A wide range of water levels in habitats contributed to the formation of four ecological forms in *S. hyperboreum* (terrestrial; sterile). In Russia, the species often grows in low- and low-mineralized, slightly acidic/neutral/slightly alkaline waters.

The results of the analysis using ecological scales make it possible to attribute the species to the hemistenobiont group. Distribution is limited by the continentality of the climate, the temperature regime, the richness of soils in nitrogen and illumination.

For the territory of the north of Western Siberia, it has been established that in tundra thermokarst and secondary intrabog lakes, the species is characterized by the formation of monodominant communities (**Sparganietum hyperborei purum** association), while PC of *S. hyperboreum* in some cases reaches 70%. In the subzone of the southern shrub tundra, *S. hyperboreum* manifests itself as an apophyte, often occurring in anthropogenically transformed areas and reservoirs of artificial origin in the **Sparganieto hyperborei** – **Hippuridetum vulgaris**, **aqui-herboso** – **Equisitetum fluviatilis**, **Utricularieto** – **Sparganietum hyperborei**, **Potameto pusilli** – **Sparganietum hyperborei** associations.

Our data suggest that the life form of *S. hyperboreum* is a herbaceous polycarp; summer-winter green, vegetatively mobile clearly polycentric long-rhizomatous pseudoannual with a racemose root system, anisotropic middle-rosette di- and tricyclic monocarpic shoots and leaves partially submerged or floating on the water surface; hemicryptophyte. A similar type of life form is apparently characteristic of all representatives of the subgenus *Xanthosparganium*. The species is characterized by high vegetative mobility and efficient vegetative reproduction, although generative reproduction is not excluded. Storage of seeds of this species in water at low positive temperatures for 8.8 months after collection, it gives a relatively high laboratory germination rate – 60.0 ± 6.7%.

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References

Belavskaya, A.P., 1979. K metodike izucheniya vodnoy rastitel’nosti [On the methods of studying the aquatic vegetation]. *Botanicheskii Zhurnal* **64** (1), 32–41. (In Russian).

Belavskaya, A.P., 1984. K morfologii plodov roda *Sparganium* (Typhaceae) flory SSSR [A contribution to the morphology of fruits of the genus *Sparganium* (Typhaceae) in the flora of the USSR]. *Botanicheskii Zhurnal* **69** (12), 1662–1668. (In Russian).

Belyakov, E.A., Philippov, D.A., 2018. The effect of changes in environmental conditions on the morphology of *Sparganium natans* L. (Typhaceae) in the taiga zone of European Russia. *Ecosystem Transformation* **1** (1), 29–41. https://doi.org/10.23859/estr-18032

Bobrov, A.A., Mochalova, O.A., 2014. Zametki o vodnykh sosudistykh rasteniyakh Yakutii po materialam Yakutskikh gerbariev [Notes on aquatic vascular plants of Yakutia on materials of the

Yakutian herbaria]. *Novosti sistematiki vysshikh rastenii [Novitates Systematicae Plantarum Vascularium]* **45**, 122–144. (In Russian).

Bobrov, A.A., Mochalova, O.A., 2017. Vodnye sosudistye rasteniya doliny Kolymy: raznoobrazie, rasprostranenie, usloviya obitaniya [Aquatic vascular plants of the Kolyma River valley: diversity, distribution, habitat conditions]. *Botanicheskii Zhurnal* **102** (10), 1347–1378. (In Russian).

Bobrov, A.A., Mochalova, O.A., Chemeris, E.V., 2014. Zametki o vodnykh i pribrezhno-vodnykh rasteniyakh Kamchatki [Notes on aquatic and semiaquatic vascular plants of Kamchatka]. *Botanicheskii Zhurnal* **99** (9), 1025–1043. (In Russian).

Casper, S.J., Krauch, H.D., 1980. Sußwasserflora von Mitteleuropa. Pteridophyta und Anthophyta. Teil 1. Lycopodiaceae bis Orchidaceae. VEB Gustav Fischer Verlag, Jena, Germany, 404 p. 9In German).

Cook, C.D.K., Nicholls, M.S., 1986. A monographic study of the genus *Sparganium*. Part 1: Subgenus *Xanthosparganium*. *Botanica Helvetica* **96** (2), 213–267.

Glushchenko, L.A., Dubovskaya, O.P., Ivanova, E.A., Shulepina, S.P., Zuev, I.V., AgeevA.V., 2009. Gidrobiologicheskii ocherk nekotorykh ozyor gornogo khrebta Ergaki (Zapadnyi Sayan) *[Hydrobiologic survey of some lakes of mountain range Ergaki (West Sayan)]. Zhurnal Sibirskogo federal'nogo universiteta. Biologiya [Journal of Siberian Federal University. Biology]* **3** (2), 355–378. (In Russian).

Harms, V.L., 1973. Taxonomic studies of North American *Sparganium*. I. *S. hyperboreum* and *S. minimum*. *Canadian Journal of Botany* **51**, 1629–1641.

Il'yina, I.S., Lapshina, E.I., Lavrenko, N.N., Mel'tzer, L.I., Romanova, E.A., Bogoyavlenskiy, B.A., Makhno, V.D., 1976. Rastitel'nost' Zapadno-Sibirskoi ravniny. Karta masshtaba 1:1500000 [Vegetation of the West Siberian Plain. Map scale 1:1500000]. Main Department of Geodesy and Cartography, Moscow, USSR, 1 p. (In Russian).

Il'yina, I.S., Lapshina, E.I., Lavrenko, N.N., Mel'tzer, L.I., Romanova, E.A., Bogoyavlenskiy, B.A., Makhno, V.D., 1985. Rastitel'nyi pokrov Zapadno-Sibirskoi Ravniny [Vegetation cover of the West Siberian Plain]. Nauka, Novosibirsk, USSR, 251 p. (In Russian).

Ivanova, M.O., Volkova, P.A., Kopylov-Guskov, Yu.O., Bobrov, A.A., 2017. Floristicheskie nakhodki v yuzhykh prirodnykh raionakh Respubliki Tuvy i v okhrannoi zone zapovednika "Ubsunurskaia Kotlovina" [Floristic findings in southern nature regions of Tuva Republic and in conservation zone of Ubsunur Hollow Biosphere Reserve]. *Turczaninowia* **20** (4): 15–25. (In Russian). https://doi.org/10.14258/turczaninowia.20.4.2

Ito, Yu, Cota-Sánchez, J.H., 2014. Distribution and conservation status of *Sparganium* (Typhaceae) in the Canadian prairie provinces. *Great Plains Research* **24** (2), 119–125. https://doi.org/10.1353/gpr.2014.0019

Kamelin, R.V., Shmakov, A.I., Djachenko, S.A., 1999. Nekotorye floristicheskie nakhodki 1995–1998 gg. na ploskogor'e Ukok [Some floristic findings made during 1995–1998 years on the Ukok Plateau]. *Turczaninowia* **2** (4), 42–43 (In Russian).

Katanskaya, V.M., 1981. Vysshaya vodnaya rastitel'nost kontinental'nykh vodoemov SSSR. Metody izucheniya [Higher aquatic vegetation of continental water bodies of the USSR. Methods of study]. Nauka, Leningrad, USSR, 187 p. (In Russian).

Khodachek, E.A., Sokolova, M.V., 2004. Botaniko-geographicheskaya kharakteristika shirotnogo profilya severo-zapadnogo poberezh'ya poluostrova Taimyr (bassein reki Lenivoi) [Botanical-geographical characteristic of a latitudinal transect through the North-Western coast of Taimyr Peninsula (the Lenivaya River Basin)]. *Botanicheskii Zhurnal* **89** (4), 563–581. (In Russian).

Korobkov, A.A., Sekretareva, N.A., 2001. Analis flory "Yuzhnoy Chukotki" (Nizhneanadyrskii okrug) [The analysis of the Flora of "Southern Chukotka" (Nizhneanadyr District)]. *Krylovia* **3** (2), 63–77. (In Russian).

Lavrinenko, O.V., Lavrinenko, I.A., 2018. Klassifikatsiya rastitel'nosti solenykh i solonovatykh marshei Bolshezemel'skoi tundry (poberezh'e Barentseva morya) [Classification of salt and brackish marshes vegetation of the Bolschezemelskaya Tundra (Barents sea coast)]. *Fitoraznoobrazie Vostochnoi Evropy [Phytodiversity of Eastern Europe]* **12** (3), 82–143. (In Russian). https://doi.org/10.24411/2072-8816-2018-10028

Mochalova, O.A., 2009. Rod *Sparganium* (Sparganiaceae) v Magadanskoi oblasti [The Genus *Sparganium* (Sparganiaceae) in the Magadan region]. *Botanicheskii Zhurnal* **94** (8), 1235–1241. (In Russian).

Mochalova, O.A., Yakubov, V.V., 2004. Flora Komandorskikh ostrovov [Flora of Commander islands]. Institute of Biology and Soil Sciences, Vladivostok, Russia, 120 p. (In Russian).

Nekratov, N.F., Nekratova, N.A., Nekratova, A.N., 2002. Vidovoy sostav sosudistykh rasteniy Kuznetskogo Alatau [Species composition of vascular plants of the Kuznetsk Alatau]. *Issledovano v Rossii* [*Researched in Russia]* **5**, 2022–2036. (In Russian).

Neshataev, V.Yu., Neshatayeva, V.V., Yakubov, V.V., 2017. Rastitel’nost’ akvatorii i poberezhii ozera Talovskoe i ego okrestnostei (Koryakskii okrug, Kamchatskii Krai) [Aquatic and shore vegetation of Talovskiye Lake and its surroundings (Koryak district, Kamchatka Territory)]. *Rastitelnost’ Rossii [Vegetation of Russia]* **31**, 59–76. (In Russian). https://doi.org/10.31111/vegrus/2017.31.59

Neshatayeva, V.Yu., 2009. Rastitelnost’ poluostrova Kamchatka [The vegetation of the Kamchatka Peninsula]. KMK Scientific Press Ltd, Moskow, Russia, 554 p. (In Russian).

Panarina, N.G., Papchenkov, V.G., 2005. Rastitel’nyi pokrov vodoemov i vodotokov Kandalakshskogo gosudarstvennogo prirodnogo zapovednika (Kandalakshskii zaliv, Beloe more) [Water-body and water-current vegetative cover of the Kandalaksha state natural reserve (Kandalaksha bay, the White sea)]. In: Raspopov, I.M. (ed.), *Trudy Kandalakshskogo zapovednika. Vyp. 11 [Transactions of Kandalaksha State Nature Reserve. Issue 11]*. Rybinsk Publishing House, Rybinsk, Russia, 3–166. (In Russian).

Papchenkov, V.G., 2001. Rastitelnyi pokrov vodoyomov i vodotokov Srednego Povolzhya [Vegetation cover of water bodies and water courses of the Middle Volga region]. International Academy of Business and New Technologies, Yaroslavl, Russia, 213 p. (In Russian).

Pospelova, E.B., 1998. Sosudistye rasteniya Taymyrskogo zapovednika [The vascular plants of the Taimyr nature reserve]. In: Yurtsev, B.A. (ed.), *Flora i fauna zapovednikov. Vyp. 66 [Flora and fauna of nature reserves. Issue 66]*. Borovichi Printing House, Borovichi, Russia, 102 p. (In Russian).

Razumovskaya, A.V., Petrova, O.V., 2017. Sosudistye rasteniya ozera Imandra [Vascular plants of Imandra lake. *Botanicheskii Zhurnal* **102** (1), 62–78. (In Russian).

Rebristaya, O.V., 1998. Analiz severnyh predelov rasprostraneniya rastenii Yamala (na urovne tsenoflor) [Analysis of plant northern limits in Yamal (on a coenoflora level)]. In: Yurtsev, B.A. (ed.), *Izuchenie biologicheskogo raznoobraziya metodami sravnitel’npi floristiki: Materialy IV rabochego soveshchaniya po sravnitel’noy floristike Berezinskogo biosfernogo zapovednika* [*Study of biological diversity by methods of comparative Floristics: Proceedings of the IV working meeting on comparative Floristics of the Berezinsky biosphere reserve*]. St. Petersburg State Universuty, St. Petersburg, Russia, 158–172. (In Russian).

Rebristaya, O.V., 2013. Flora poluostrova Yamal. Sovremennoe sostoyanie i istoriya formirovaniya [Flora of the Yamal Peninsula: current status and history of formation’. Saint Petersburg Electrotechnical University, St. Petersburg, Russia, 312 p. (In Russian).

Schaulo, D.N., Doduk, A.D., Molokova N.I., 2003. Floristicheskie nakhodki v Respublike Tyva (3) [The floristic findings in the Tyva Republic (3)]. *Turczaninowia* **6** (4), 35–42. (In Russian).

Sekretareva, N.A., 2004. Sosudistye rasteniya Rossiyskoy Arktiki i sopredelnykh territorii [Vascular plants of Russian Arctic and adjacent territories]. KMK Scientific Press Ltd, Moskow, Russia, 131 p. (In Russian).

Scherbina, S.S., 2009. Flora sosudistykh rastenii Tsentral’nosibirskogo gosudarstvennogo biosfernogo zapovednika i sopredelnykh territorii [Flora of vascular plants of the Central Siberian State biosperic reserve and neighboring territories]. *Turczaninowia* **12** (1–2), 71–241. (In Russian).

Sulman, J.D., Drew, B.T., Drummond, C., Hayasaka, E., Sytsma, K.J., 2013. Systematics, biogeography, and character evolution of *Sparganium* (Typhaceae): diversification of a widespread, aquatic lineage. *American Journal of Botany* **100** (10), 2023–2039. https://doi.org/10.3732/ajb.1300048

Sviridenko, B.F., Sviridenko, T.V., Mamontov, Yu.S., 2013. Ekologicheskie tablitsy dlya tselei fitoindikacii sostoyaniya vodnyh ob’ektov pri inzhenerno-ekologicheskikh izyskaniyakh na territorii Khanty-Mansiiskogo Avtonomnogo Okruga – Yugry

[Ecological tables for the purposes of phyto-indication of the state of water bodies during engineering and environmental surveys on the territory of the Khanty-Mansi Autonomous Okrug – Yugra]. *Severnyy region: nauka, obrazovanie, kul'tura* [*The Northern Region: Science, Education, Culture*] **1** (27), 40–70 (In Russian).

Takahashi, H., Volotovskyi, K.A., Sato, T., 2000. A quantitative comparison of distribution patterns in four common *Sparganium* species in Yakutia, Eastern Siberia. *Acta Phytotaxonomica et Geobotanica* **51** (2), 155–167.

Teteryuk, B.Yu., 2014. Flora ozyor Kharbeiskoi sistemy (vostok Bol'shezemel'skoi Tundry) [Flora of the Kharbey Lakes (the East of Bolshezemelskaya Tundra)]. *Zhurnal Sibirskogo federalnogo universiteta. Biologiya [Journal of Siberian Federal University. Biology]* **7** (3), 291–302. (In Russian).

Teteryuk, B.Yu., Lavrinenko, O.V., Kipriyanova, L.M., 2022. Sparganion hyperborei – new alliance in water-bodies of the Arctic and mountainous regions of Eurasia. *Botanica Pacifica* **11** (2), 1–8. https://doi.org/10.17581/bp.2022.11208

Timokhina, S.A., 1988. *Sparganium* L. – ezhegolovnik [*Sparganium* L. – bur-reed]. In: Krasnoborov, I.M. (ed.), *Flora Sibiri. Tom 1. Lycopodiaceae – Hydrocharitaceae* [*Flora of Siberia. Vol. 1. Lycopodiaceae – Hydrocharitaceae*]. Nauka, Novosibirsk, Russia, 88–92. (In Russian).

Tsyganov, D.N., 1983. Fitoindikatsiya ekologicheskikh rezhimov v podzone khvoino-shirokolictvennykh lesov [Phytoindication of environmental regimes in the subzone of coniferous and broad-leaved Forests]. Nauka, Moscow, USSR, 197 p. (In Russian).

Vekhov, N.V., 1991. Gidro- i gidatofity Vorkutinskogo promyshlennogo raiona (vostok Bol'shezemel'skoi tundry: sostav i dinamika rasseleniia v estestvennykh biotopakh [Hydro- and hydatophytes of artificial reservoirs of urban landscapes of Vorkuta and its neighbourhood (the East of the Bolshezemelskaya Tundra): composition and dynamics of dispersion in natural biotopes]. *Botanicheskii Zhurnal* **76** (6), 852–859. (In Russian).

Yuzepchuk, S.V., 1934. Sem. XVI. Ezhegolovnikovye – Sparganiaceae Engl. [Fam. XVI. Sparganiaceae Engl.]. In: Komarov, V.L. (ed.), *Flora SSSR. Tom I [Flora of the USSR. Vol. I]*. USSR Academy of Sciences, Leningrad, USSR, 219–229. (In Russian).

Zarubina, E.Yu., 2016. Vidovoe raznoobrazie i struktura rastitelnogo pokrova raznotipnykh vodoyomov i vodotokov territorii Bovanenkovskogo neftegasokondensatnogo mestorozhdeniya (Poluostrov Yamal) [The species diversity and the plant community structure of heterogeneous water bodies and channels of Bovanenkovo oil-gas condensate field site (Yamal Peninsula)]. *Nauchnyi vestnik Yamalo-Nenetskogo avtonomnogo okruga [Scientific Bulletin of the Yamalo-Nenets Autonomous District]* **2** (91), 50–55. (In Russian).

Zhukova, L.A., Dorogova, Yu.A., Turmukhametova, N.V., Gavrilova, M.N., Polyanskaya, T.A., 2010. Ekologicheskie shkaly i metody analiza ekologicheskogo raznoobraziya rastenii [Ecological scales and methods of analysis of ecological diversity of plants]. Mari State University, Yoshkar-Ola, Russia, 368 p. (In Russian).