

Littoral phytocenoses of marshes located in different tidal conditions of the White Sea

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Abstract

This paper describes the distribution of plant communities from various associations, identified from the standpoint of the ecological-phytocenotic approach, occupying the tidal flat of low and medium marshes, which are under the influence of tide range, different values of pH and water salinity. According to the degree of pH influence, we identified acidotrophic, alkalotrophic, and indifferent phytocenoses, combined into different associations. Most associations of the estuaries with different tide range are alkalotrophic, there are noticeably fewer acidotrophic ones; a few eurytopic communities from the *Phragmitetum australis*, *Bolboschoenetum maritimae*, and *Caricetum aquatilis* associations are classified as indifferent. The study shows that the coastal vegetation of the marshes of the mesotidal estuaries of the White Sea develops in stable pH conditions in the range from 7.2 to 7.6. The formation of coastal vegetation is less stable in the macrotidal estuaries of the Mezen Bay, most of them form at pH = 7.0-8.3. Halophyte vegetation forms in the widest range of pH (6.2-8.3) in the marshes of microtidal estuaries in the Dvina Bay of the White Sea, which are more affected by floods than other estuaries. The halophytic vegetation of the White Sea develops in a wide range of salinity fluctuations from brackish to marine waters. However, the majority of plant associations in the rivers estuaries occupy the habitats of weakly saline waters with 10 to 25% salinity.

Key words: the White Sea, littoral phytocenoses, estuaries, marshes, tides, salinity, pH

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¹ Marshes are considered as independent biocenoses, with a characteristic species composition of animals and plants of the littoral zone and a part of the supralittoral zone of the tidal seas. (Dijkema et al. 1984, Bakker 2014).

Introduction

Salt marshes¹ are transitional ecosystems that link land and sea, can occur globally and take on a variety of forms, differing in structure and function. They are formed under the influence of sea tides, by bringing silt and sand sediments into the dry zone of the seas (Leont'yev *et al.* 1975). Low coasts with salt marshes vegetation are formed in estuaries of the White Sea. Estuaries are one of the most productive ecosystems on the borders of freshwater and marine environments, where plant and animal representatives of euryhaline and stenohaline brackish water species live (Safyanov 1987, Morozov *et al.* 2021). Estuary-type ecosystems include many mouths of rivers flowing into the White Sea, such as the Mezen, the Onega, as well as most of the small rivers. Brackish-water lagoons of the White Sea, the Unskaya Inlet (Safyanov and Repkina 2013) and the Sukhoe More Inlet (Misevich *et al.* 2018a), desalinated by small rivers, are also considered as estuaries.

In the modern European classification, saline and brackish marshes are distinguished according to the type of vegetation cover and salinity of substrates (Bakker 1993, Beefink 1977, Dijkema *et al.* 1984). This classification is currently often used in Russia to separate marsh biotopes (Lavrinenko and Lavrinenko 2018, Moseev *et al.* 2021). According to the features of the tidal sea influence, the following marshes are distinguished: low, medium, and high marshes (Belikov *et al.* 2011). Tidal waters cover the tidal flat of low marshes 2 times a day under the conditions of semidiurnal tides of the synodic type. The influence of tides, riverine inputs, and waves vary in their contribution with distinct impacts on salt marsh functions such as floral and faunal assemblages. Tidal flats of the medium marshes are under the influence of spring tides, they are covered with water only on the new moon and full moon in the syzygy. High marshes are not covered

by tides, but they are subject to the influence of storm surges that flood the coast at different intervals. It should be noted that marshes of different levels are independent biotopes with specific inhabitants of plants, animals, and microorganisms (Bertness and Aaron 1987, Adam 1993, Bakker 2014). The climate of the White Sea is transitional from temperate maritime climate to subarctic maritime climate ([1] - Scientific and Applied Reference Book on the Climate of the USSR 1989). In the western part of the sea, in a temperate climate, northern European marshes are characteristic with a predominance of boreal vegetation: Arctic marshes along the eastern coast of the sea are characteristic for subarctic climate conditions. It should be noted that both types of marshes are distinguished according to the classification of W. Chapman, which reflects their geographical position (Chapman 1964, Dawes 1998).

Nowadays, marsh phytocenoses have been well studied alongside a significant in terms of length coast of the White Sea (Sergienko 2013a, 2013b, c; Babina 2002, Koroleva *et al.* 2011, Moseev and Sergienko 2016, 2020; Kemp *et al.* 2017, Sergienko and Moseev 2020). The phytocenoses of many estuaries in the southeast of the White Sea, including the estuary of the Kuloy River and the Unskaya Inlet, have been poorly studied.

Marshes occupy buffer zones at the junction of sea and land. Some studies addressed the influence of geochemical conditions of the habitat (namely salinization of soils, expressed in the content of chlorides and sulfates, and soil pH variability) on the halophytic vegetation of the coasts of the Bering and Chukchi Seas (*e.g.* Sergienko 2013a). Their phytocenoses are covered by tidal waters for several hours, the part of the coastal vegetation is occupied by saline waters of microdepressions; which also indicates a significant influence of hydrological and

hydrochemical environmental factors on the development of halophytic vegetation. However, there is little information on the effect of water salinity and pH on the composition of vegetation cover of tidal shores (Sergienko 2013a, Moseev 2019), which is the subject of this publication.

This manuscript does not focus on the classification of vegetation, as we provided that information in previously pub-

lished works (Moseev 2019, Moseev and Sergienko 2016, 2020). The paper analyzes the influence of abiotic environmental factors on salt marshes. The work is aimed at studying the features of the halophyte vegetation's phytocenoses distribution in the tidal zone of the White Sea with regard to the impact of hydrological and hydrochemical environmental factors (tide, salinity, pH).

Material and Methods

The vegetation structure of the marshes of the tidal zone was studied for 6 estuaries of the White Sea with different tide range, namely, the estuaries of the Keret', the Kyanda, the Kuloy and the Chizhi rivers, Unskaya Inlet, and Sukhoe More Inlet (Fig. 1). In each estuary, water measurements were conducted using standard instruments: portable conductometer IDS Meter (HACH), multi-parameter liquid analyzer Multi 3420 (WTW), and pH meter Checker HI 98103 to determine pH, salinity, total mineralization, oxygen and oxygen saturation, as hydrological and hydrochemical factors influencing the marshes hygrophilous phytocenoses formation.

Hydrobotanical studies of the vicinity of water bodies were carried out using geobotanical methods with the laying of test plots 3×3 m or 1×2 m in size, in littoral and supralittoral phytocenoses homogeneous in composition and structure. Test plots, linked to a geographic coordinates grid using a Garmin62S GPS navigator (Taiwan), were laid in the direction from the coastline to the land. On all test plots, the species composition and projective cover (in %) of all types of vascular plants, their longline position, soil type, relief features, moisture degree, salinity, and pH were determined. The phytocenoses under analyses are combined into plant associations, identified from the standpoint of the methods of the ecological-phytocenotic approach (Neshatayev 2001). In our opin-

ion, this approach is universal for studying the influence of environmental factors on phytocenoses and vegetation, which is also emphasized by other classical hydrobotanists (Papchenkov 2001).

In accordance with certain ranges of salinity and pH values, the correlation matrix was used to rank phytocenoses united into plant associations. The ranges of water salinity (S, ‰) are given according to L. Skibinsky (2003): <1‰ – fresh water, 1-10‰ – brackish, 10-25‰ – slightly saline, > 25‰ – saline or marine waters. In accordance with the water salinity index, the following types of plant associations were distinguished for marshes: freshwater – < 1‰, slightly brackish water – 1-10‰, brackish water – 10-25‰, saline – > 25‰. In accordance with the pH value, based on the classification used for river ecosystems (Zinovyeva and Durnikin 2012a, Sviridenko 2000, Salazkin 1976), the following types of plant associations were identified: acidotrophic – they are formed at pH 6.7-7.2; alkalotrophic or basotrophic – are formed at pH 7.3-8.4; indifferent – are formed at pH 6.2-10.0. Salinity and pH values in the maximum full water of the tidal cycle are taken as threshold values. Both factors are directly dependent on the tidal range, which is well expressed in the estuaries of the White Sea (Leshchev et al. 2015, Miskevich et al. 2014, 2018a, b, 2021).

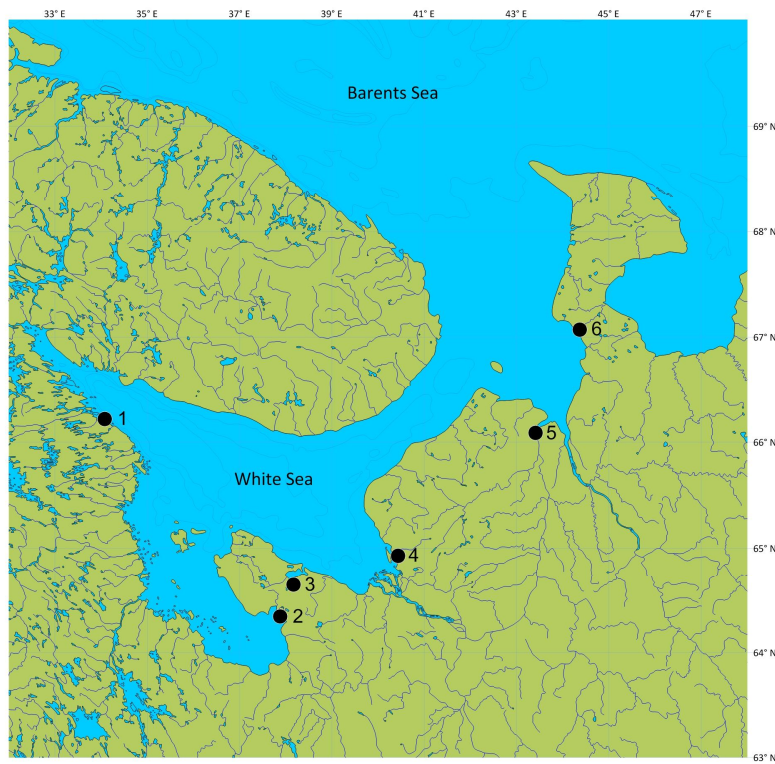


Fig. 1. Map of the research area in the White Sea.

Estuaries are marked with numbers: 1 – the Keret', 2 – the Kyanda, 3 – the Unskaya Inlet, 4 – the Sukhoe More Inlet, 5 – the Kuloy, 6 – the Chizha.

Depending on the tide level range in the estuarine section of the sea, river mouths are distinguished into three groups: with microtidal conditions – with a spring tide amplitude of less than 1.6 m; with mesotidal conditions – a spring tide amplitude of 1.6-2.8 m; and with macrotidal conditions – a spring tide amplitude of more than 2.8 m (Mikhailov 1997). Microtidal estuaries – the Sukhoye More Inlet and the Unskaya Inlet, mesotidal estuaries – the Keret' and the Kyanda rivers, macrotidal estuaries – the Kuloy and the Chizha rivers. The estuaries hydrological and hydrochemical features are heterogeneous. In 2020, the research of the Unskaya Inlet was carried out in the area of the confluence of the Unskaya Inlet in the Una

river mouth. According to measurements in September 2020, in the "kut" (a blind inlet end) part of the bay in the high water of the tidal cycle, the salinity of the water was 11.3-14.2‰ near the mouth of the Una river, and pH value was about 7.2-7.63. In the sublittoral zone, water salinity was 11.2‰ at the blind inlet end, and 15.3‰ at the exit from the inlet end to the wide inlet part with the pH 7.41-7.62. In the Sukhoye More Inlet the desalination effect of the rivers is expressed throughout the entire length of the inlet, but most of all in its southern part, where the salinity even in low water of the tidal cycle does not exceed 5.8‰. In the northern part the salinity reaches 15‰, at the mouth of the Bolshaya Nitsa river is only about 9‰. At

the narrowing inlet site salinity did not exceed 2.32‰ in July 2019 (Miskevich and Moseev 2019). In the estuary of the Keret' River, the seashore is fenced off by Sredniy Goreliy and Bolshoi Goreliy islands (Smagin et al. 2009). According to measurements made in July 2014 during the low water period, the salinity at the estuary head was 5.21‰, and at the sea boundary – 23.1‰. The average tide range in the estuary of the Kyanda River is 2.5 m (according to measurements at the station of semi-diurnal observations), so this estuary is mesotidal (Leshchev et al. 2015, Miskevich et al. 2018b). Tidal dry areas width range from several tens of meters at the estuary head to 1 km at the exit to the Onega Inlet of the White Sea. They are covered with silty-clayish and silty-sand sediments.

According to measurements in July 2015 during low water period, salinity at

the estuary head was 0.21 ‰, and at the sea boundary – 25.1‰. In the estuaries of the Kuloy River the maximum salinity in the summer low water, according to measurements carried out in August 2021 at the sea boundary of the estuary, reached 23.6‰, dropping to 0.5‰ at the top of the river estuary. Due to the presence of karst rocks in its catchment area, the Kuloy River mouth water is distinguished by elevated pH values, which determines the presence of well-expressed alkaline properties. The maximum pH value is 8.4 at the estuary boundary, which is explained by the photosynthetic activity of phytoplankton. At the top of the estuary, the pH value in the full water of the tidal cycle is 8.06; at the sea boundary it is 7.87. In the Chizha River at the sea boundary, the salinity in the full water of the tidal cycle reaches 26‰, at the top of the estuary – 0.23-14.23‰.

Results

With regard to the ecological-phytocenotic approach, we identified 30 plant associations and one type community, which differed in floristic composition and structure. The largest in vegetation area are *Alopecuretum arundinaceus subpurum Bolboschoenetum maritimi*, *Caricetum subspathaceae subpurum*, *Phragmitetum australis*, *Plantaginetum subpolaris*, *Salicornietum pojarkovae*, *Triglochinetum maritimae*.

Only 4-10 species were floristically poor, these were mainly pioneer communities of low marshes, united in the following associations: *Alopecureto-Caricetum salinae*, *Bolboschoenetum maritimi*, *Bolboschoenetum maritimi* subass. *potamogenosum pectinati*, *Caricetum aquatilis*, *Caricetum salinae*, *Caricetum subspathaceae subpurum*, *Eleocharietum uniglumis*, *Glaucetum maritimae*, *Hippuridetum tetraphyllae*, *Hippuridetum tetraphyllae* subass. *vaucheriosum velutinae*, *Phragmitetum australis* subass. *eleochariosum uniglumis*, *Plantaginetum maritimae*, *Puccinellietum phryganodis*, *Rupprietum maritimae*, *Salicornietum pojarkovae*, *Scirpetum tabernaemontanae*, *Triglochinetum maritimae caricosum subspathaceae*, *Triglochinetum maritimae tripoliosum vulgaris*. The sublittoral and lower littoral associations were distinguished by low species variety composition: *Potamogenetum pectinati*, *Rupprietum maritimae*, *Zosteretum marinae*, as well as communities dominated by *Ulva prolifera* green algae. The species composition was richer in the associations of medium marshes – it included more than 10 species. These were: *Alopecuretum arundinaceus subpurum*, *Caricetum mackenziei*, *Caricetum subspathaceae potentillosum egedae*, *Eleocharietum uniglumis triglochinosum maritimae*, *Juncetum gerardii*, *Plantaginetum maritimae* subass. *puccinelliosum coarctatae*, *Plantaginetum subpolaris*, *Phragmitetum australis*, *Triglochinetum maritimae*.

Majority associations communities under study were formed in a temperate climate (for the White Sea western and south-western coasts, which include the Keret' and Kyanda rivers estuaries, the Unskaya Inlet and the Sukhoe More Inlet): *Alopecuretum arundinaceus subpurum*, *Bolboschoenetum maritimi*, *Bolboschoenetum maritimi* subass. *potamogenosum pectinati*, *Caricetum aquatilis*, *Caricetum mackenziei*, *Eleocharietum uniglumis*, *Eleocharietum uniglumis triglochinosum maritimae*, *Glaucetum maritimae*, *Hippuridetum tetrrophyllae*, *Hippuridetum tetrrophyllae* subass. *vaucheriosum velutinae*, *Juncetum gerardii*, *Plantaginetum maritimae*, *Potamogenetum pectinati*, *Phragmitetum australis*, *Ruppisetum maritimae*, *Salicornietum pojarkovae*, *Scirpetum tabernaemontanae*, *Triglochinetum maritimae*, *Triglochinetum maritimae tripoliosum vulgaris*, *Zosteretum maritimae*, *Ulva prolifera*. According to the geographical classification (Chapman 1959, 1960, 1964), marshes with such vegetation are more characteristic of the seas of moderate latitudes in Europe and North America, so they should be attributed to the North European group.

On the eastern coast of the White Sea, including the estuaries of the Kuloy and the Chizha rivers, there were no such phytocenoses as: *Bolboschoenetum maritimi*, *Bolboschoenetum maritimi* subass. *potamogenosum pectinati*, *Eleocharietum uniglumis*, *Eleocharietum uniglumis triglochinosum maritimae*, *Glaucetum maritimae*, *Potamogenetum pectinati*, *Ruppisetum maritimae*, *Scirpetum tabernaemontanae*, *Triglochinetum maritimae tripoliosum vulgaris*, *Zosteretum marinae*, which is due to their boreal distribution in moderate latitudes and was also confirmed by Korchagin (1935), Miskevich *et al.* (2014), Moseev and Sergienko (2020). The following associations were found up to the Kuloy estuary, but absent near the Chizha River: *Plantaginetum maritimae* subass. *puccinelliosum coarctatae*, *Phragmitetum australis*, since the ranges of their diagnostic species, *Plantago maritima* and *Phragmites australis*, are limited to the forest-tundra subzone on the White Sea coast. Plant associations that were distinguished only within the Chizha river estuary were: *Alopecureto-Caricetum salinae*, *Plantaginetum subpolaris*. Arctic group of marshes associations occupied noticeably larger areas of the White Sea eastern part coasts (at the Kuloy and Chizha rivers mouths) with the dominance of arctic and hypoarctic species (Moseev and Sergienko 2020) as compared to the western part coasts: *Alopecuretum arundinaceus subpurum*, *Alopecureto-Caricetum salinae*, *Caricetum salinae*, *Caricetum subspathaceae subpurum*, *Hippuridetum tetrrophyllae*, *Puccinellietum phryganodis*, *Salicornietum pojarkovae*.

Phytocenoses found along the entire White Sea coast were *Alopecuretum arundinaceus subpurum*, *Caricetum aquatilis*, *Caricetum mackenziei*, *Caricetum subspathaceae subpurum*, *Hippuridetum tetrrophyllae*, *Hippuridetum tetrrophyllae* subass. *vaucheriosum velutinae*, *Juncetum gerardii*, *Plantaginetum maritimae*, *Puccinellietum phryganodis*, *Salicornietum pojarkovae*, *Triglochinetum maritimae*, *Triglochinetum maritimae caricosum subspathaceae*, *Ulva prolifera*.

Optimal values of salinity and pH of water for the stable formation of halophyte communities in estuaries with different tides have been identified. These values influence well the projective coverage of the dominant species (Table 1).

Estuaries with different tide levels have similar conditions for association communities development which not equally tolerant the salinity and pH of water. Water salinity values more than $> 15\text{‰}$ favorably influence forming of the low and medium marches communities with the obligate halophytes dominance. These associations are *Caricetum subspathaceae subpurum*, *Caricetum subspathaceae potentillosum egedae*, *Plantaginetum maritimae*, *Triglochinetum maritimi*, *Plantaginetum subpolaris*, *Zosteretum marinae*.

| Parameters | Correlation coefficient | |
|--|-------------------------|---------|
| | S, ‰ | pH |
| Association microtidal of the White Sea estuaries | | |
| <i>Plantaginietum maritimae</i> | >14 | 7.3-8.3 |
| <i>Zosteretum marinae</i> | >16 | 8.0-8.2 |
| <i>Triglochinietum maritimi</i> | >14 | 7.3-8.3 |
| <i>Caricetum aquatilis</i> | <1 | 6.5-7.0 |
| <i>Bolboschoenetum maritimi</i> | >3 | 7.4-8.2 |
| <i>Juncetum gerardii</i> | ~14 | ~8 |
| <i>Potamogenetum pectinati</i> | >3 | 7.3-8.3 |
| <i>Scirpetum tabernaemontanae</i> | >2 | 7.0-8.5 |
| <i>Phragmitetum australis</i> | >0 | 6.5-8.5 |
| Association mesotidal of the White Sea estuaries | | |
| <i>Eleocharietum uniglumis triglochinsum maritimi</i> | >11 | 7.0-7.5 |
| <i>Ruppium maritimae</i> | 15-18 | 7.0-8.0 |
| <i>Triglochinietum maritimi</i> | >15 | 7.0-8.0 |
| <i>Caricetum subspathaceae subpurum</i> | >15 | 7.0-8.0 |
| <i>Zosteretum marinae</i> | >15 | 7.0-8.0 |
| <i>Phragmitetum australis</i> | >0 | 6.5-8.5 |
| <i>Bolboschoenetum maritimi</i> | >15 | 7.3-7.8 |
| Association macrotidal of the White Sea estuaries | | |
| <i>Triglochinietum maritimi</i> | >15 | 7.0-8.0 |
| <i>Plantaginietum subpolaris</i> | >15 | 7.2-7.8 |
| <i>Alopecuretum arundinaceus subpurum</i> | <14 | 6.5-8.5 |
| <i>Caricetum subspathaceae potentillosum egedae</i> | >15 | 7.5-8.0 |
| <i>Triglochinietum maritimae caricetum subspathaceae</i> | >15 | 7.4-8.0 |
| <i>Salicornietum pojarkovae</i> | >15 | 7.2-7.8 |
| <i>Caricetum subspathaceae subpurum</i> | >15 | 7.0-8.0 |
| <i>Hippuridetum tetraphyllae</i> | >1 | 6.5-8.0 |
| <i>Alopecureto-Caricetum salinae</i> | >1 | 6.5-8.0 |

Table 1. The most favorable conditions for halophyte vegetation associations of the White Sea coast.

Salinity value less than <14‰ favorably influence forming of association communities with the facultative halophytes dominance. These associations are *Alopecuretum arundinaceus subpurum*, *Juncetum gerardii*, *Potamogenetum pectinati*, *Scirpetum tabernaemontanae*. *Phragmitetum australis* association communities develop under different salinity conditions.

The *Alopecureto* association communities species – *Caricetum salinae*, *Hippuridetum tetraphyllae* are also resistant to different water salinity.

Most of the coastal communities develop in conditions of a wide ecological optimum pH – 7.0-8.5 units. Large hygrophilous cereals are dominant in communities structure such as *Phragmitetum australis* and *Alopecuretum arundinaceus subpurum*. These associations are significantly dependent on tides with water pH values in range 6.5–8.5.

| Group of associations by type of pH and salinity | Ranges | the Unskaya Inlet | the Sukhoe More Inlet |
|--|----------|--|---|
| pH factor group | | | |
| | | Associations | |
| Acidotrophic | 6.5-7.2 | <i>Hippuridetum tetrphyllae</i> , <i>Hippuridetum tetrphyllae</i> subass. <i>vaucheriosum</i> <i>velutinae</i> | . |
| Alkalilotropic | 7.3-8.4 | <i>Bolboschoenetum maritimi</i> subass. <i>potamogenosum pectinati</i> , <i>Eleocharietum uniglumis</i> , <i>Plantagnetum maritimae</i> , <i>Potamogenetum pectinati</i> , <i>Puccinellietum phryganodis</i> , <i>Rupprietum maritimae</i> , <i>Salicornietum pojarkovae</i> , <i>Triglochinetum maritimi</i> , <i>Zosteretum marinae</i> | <i>Bolschoenetum maritimi</i> , <i>Eleocharietum uniglumis</i> , <i>Juncetum gerardii</i> , <i>Plantagnetum maritimae</i> , <i>Potamogenetum pectinati</i> , <i>Puccinellietum phryganodis</i> , <i>Scirpetum tabernaemontanae</i> , <i>Triglochinetum maritimi</i> , <i>Salicornietum pojarkovae</i> , <i>Rupprietum maritimae</i> , <i>Zosteretum marinae</i> |
| Indifferent | 6.5-10.0 | <i>Bolboschoenetum maritimi</i> , <i>Phragmitetum australis</i> | <i>Phragmitetum australis</i> , <i>Caricetum aquatilis</i> |
| Salinity factor group | | | |
| Fresh water | <1 | . | <i>Caricetum aquatilis</i> |
| Brackish water | 1-10‰ | <i>Bolboschoenetum maritimi</i> , <i>Eleocharietum uniglumis</i> , <i>Hippuridetum tetrphyllae</i> , <i>Hippuridetum tetrphyllae</i> subass. <i>vaucheriosum velutinae</i> , <i>Phragmitetum australis</i> | <i>Bolschoenetum maritimi</i> , <i>Eleocharietum uniglumis</i> , <i>Phragmitetum australis</i> , <i>Potamogenetum pectinati</i> , <i>Scirpetum tabernaemontanae</i> |
| Slightly saline water | 10-25‰ | <i>Bolboschoenetum maritimi</i> , <i>Bolboschoenetum maritimi</i> subass. <i>potamogenosum pectinati</i> , <i>Eleocharietum uniglumis</i> , <i>Phragmitetum australis</i> , <i>Plantagnetum maritimae</i> , <i>Potamogenetum pectinati</i> , <i>Puccinellietum phryganodis</i> , <i>Rupprietum maritimae</i> , <i>Salicornietum pojarkovae</i> , <i>Triglochinetum maritimi</i> , <i>Zosteretum marinae</i> | <i>Juncetum gerardii</i> , <i>Phragmitetum australis</i> , <i>Plantagnetum maritimae</i> , <i>Potamogenetum pectinati</i> , <i>Puccinellietum phryganodis</i> , <i>Salicornietum pojarkovae</i> , <i>Triglochinetum maritimi</i> , <i>Zosteretum maritimae</i> |

| | | | |
|---|------|--|----|
| Saline or marine waters | >25‰ | | |
| Results | | | |
| Total associations in microtidal conditions | 13 | | 12 |
| of which by pH group: | | | |
| Acidotrophic | 2 | | 0 |
| Alkalilithotrophic | 9 | | 10 |
| Indifferent | 2 | | 2 |
| by salinity group: | | | |
| Fresh water | 0 | | 1 |
| Brackish | 5 | | 5 |
| Slightly saline | 11 | | 8 |
| Saline | 0 | | 0 |

Table 2. Distribution of associations by pH and salinity factors in estuaries with microtidal conditions.

Some communities development conditions are formed in a narrow ecological optimum pH. This was true for the associations: *Alopecureto-Caricetum salinae*, *Caricetum aquatilis*, *Caricetum subspathaceae potentillosum egedae*, *Juncetum gerardii*, *Hippuridetum tetraphyllae*, *Plantaginetum subpolaris*, *Scirpetum tabernaemontanae*, *Zosteretum marinae*.

Phytocenoses of marshes in microtidal conditions of the White Sea estuaries

In the studied area of the White Sea, microtidal conditions with a spring tide of less than 1 m are characteristic for all the mouths of the rivers flowing into the Unskaya Inlet (the Una, the Babia, the Karbasovka, the Seitsa), and into the Sukhoe More Inlet (the Mudyuga, the Kad', the Bolshaya Nitsa).

In the head of the Unskaya Inlet and the southern part of the Sukhoe More Inlet water area, the desalination effect of the rivers contributes to the formation of brackish marshes, with the dominance of tall-grass hygrophilous species *Phragmites australis*, *Bolboschoenus maritimus*. In the north of the Sukhoe More Inlet and at the exit from the Unskaya Inlet to the Dvina Bay, salt marshes are formed with the dominance of obligate halophytes: *Salicornia pojarkovae*, *Plantago maritima*, *P. subpolaris*, *Triglochin maritima*, *Carex subspathacea* (Table 2).

Despite the low level of the tide, the extensive wetlands of the marshes of the Unskaya Inlet and the Sukhoe More Inlet contribute to the high phytocenotic diversity of halophyte vegetation. Most of the communities on the middle and low marshes of these bays are confined to silty wetlands covered with weakly saline waters of the tides (10-25‰): *Zosteretum marinae*, *Potamogenetum pectinati*, *Bolboschoenetum maritimi potamogenosum pectinati*, *Triglochinnetum maritimi*, *Juncetum gerardii*, *Plantaginetum maritimae*, *Salicornietum pojarkovae*. Under the influence of brackish tidal waters (1-10‰), communities of the associations *Hippuridetum tetraphyllae*, *Eleocharietum uniglumis*, and *Scirpetum tabernaemontanae* were formed. In the fresh water conditions of river deltas flowing into the Sukhoe More Inlet, cenoses of *Caricetum aquatilis* were common.

| Group of associations by type of pH and salinity | Range | the Keret' | the Kyanda |
|--|----------|---|--|
| pH factor group | | | |
| | | Associations | |
| Acidotrophic | 6.5-7.2 | . | . |
| Alkalilotrophic | 7.3-8.4 | <i>Blysmetum rufi</i> , <i>Eleocharietum uniglumis triglochinosum maritimae</i> , <i>Caricetum subspathaceae subpurum</i> , <i>Hippuridetum tetrphyllae</i> , <i>Phragmitetum australis eleochariosum uniglumis</i> , <i>Rupprietum maritimae</i> , <i>Triglochinetum maritimi</i> , <i>Zosteretum marinae</i> | <i>Bolboschoenetum maritimi</i> , <i>Caricetum salinae</i> , <i>Glaucetum maritimae</i> , <i>Triglochinetum maritimi tripoliosum vulgare</i> |
| Indifferent | 6.5-10.0 | <i>Caricetum aquatilis</i> | <i>Phragmitetum australis</i> , <i>Caricetum aquatilis</i> |
| Salinity factor group | | | |
| Fresh water | <1 | <i>Caricetum aquatilis</i> | <i>Caricetum aquatilis</i> , <i>Phragmitetum australis</i> |
| Brackish water | 1-10‰ | <i>Caricetum aquatilis</i> , <i>Eleocharietum uniglumis triglochinosum maritimi</i> , <i>Hippuridetum tetrphyllae</i> | <i>Caricetum salinae</i> , <i>Phragmitetum australis</i> |
| Slightly saline water | 10-25‰ | <i>Blysmetum rufi</i> , <i>Caricetum subspathaceae</i> , <i>Eleocharietum uniglumis triglochinosum maritimi</i> , <i>Hippuridetum tetrphyllae</i> , <i>Phragmites australis eleocharietum uniglumis</i> <i>Rupprietum maritimae</i> , <i>Triglochinetum maritimi</i> , <i>Zosteretum marinae</i> | <i>Bolboschoenetum maritimi</i> , <i>Glaucetum maritimae</i> , <i>Phragmitetum australis</i> , <i>Triglochinetum maritimi tripoliosum vulgare</i> |
| Saline or marine waters | >25‰ | . | . |
| Results | | | |
| Total associations in microtidal conditions | | 9 | 6 |
| of which by pH group: Acidotrophic | | 0 | 0 |

| | | | |
|--------------------|--|---|---|
| Alkalilotropic | | 8 | 4 |
| Indifferent | | 1 | 2 |
| by salinity group: | | 1 | 2 |
| Fresh water | | | |
| Brackish | | 3 | 2 |
| Slightly saline | | 8 | 4 |
| Saline | | 0 | 0 |

Table 3. Distribution of associations by pH and salinity factors in estuaries with mesotidal conditions.

The communities of *Bolboschoenetum maritimi*, *Potamogenetum pectinati*, and *Phragmitetum australis* associations, which are the most eurytopic in relation to water salinity, occupy silty wetlands of the low-level marshes within a wide range of water salinity counting from 1 to 25‰.

The pH factor is significant for all phytocenoses. As the analysis showed, most communities of the White Sea marshes are alkalotropic, *i.e.*, they occupy habitats with a pH of alkaline and weakly alkaline environment in the range of 7.2-8.4. They were grouped into *Bolschoenetum maritimi*, *Bolboschoenetum maritimi potamogenosum pectinati*, *Eleocharietum uniglumis*, *Plantaginetum maritimae*, *Potamogenetum pectinati*, *Puccinellietum phryganodis*, *Salicornietum pojarkovae*, *Scirpetum tabernaemontanae*, *Triglochinietum maritimi*, *Zosteretum marinae* associations. Communities of the *Hippuridetum tetraphyllae* association, characteristic of small shallow lakes located within marshes, and ecologically similar communities of *Hippuridetum tetraphyllae subass. vaucheriosum velutinae* develop at slightly acidic and neutral pH 6.5-7.2, therefore they are classified as acidotrophic. The most eurytopic plant associations, *Caricetum aquatilis* and *Phragmitetum australis*, were indifferent and can develop in a wide range of water pH from 6.5 to 10.3.

Phytocenoses of marshes in mesotidal conditions of the White Sea estuaries

Mesotidal conditions are formed in the estuaries of the rivers flowing into the Onega and the Kandalaksha bays of the White Sea (Miskevich 1988) and were studied by us on the example of the estuaries of the Keret' and the Kyanda rivers. Estuary marshes in the Keret' river have a low location and are almost completely flooded during the high tide phase (Moseev 2019). In the estuary of the Kyanda River, a significant part of the marshes occupied an accumulative terrace located slightly above sea level; most of the marshes are covered with water during spring tides. Only those foreshores are covered by the tide twice a day, which are closer to the sea and are located below the accumulative terrace.

The phytocenotic diversity in the mesotidal conditions of the estuaries is rich due to the large length and width of the marshes, but, for example, the composition and structure of plant associations on the Kyanda and the Keret' rivers differ significantly. This is due to the different mechanical composition of soils, salinity and the influence of flooding of the coast by the tide (Table 3).

| Group of associations by type of pH and salinity | Range | the Chizha | the Kuloy |
|--|----------|---|---|
| pH factor group | | | |
| | | Associations | |
| Acidotrophic | 6.5-7.2 | <i>Alopecuretum arundinaceus subpurum</i> , <i>Alopecureto-Caricetum salinae</i> , <i>Caricetum aquatilis</i> | . |
| Alkalilotropic | 7.3-8.4 | <i>Caricetum subspathaceae subpurum</i> , <i>Puccinellietum phryganodis</i> , <i>Plantaginetum subpolaris</i> , <i>Salicornietum pojarkovae</i> , <i>Triglochinetum maritimi</i> , <i>Triglochinetum maritimi caricosum subspathaceae</i> | <i>Caricetum subspathaceae subpurum</i> , <i>Plantaginetum maritimae</i> , <i>Plantaginetum maritimae</i> subass. <i>puccinellietum coarctatae</i> , <i>Puccinellietum phryganodis</i> , <i>Triglochinetum maritimi</i> , <i>Ulva prolifera</i> |
| Indifferent | 6.5-10.0 | <i>Caricetum subspathaceae potentillosum egedae</i> , <i>Hippuridetum tetraphyllae</i> | <i>Alopecuretum arundinaceus subpurum</i> , <i>Phragmitetum australis</i> , <i>Caricetum aquatilis</i> |
| Salinity factor group | | | |
| Fresh water | <1 | <i>Caricetum aquatilis</i> | . |
| Brackish water | 1-10‰ | <i>Alopecuretum arundinaceus subpurum</i> , <i>Alopecureto-Caricetum salinae</i> , <i>Hippuridetum tetraphyllae</i> | <i>Alopecuretum arundinaceus subpurum</i> , <i>Caricetum aquatilis</i> , <i>Phragmitetum australis</i> |
| Slightly saline water | 10-25‰ | <i>Alopecuretum arundinaceus subpurum</i> , <i>Alopecureto-Caricetum salinae</i> , <i>Caricetum subspathaceae potentillosum egedae</i> , <i>Hippuridetum tetraphyllae</i> , <i>Plantaginetum subpolaris</i> , <i>Puccinellietum phryganodis</i> , <i>Salicornietum pojarkovae</i> , <i>Triglochinetum maritimi</i> , <i>Triglochinetum maritimi caricosum subspathaceae</i> | <i>Alopecuretum arundinaceus subpurum</i> , <i>Caricetum subspathaceae subpurum</i> , <i>Plantaginetum maritimae</i> subass. <i>puccinellietum coarctatae</i> , <i>Triglochinetum maritimi</i> , <i>Ulva prolifera</i> , <i>Phragmitetum australis</i> |
| Saline or marine waters | >25‰ | <i>Caricetum subspathaceae subpurum</i> , <i>Caricetum subspathaceae potentillosum egedae</i> , <i>Hippuridetum tetraphyllae</i> , | <i>Caricetum subspathaceae subpurum</i> , <i>Puccinellietum phryganodis</i> |

| | | | |
|---|----|--|---|
| | | <i>Plantaginetum sub-polaris</i> , <i>Puccinellietum phryganodis</i> , <i>Salicornietum pojarkovae</i> , <i>Triglochinietum maritimi</i> , <i>Triglochinietum maritimi caricosum subspathaceae</i> | |
| Results | | | |
| Total associations in microtidal conditions | 11 | | 9 |
| of which by pH group: | 3 | | |
| Acidotrophic | | | |
| Alkalilotrophic | 6 | | 6 |
| Indifferent | 2 | | 3 |
| by salinity group: | 1 | | |
| Fresh water | | | |
| Brackish | 3 | | 3 |
| Slightly saline | 9 | | 6 |
| Saline | 8 | | 2 |

Table 4. Distribution of associations by pH and salinity factors in estuaries with macrotidal conditions.

Most plant associations formed mainly by obligate halophytes are developed on silt-clay wetlands in slightly saline waters (10-25‰) – such as *Blysmetum rufi*, *Bolboschoenetum maritimi*, *Caricetum subspathaceae*, *Phragmites australis* subass. *Eleocharietum uniglumis*, *Ruppium maritima*, *Triglochinietum maritima*, *Triglochinietum maritimi* subass. *tripoliosum vulgare*, *Zosteretum marinae*. Phytocenoses of the *Caricetum salinae* association develop in the conditions of brackish waters of the estuary of the Kyanda River. The *Caricetum aquatilis* association is predominantly freshwater, but its communities in the Keret' Inlet are also covered by tidal waters with a salinity of up to 5‰. The *Phragmitetum australis* association from the mouth of the Kyanda River, as well as *Eleocharietum uniglumis triglochinosum maritimi* and *Hippuridetum tetraphyllae*, occupy the muddy tidal flat of the Keret' Inlet. They are more eurytopic and are formed under the conditions of a wide range of brackish waters with salinity level from 1 to 25‰. In the Keret' Inlet, the formation of *Zosteretum marinae* communities is influenced by the halocline, which is formed in the bottom layers (Moseev 2019). Thanks to the halocline, the water salinity in the bottom layers does not drop below 10 ‰, and its temperature is much lower compared to the water surface of the bay.

In accordance with the pH factor, most estuary communities with mesotidal conditions get into the alkalotrophic group: *Bolboschoenetum maritimi*, *Blysmetum rufi*, *Caricetum salinae*, *Caricetum subspathaceae*, *Eleocharietum uniglumis triglochinosum maritimi*, *Glaucetum maritima*, *Hippuridetum tetraphyllae*, *Phragmitetum australis eleochariosum uniglumis*, *Ruppium maritima*, *Triglochinietum maritima*, *Triglochinietum maritima tripoliosum vulgare*. Only hygrophilous communities of two eurytopic associations, *Phragmitetum australis* and *Caricetum aquatilis*, with a predominance of tall-grass hygrophilous species, are indifferent to the formation on marshes in terms of pH value.

Phytocenoses of marshes in the macrotidal conditions of the White Sea estuaries

In the White Sea, macrotidal conditions are manifested for the mouths of those rivers which flow into the Mezen' Bay and its wide part at the outlet to the Barents Sea, called the "Vorotka". Phytocenoses of marshes formed under macrotidal conditions were studied on the example of the Kuloy and the Chizha rivers' estuaries (Table 4).

These marshes should be attributed to the Arctic group according to the geographical location of the mouth of the Chizha River which flows in the tundra zone off the eastern coast of the White Sea. Many boreal species of coastal vegetation disappeared recently. At the mouth of the Kuloy River, on the border of the taiga and the forest-tundra zones. The marshes should rather be attributed to the transitional type between the North European and the Arctic ones. However, despite the geographical location and high tides, diverse ecotopes with wide littoral tidal flat contribute to the rich phytocenotic diversity of the tidal zone of macrotidal estuaries. Seaside phytocenoses here are combined into 15 associations and subassociations.

Communities of associations with dominance and numerical predominance of obligate halophytes are formed during flooding with slightly saline and sea waters (Table 4). These associations are: *Caricetum subspathaceae potentillosum egedae*, *Caricetum subspathaceae subpurum*, *Plantaginetum maritimae*, *Plantaginetum maritimae* subass. *puccinellietum coarctatae*, *Plantaginetum subpolaris*, *Salicornietum pojarkovae*, *Triglochinetum maritimi*, *Triglochinetum maritimi caricosum subspathaceae*, and the green algae *Ulva prolifera*. Monodominant communities of *Puccinellietum phryganodis* are covered only by sea waters with >25‰. The most eurytopic in terms of salinity are phytocenoses of *Hippuridetum tetraphyllae*, occupying small lakes with salt water from 1 to 26‰. Hygrophytic tall grass phytocenoses *Alopecuretum arundinaceus subpurum*, *Alopecureto-Caricetum salinae*, *Phragmitetum australis*, where facultative halophytes and species tolerant to salinity dominate, are covered with brackish and slightly saline waters of the tides. The *Caricetum aquatilis* association occupies narrow clay drains, where it is flooded with water below 10‰.

Thus, in contrast to meso- and microtidal conditions, associations in macrotidal conditions cover a wider range of water salinity (Fig. 3).

In accordance with the pH index, most communities in macrotidal conditions are alkalotrophic, for example: *Alopecuretum arundinaceus subpurum*, *Caricetum subspathaceae subpurum*, *Phragmitetum australis*, *Plantaginetum maritimae*, *Plantaginetum maritimae puccinellietum coarctatae*, *Plantaginetum subpolaris*, *Puccinellietum phryganodis*. In the estuary of the Chizha River, in a slightly acidic or almost neutral environment, phytocenoses of *Alopecuretum arundinaceus subpurum*, *Alopecureto-Caricetum salinae*, *Caricetum aquatilis* associations are developed. Associations of *Caricetum subspathaceae potentillosum egedae*, *Hippuridetum tetraphyllae*, *Phragmitetum australis* are formed over a wide pH range.

Discussion and Summary

The influence of abiotic factors (pH index and water salinity) had an ambiguous effect on the structure of halophytic vegetation in the conditions of the White Sea estuaries with different tide values. It was manifested in the distribution of coastal phytocenoses within the biotopes of the tidal zone of marshes. These factors were limiting for coastal phytocenoses and halophyte plants included in them. The salinity and pH index

of the water mainly affected the coastal phytocenoses, which occupied the tidal flat of low and medium marshes under the direct influence of the tide, *i.e.* they are covered with water either 2 times a day or periodically 2 times a month during the syzygy.

Analysis of estuary phytocenoses according to the pH index. A graphical interpretation of the distribution of plant associations shows (Fig. 3) that in mesotidal estuaries, most plant associations develop under conditions of stable pH with a small range of this indicator from 7.2 to 7.6, which can be explained by the weak effect of floods on halophyte vegetation in a wide funnel-shaped estuary of the Keret' river. Phytocenoses develop less stably in macrotidal conditions, and most of them are alkalotrophic. In an even larger pH range, vegetation develops on the marshes of macrotidal estuaries, where there are many both alkalotrophic and acidotrophic associations.

Most communities in estuaries with macro-, meso- and microtidal conditions fall into the alkalotrophic group; their ecological-coenotic optimum of stable existence is within 7.2-8.4 pH units (Fig. 3). These include: *Blysmetum rufti*, *Bolboschoenetum maritimi* subass. *potamogenosum pectinati*, *Caricetum subspathaceae subpurum*, *Eleocharietum uniglumis*, *Eleocharietum uniglumis triglochinosum maritimi*, *Juncetum gerardii*, *Plantaginietum maritimae*, *Plantaginietum subpolaris*, *Potamogenetum pectinati*, *Puccinellietum phryganodis*, *Salicornietum pojarkovae*, *Scirpetum tabernaemontanae*, *Triglochinetum maritimi*, *Triglochinetum maritimi caricetum subspathaceae*, *Phragmitetum australis eleochariosum uniglumis*, *Ruppium maritimae*, *Triglochinetum maritimi*, *Zosteretum marinae*. Phytocenoses of *Bolboschoenetum maritimi* are very large in area. In many estuaries they occupy habitats with a pH of 7.2-8.4, however in the Unskaya Inlet they are found in brackish lakes with a pH of 6.82. On silty tidal wetlands of the inlet, they are formed at pH > 7.2, *i.e.*, they can exist in a wide pH range, depending on the biotopes they occupy.

The acidotrophic group of associations was identified in estuaries with micro- and macrotidal conditions; these are associations of *Hippuridetum tetraphyllae*, *Hippuridetum tetraphyllae* subass. *vaucheriosum velutinae*, *Alopecuretum arundinaceus subpurum*, *Alopecureto-Caricetum salinae*. At the same time, the phytocenoses of the *Hippuridetum tetraphyllae* association in the mesotidal conditions of the Keret' and the Chizha estuaries manifest themselves as indifferent ones. Phytocenoses of *Alopecuretum arundinaceus subpurum* have an ecological-coenotic optimum with a pH of 7.2-8.4 in the Kuloy and the Chizha estuaries (Fig. 2, point 7).

Phragmitetum australis, *Caricetum aquatilis*, *Hippuridetum tetraphyllae* phytocenoses are formed in all estuaries in a wide range of ecological-coenotic pH optimum – from 6.5 to 10.0 (Fig. 3, points 1, 18, 19).

According to L. A. Sergienko (Sergienko 2013a), a number of plant associations on the coasts of the Bering and the Chukchi Seas, which are similar in species composition and structure, occupy habitats with different pH values in soil and are alkalotrophic (basotrophic) and acidotrophic. Good examples are phytocenoses *Caricetum subspathaceae*, *Caricetum subspathaceae potentillosum egedae*, *Puccinellietum phryganodis* associations. The phytocenoses of the *Hippuridetum tetraphyllae* association are confined to neutral and slightly acidic soil and water pH values, which brings them closer to our data (Sergienko 2013a). Phytocenoses of marsh associations of the southeastern coast of the Barents Sea occupy habitats with a slightly acidic environment (pH = 5.7-6.5) (Matveeva and Lavrinenko 2011). In this paper, the classification of halophyte vegetation was carried out on the basis of the ecological and floristic approach. The species composition of the communities is, in fact, similar to our descriptions for the *Caricetum*

mackenziei, *Caricetum subspathaceae subpurum*, *Hippuridetum tetraphyllae*, *Puccinellietum phryganodis* associations (Moseev and Sergienko 2016, 2020). According to the literature data for the Atlantic coast in the northeast of North America (New England), *Juncus gerardii* lives at pH = 6.42–6.45, which is significantly lower than in the studied habitats of the White Sea coast communities (Beefink 1977).

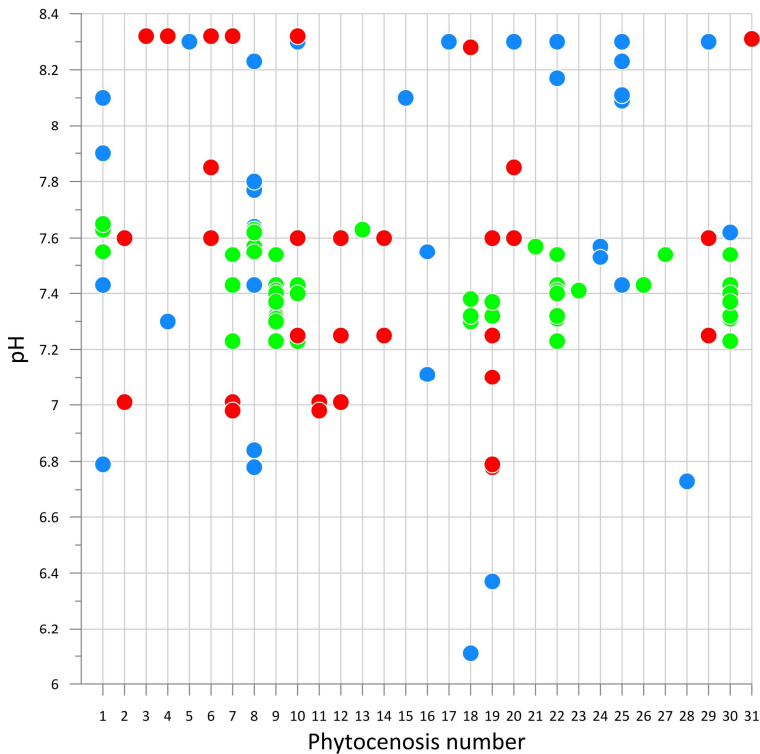


Fig. 2. Influence of the pH factor on phytocenoses of estuaries with different tide levels. Associations of microtidal estuaries are blue, mesotidal estuaries – green, and macrotidal estuaries – red.

Association numbers: 1 – *Phragmitetum australis*, 2 – *Caricetum subspathaceae potentillosum egedae*, 3 – *Plantaginetum maritimae* subass. *puccinelliosum coarctatae*, 4 – *Caricetum mackenziei*, 5 – *Juncetum gerardii*, 6 – *Caricetum subspathaceae subpurum*, 7 – *Alopecuretum arundinaceus subpurum*, 8 – *Bolboschoenetum maritimi*, 9 – *Eleocharietum uniglumis triglochinosum maritimi*, 10 – *Triglochinatum maritimi*, 11 – *Alopecureto-Caricetum salinae*, 12 – *Plantaginetum subpolaris*, 13 – *Caricetum salinae*, 14 – *Triglochinatum maritimi caricosum subspathaceae*, 15 – *Eleocharietum uniglumis*, 16 – *Scirpetum tabernaemontanae*, 17 – *Plantaginetum maritimae*, 18 – *Caricetum aquatilis*, 19 – *Hippuridetum tetraphyllae*, 20 – *Puccinellietum phryganodis*, 21 – *Triglochinatum maritimi tripoliosum vulgare*, 22 – *Zosteretum marinae*, 23 – *Phragmitetum australis* subass. *eleochariosum uniglumis*, 24 – *Bolboschoenetum maritimi* subass. *potamogenosum pectinati*, 25 – *Potamogenetum pectinati*, 26 – *Blysmetum rufi*, 27 – *Glaucetum maritimae*, 28 – *Hippuridetum tetraphyllae* subass. *vaucheriosum velutinae*, 29 – *Salicornietum pojarkovae*, 30 – *Ruppisetum maritimae*, 31 – *Ulva prolifera*.

In total, 16 associations of the alkalotrophic group were identified within the marshes with microtidal conditions, 12 associations on marshes with mesotidal conditions, and 8 associations on marshes with macrotidal conditions. There are not many acidotrophic associations at different tide values (Tables 2, 3, 4).

Analysis of estuary phytocenoses by salinity factor

At different tide values, most plant associations are confined to the zone of influence of brackish waters in the range from 1 to 25‰ (Fig. 4). Therefore, the communities of the White Sea marshes can be named the estuary ones to some extent. In microtidal conditions, the brackish water group includes such associations as *Bolboschoenetum maritimi*, *Bolboschoenetum maritimi* subass. *potamogenosum*, *Eleocharietum uniglumis*, *Plantaginetum maritimae*, *Potamogenetum pectinati*, *Puccinellietum phryganodis*, *Ruppium maritimae*, *Zosteretum marinae*, *Juncetum gerardii*, *Phragmitetum australis*, *Plantaginetum maritimae*, *Potamogenetum pectinati*, *Puccinellietum phryganodis*, *Salicornietum pojarkovae*, *Triglochinietum maritimi*, *Zosteretum marinae*. Similar associations in this group concerning water salinity can also be observed in mesotidal conditions, these are: *Bolboschoenetum maritimi*, *Blysmetum rufi*, *Caricetum subspathaceae*, *Eleocharietum uniglumis triglochinosum maritimi*, *Glaucetum maritimae*, *Hippuridetum tetraphyllae*, *Phragmites australis eleocharietum uniglumis*, *Ruppium maritimae*, *Triglochinietum maritimi*, *Triglochinietum maritimi tripoliosum vulgaris*, *Zosteretum marinae*. The communities of this salinity group differ slightly in macrotidal conditions, which is associated with a colder climate, since the marshes of the Chizha and the Kuloy rivers estuaries are located to the north of the other estuaries and are arctic according to the Chapman's climatic zoning. These associations are: *Alopecuretum arundinaceus subpurum*, *Alopecureto-Caricetum salinae*, *Caricetum subspathaceae potentillosum egedae*, *Hippuridetum tetraphyllae*, *Plantaginetum subpolaris*, *Plantaginetum maritimae* subass. *puccinellietum coarctatae*, *Puccinellietum phryganodis*, *Salicornietum pojarkovae*, *Triglochinietum maritimi*, *Triglochinietum maritimi caricosum subspathaceae*, *Ulva prolifera*.

A small number of phytocenoses of the Unskaya Inlet and the Sukhoe More Inlet fall into the group of influence of slightly brackish waters (with water salinity from 1 to 10‰). These are: *Hippuridetum tetraphyllae*, *Hippuridetum tetraphyllae* subass. *vaucheria velutina*, *Scirpetum tabernaemontanae*. *Bolboschoenetum maritimi* and *Eleocharietum uniglumis* phytocenoses are also developed in microtidal conditions at such salinity. Under mesotidal conditions, the *Eleocharietum uniglumis triglochinosum maritimi* and *Caricetum salinae* associations develop, the ones which can also develop in a larger range of brackish waters (from 10 to 25‰).

At different tide levels at the tops of all estuaries, where the salinity usually does not exceed 1‰, communities of *Caricetum aquatilis* are formed. They can be covered with waters with a salinity of 1-2‰ only in the Keret' and the Kuloy estuaries (Fig. 4, point 18). Halophytic communities of *Triglochinietum maritimi* and *Triglochinietum maritimi caricosum subspathaceae* are, on the contrary, found only in waters with a salinity of at least 10‰.

Phytocenoses of silty drying heights were formed only in macrotidal conditions at the sea boundaries of the Chizha and the Kuloy estuaries, covered with saline waters > 25‰. This vegetation dominated by euhalophytes belongs to the *Caricetum subspathaceae subpurum*, *Caricetum subspathaceae potentillosum egedae*, *Hippuridetum tetraphyllae*, *Plantaginetum subpolaris*, *Puccinellietum phryganodis*, *Salicornietum pojarkovae*, *Triglochinietum maritimi*, *Triglochinietum maritimi caricosum subspathaceae* associations.

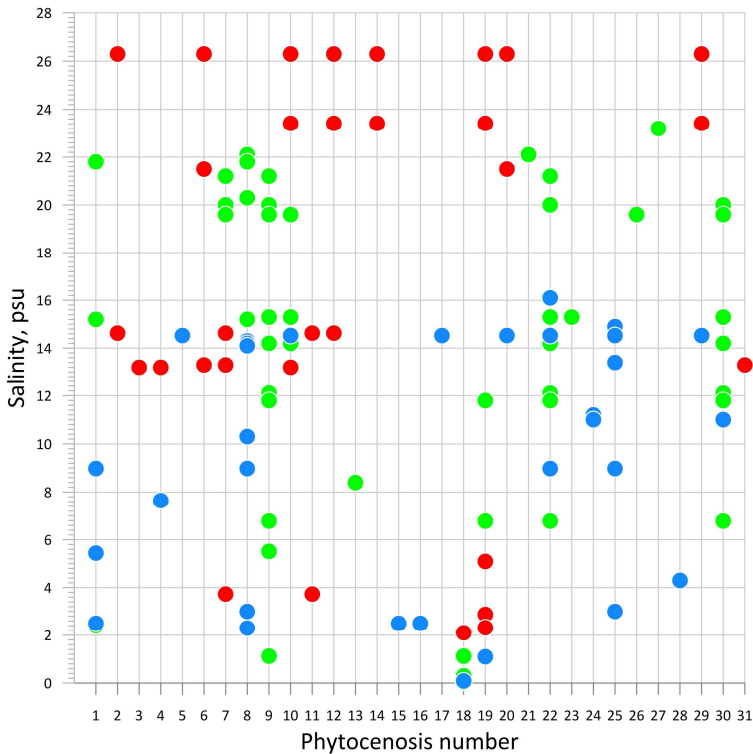


Fig. 3. Influence of water salinity factor on phytocenoses of estuaries with different tide levels. Associations of microtidal estuaries are highlighted in blue, mesotidal estuaries in green, and macrotidal estuaries in red.

Association numbers: 1 – *Phragmitetum australis*, 2 – *Caricetum subspathaceae potentillosum egedae*, 3 – *Plantaginetum maritimae* subass. *puccinelliosum coarctatae*, 4 – *Caricetum mackenziei*, 5 – *Juncetum gerardii*, 6 – *Caricetum subspathaceae subpurum*, 7 – *Alopecuretum arundinaceus subpurum*, 8 – *Bolboschoenetum maritimi*, 9 – *Eleocharietum uniglumis triglochinosum maritimi*, 10 – *Triglochinetum maritimi*, 11 – *Alopecureto-Caricetum salinae*, 12 – *Plantaginetum subpolaris*, 13 – *Caricetum salinae*, 14 – *Triglochinetum maritimi caricosum subspathaceae*, 15 – *Eleocharietum uniglumis*, 16 – *Scirpetum tabernaemontanae*, 17 – *Plantaginetum maritimae*, 18 – *Caricetum aquatilis*, 19 – *Hippuridetum tetraphyllae*, 20 – *Puccinellietum phryganodis*, 21 – *Triglochinetum maritimi tripoliosum vulgaris*, 22 – *Zosteretum maritimae*, 23 – *Phragmitetum australis* subass. *eleochariosum uniglumis*, 24 – *Bolboschoenetum maritimi* subass. *potamogenosum pectinati*, 25 – *Potamogenetum pectinati*, 26 – *Blysmetum rufi*, 27 – *Glaucetum maritimae*, 28 – *Hippuridetum tetraphyllae* subass. *vaucheriosum velutinae*, 29 – *Salicornietum pojarkovae*, 30 – *Ruppietum maritimae*, 31 – *Ulva prolifera*.

On the coasts of the Bering and the Chukchi Seas, phytocenoses of most coastal associations occupy habitats with different soil salinity (Sergienko 2013a, c), which, in our case, is also characteristic of phytocenoses of halophytic vegetation of marshes in micro- and mesotidal estuaries of the White Sea. Phytocenoses of the southeastern coast of the Barents Sea also develop under conditions of varying soil salinity (Matveeva and Lavrinenko 2011). For the northeastern coast of North America (New England), data are given on the habitats of *Juncetum gerardii* communities at salinities from 16.6 to 23.0‰

(Bertness and Aaron 1987). In the brackish lakes of southern Siberia, communities of *Potamogeton pectinatus* develop at a high mineralization of 0.603–2.587 g/dm³, but in the same region, communities of *Ruppia maritima* occupy habitats with a wide range of water salinity (9.350 – 42‰) (Kipriyanova 2022).

In a wide range of water salinity from < 1‰ to 25‰, boreal eurytopic phytocenoses of the *Phragmitetum australis* association are formed. These are characteristic of almost all estuaries except for the Chizha River estuary (Fig. 6, point 1), where the dominant species *Phragmites australis* is not found due to the unfavorable climatic conditions. Such distribution of this association in different ecological conditions of the White Sea estuaries is associated with the peculiarities of the root system morphology of the dominant glycophyte *Phragmites australis*. The extensive root system of the reed penetrates deep into the soil, reaching non-saline horizons with different pH values (Babina 2002). It should be noted that the habitat conditions of *Phragmites australis* in a wide range of salinity and mineralization have been established in different research areas, both on the sea coasts and inland waters (Zinovyeva and Durnikin 2012b, Moseev and Sergienko 2016).

However, some phytocenoses of plant associations which are found in the macrotidal estuaries of the Kuloy and the Chizha rivers of the White Sea coast, tend to marshes, covered with saline waters of tides with the salinity > 25‰.

Conclusion

For the first time, the analysis of phytocenoses from 30 associations of the White Sea marshes was carried out evaluating pH and salinity factors. It was conducted for 6 estuaries with different tide values: (1) the Unskaya and the Sukhoe More Inlets, where microtidal conditions are observed; (2) estuaries of the Keret' and the Kyanda rivers, with mesotidal conditions; and (3) estuaries of the Kuloy and the Chizha rivers with macrotidal conditions.

The tidal range factor is significant for all coastal plant associations, but it acts more essentially in macrotidal estuaries, when sea tides have greater influence on the halophyte vegetation formation than other environmental factors. Most phytocenoses under different tidal conditions belong to the alkotrophic group in terms of pH value. At different tide values, coastal phytocenoses are mainly formed in the

range of brackish water influence from 10 to 25‰. However, near the seashore in the macrotidal estuary of the Chizha river they also occupy marshes covered with saline waters with the salinity value > 25‰.

As indicators of the acidity of estuarine waters, we can distinguish stenotopic phytocenoses, which occupy habitats in a narrow range of pH 7.4–8.4. At the tops of almost all estuaries, a transitional association *Caricetum aquatilis* from salty to fresh waters has been identified.

In estuaries with different tide values, the communities of the *Phragmitetum australis* association are the most eurytopic with respect to different pH and water salinity. The latter currently occupy very large areas on the coast of the Unskaya Inlet, in the Sukhoe More Inlet and at the mouth of the Kyanda River.

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