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## Article

# Common reed *Phragmites australis* in the ecotopes of the White Sea coastal zone

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**Abstract.** The tall emergent perennial common reed *Phragmites australis* is widespread across a vast area from the western to the eastern coast of the White Sea. Studies of phytocenoses dominated by or containing *P. australis* were conducted on the White Sea coast during the summer periods of 2012–2023. This species forms extensive stands in various ecotopes along the shores of river mouths and shallow marine bays. The results of ordination of phytocenoses dominated by *P. australis* show that its characteristic ecotope is the brackish water coastal marsh of estuaries. At the same time, the species colonizes and even forms communities in other coastal ecotopes: salt marshes, beaches, shoals of the littoral zone, and tidal flats in the upper reaches of estuaries. In the ecotope of coastal water marshes, communities it dominates can be grouped into the association **Phragmitetum australis maritimae**. Within the rank of association, numerous ecologically similar subassociations have been identified. In these communities, the codominants with *P. australis* are the halophytes *Juncus gerardii*, *Bolboschoenus maritimus*, *Alopecurus arundinaceus*, and *Glaux maritima*. On the beaches of the Unskaya Bay and Onega Bay of the White Sea, codominance of the reed with *Honckenya peploides*, *Leymus arenarius*, and *Leymotrigia bergrothii* is observed. Its spread onto salt marshes, where the species grows alongside obligate halophytes (*Plantago maritima*, *Carex subspathacea*, *Carex glareosa*), indicates its tolerance to soil salinity and saltwater. The development of *P. australis* in estuaries occurs under varying salinity, but in our studies its communities are limited to waters with a salinity of 22‰. In the spatial structure of the coastal vegetation of the White Sea, *P. australis* communities often completely encompass the shores of river mouths, where their development is facilitated by spring floods. In shallow lagoons, they frequently occupy areas on the boundary between high-level marshes and forests.

**Keywords:** coast, plant communities, river mouths, salt marsh, estuary

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*Научная статья*

## **Тростник обыкновенный *Phragmites australis* в экотопах береговой зоны Белого моря**

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**Аннотация.** Высокий воздушно-водный многолетник тростник обыкновенный *Phragmites australis* распространен на обширной территории от западного до восточного побережья Белого моря. Исследования фитоценозов с доминированием и участием *P. australis* были проведены на побережье Белого моря в летний период 2012–2023 гг. Этот вид образует обширные заросли в разных экотопах берегов устьев рек и мелководных морских заливов. Результаты ординации фитоценозов с доминированием *P. australis* показывают, что его характерным экотопом является прибрежно-водный солоноватый марш эстуариев. В то же время вид осваивает и даже образует сообщества в других экотопах берегов: соленых маршах, пляжах, отмелях литоральной зоны и приливных осушках в вершинах эстуариев. В экотопе прибрежно-водных маршей сообщества с его доминированием можно объединить в ассоциацию **Phragmitetum australis maritimae**. В ранге ассоциации выделено множество экологически сходных субассоциаций, в составе сообществ которых содоминантами *P. australis* являются галофиты *Juncus gerardii*, *Bolboschoenus maritimus*, *Alopecurus arundinaceus*, *Glaux maritimus*. На пляжах Унской губы и Онежского залива Белого моря наблюдается содоминирование тростника с *Honckenya peploides*, *Leymus arenarius*, *Leymotrigia bergrotii*. Расселение на соленые марши, где вид соседствует с облигатными галофитами (*Plantago maritima*, *Carex subspathacea*, *Carex glareosa*), свидетельствует о его устойчивости к засолению почвы и соленым водам. Развитие *P. australis* в эстуариях происходит при различной солености, но в наших исследованиях его сообщества ограничиваются водами с соленостью 22‰. В пространственной структуре приморской растительности Белого моря сообщества *P. australis* часто полностью охватывают берега устьев рек, где их развитию способствуют весенние паводки. В мелководных лагунах они нередко занимают участки на границе маршей высокого уровня и леса.

**Ключевые слова:** побережье, растительные сообщества, устья рек, соленый марш, эстуарий

**Финансирование.** Работы на побережье Белого моря (устья рек Онеги, Кянды, Кулоя, Тамицы, губы Сухое Море) проведены в рамках государственного задания FMWE-2024-0020 «Осадкообразование в современном и древнем океане – рассеянное осадочное вещество и донные отложения как геологические архивы изменения климата и природных систем ключевых районов Мирового океана, морей России и пограничной области море–суша». Исследования на территории национального парка «Онежское Поморье» проведены в рамках научно-исследовательской работы по теме № 1-25-104-2 "Комплексное исследование структуры и динамики растительных и животных сообществ побережья Белого моря и прилегающей к нему акватории, с целью установления взаимосвязей между разными биоценозами в зоне экотона и создания устойчивой модели природоохранного менеджмента в национальном парке «Онежское Поморье».

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## Introduction

The common reed *Phragmites australis* (Cav.) Trin. ex Steud. is a Eurasian-American plurizentral species that spread from Europe to North America and even to the subtropical regions of South America, southern Africa, and Australia, thereby now being nearly cosmopolitan (Babina, 2002; Shafranov, 1961). This is primarily a freshwater species belonging to the ecological group of helophytes. Within its range, it has colonized various freshwater habitats, river and lake shores, lowland bogs; however, due to its broad ecological valence, it has also adapted to living in the tidal zone of estuaries and lagoons of seas with brackish waters.

Habitat conditions on saline sea coasts are optimal for halophytes – plants tolerant to substrate salinity. According to the classifications by V.G. Barbour (1970) and E. Tsopa (1939), two ecological groups of halophytes are distinguished: obligate halophytes, which inhabit strongly saline substrates, and facultative halophytes, which grow under moderate or weak salinity.

In relation to substrate salinity, *P. australis* belongs to the group of glycophytes – plants lacking specific physiological adaptations for growth in conditions of soil and saltwater salinity. One of the reasons for the species' tolerance to saline waters and soils lies in its strategy of avoiding salinity through a developed, deep root system that reaches freshwater in its habitats (Babina, 2002). According to O.V. Rebristaya's (1997) classification of coastal plants, *P. australis* should be classified as a "tolerant" species. Thus, we believe it is most accurate to characterize this species as a «glycophyte tolerant to substrate salinity».

The reed is a highly competitive plant that displaces other species, including halophytes, from their previously occupied habitats. For instance, in communities with *Juncus gerardii* Loisel., the reed regenerates successfully. At the same time, *P. australis* often coexists with other halophytes that compete for the same ecological niche (e.g., *Spartina patens* (Aiton) Muhl. and *S. alterniflora* Loisel.), which are capable of suppressing its growth and development (Burdick and Konisky, 2003).

In Europe, the species colonizes the shores of the Sea of Azov (Grechushkina et al., 2011), the river mouths and limans of the Black Sea (Dvoreckiy and Gubanov, 2023), and forms communities in the bays of the Baltic Sea (Rebassoo, 1975, 1987). At present, extensive reed stands are forming on the Atlantic coast of North America (Bart and Hartman, 2003; Burdick and Konisky, 2003; Chambers et al., 1998; Lissner and Schierup, 1997; Smith, 2013). On the northern coast of the Caspian Sea, phytocenoses dominated by *P. australis* occupy vast areas in the Volga Delta (Golub and Mirkin, 1986; Golub et al., 2015). On the shores of the non-tidal southern seas of Russia with wind-induced shallows (the Black and Azov Seas), dense reed stands form so-called «floodplain reed beds» (plavni). Plavni can be considered as a biocoenosis of marine alluvia similar to marshes, as was noted by A.A. Korchagin (1935). We refer to the coastal ecotopes formed by reeds as brackish coastal-water marshes. Within the general ordination system of the White Sea coastal vegetation, they are differentiated from other ecotopes, including salt marshes (Moseev, 2024).

Marine geomorphologist O.K. Leontiev termed biogenic shores dominated by reed and ecologically similar emergent aquatic plants (*Typha angustifolia* L., *T. latifolia* L.) as «reed coasts» (Kaplin et al., 1991; Morskaya geomorphologiya, 1980). Coasts of the same type have formed in the river mouths and lagoons of the southern White Sea (Miskevich et al., 2018b; Moseev, 2014).

Currently, the reed is actively colonizing the White Sea coast, where it forms extensive communities, as demonstrated by research over recent decades (Babina, 2002, 2003; Moseev, 2016a, b; Moseev and Sergienko, 2016, 2017; Moseev et al., 2022, 2023a, b). The primary habitats of this species here are marshes – low tidal shores formed under the influence of tides due to the deposition of suspended and bedload sediments in the intertidal zone of the sea, which are covered with subaerial moisture-loving vegetation (Leontiev, 1961). In modern classifications, all marshes are also divided according to the levels of marine water influence (Belikov et al., 2011):

Low marshes (low-level marshes) have distinct boundaries that coincide with the boundaries of the middle horizon of the littoral zone. From sea to land, they extend from the level of the quadrature low tide to the level of the quadrature high tide.

Middle marshes (mid-level marshes), whose boundaries coincide with the boundaries of the upper horizon of the littoral zone. From sea to land, they extend from the level of the quadrature high tide to the level of the spring high tide. Typically, such marshes occupy the largest areas on the coast.

High marshes (high-level marshes) are located within the supralittoral zone and are covered by seawater only during storm surges. Their lower boundary runs along the level of the spring high tide, and their upper boundary is limited by the influence of surges.

On the White Sea, the common reed has become most widespread along the entire western coast (Babina, 2002; Sergienko, 2013), as well as along almost the entire southeastern coast (Moseev, 2016a, b; Moseev and Sergienko, 2016; Sergienko, 1983). On the eastern coast of the sea, it occurs up to the latitude of the Nes River mouth on the Kanin Peninsula (Korchagin, 1935). On the western coast, its communities have been described at the mouth of the Keret River (Moseev et al., 2022), and at the mouths of the Kudma, Nyukhcha, Kolezhma, and Kem rivers (Babina, 2002).

Previously, during studies conducted on the western coast of the White Sea, it was suggested that the reed is capable of occupying significant areas, displacing halophytic vegetation (Babina, 2002), a phenomenon which, in our opinion, is already being observed at present. The aim of the present work is to demonstrate the features of the formation and geographical distribution of plant communities dominated by or containing *Phragmites australis* on the White Sea shores and this species' colonization of coastal ecotopes.

## Materials and methods

### Research methodology

The study area, investigated during the growing seasons from 2012 to 2023, encompasses various types of accumulative shores in river mouths, lagoons, and open coasts of bays near capes across a vast territory from the western to the eastern coast of the White Sea (Fig. 1).

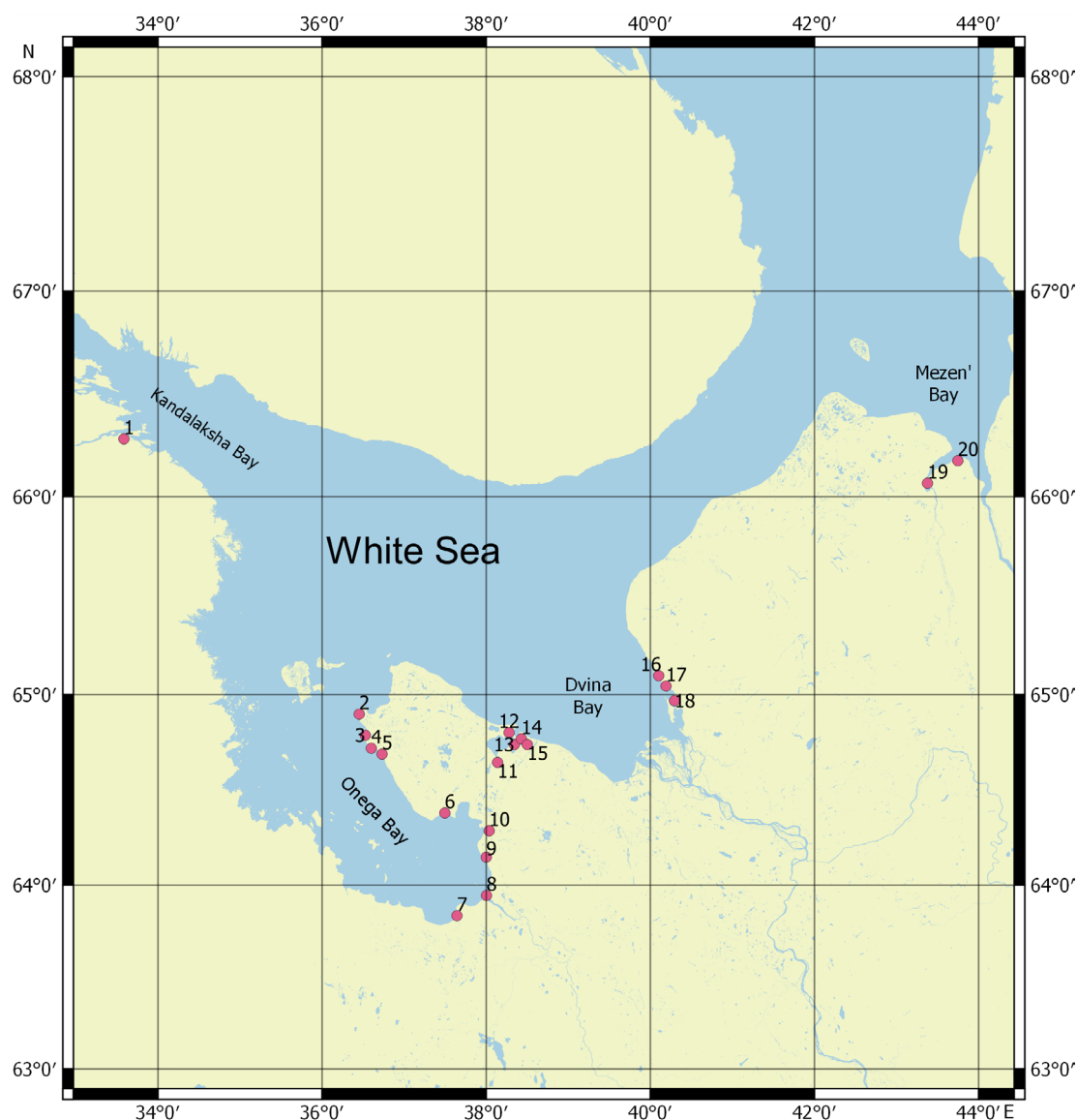
To study plant communities containing common reed, 203 sample plots sized 3×3 m were established. Geobotanical descriptions were conducted on these plots, recording total projective cover (TPC), projective cover of each species, layer structure, frequency of tidal inundation, and the mechanical composition of the substrate. Plant communities dominated by *P. australis* or containing it were grouped into associations identified from the standpoint of an ecological-phytocoenotic approach. Association names are given in accordance with the provisions of the article "Draft All-Russian Code of Phytocoenological Nomenclature" (Neshatayev, 2001). For rankless syntaxa with a single description, the term "community type" is used. Names of vascular plant species follow the database "Plants and Lichens of Russia and Neighboring Countries"<sup>1</sup>. The species name *Tripolium vulgare* Nees is given according to the systematic checklist by S.K. Cherepanov (1995). The name of the green alga *Ulva prolifera* follows the AlgaeBase database<sup>2</sup>.

To study the influence of seawater on communities in river mouths, hydrological and hydrochemical research was linked to hydrological observation stations, where measurements of tidal range, pH, salinity, and total dissolved solids (TDS) of water were conducted. Salinity, TDS, and pH were measured using a Multi 3420 multiparameter liquid analyzer (Germany), a MARK 603 conductivity/salinity meter (VZOR, Russia), and a MARK 903 pH meter (VZOR, Russia).

Ordination of phytocoenoses for ecotopes with different growing conditions was performed using the non-metric multidimensional scaling (NMDS) method. Calculations were performed using the R language (R Core Team, 2019), and data visualization was carried out using the ggplot2 package (Wickham, 2016). For the analysis of species composition similarity, a dissimilarity matrix was calculated using the Bray-Curtis distance. The ordination was based on data on species composition and projective cover of species in communities described in different habitats.

<sup>1</sup> Plantarium. Web page. URL: [www.plantarium.ru](http://www.plantarium.ru) (accessed: 12.12.2025).

<sup>2</sup> Algaebase. Web page. URL: <http://www.algaebase.org> (accessed: 12.12.2025).



**Fig. 1.** Map showing surveyed areas with *Phragmites australis* communities along the White Sea coast. Figures on the map indicate: 1 – mouth of the Keret River, 2 – Mokraya Bay and Cape Letny Orlov, 3 – Pushlakhta Bay and the mouth of the Shidrovka River, 4 – Cape Chesmensky, 5 - mouth of the Kotova River, 6 – mouth of the Veiga River, 7 – mouth of the Tapshenga River, 8 - mouth of the Onega River, 9 – mouth of the Tamitsa River, 10 – mouth of the Kyanda River, 11 – mouth of the Una River, 12 – Zayatsky Peninsula in the north of Una Bay, 13 – southern shore of Una Bay, 14 – Sosnovy Cape, 15 – Kinzhuga Bay, 16 – mouth of the Kuya River, 17 – northern part of Sukhoye More Bay, 18 – mouths of the Mudyuga and Kad Rivers in Sukhoye More Gulf, 19 – mouth of the Kulovka River, 20 – mouth of the Kargovka River.

### **Natural conditions of the White Sea**

The White Sea is an inland sea with an area of 90 thousand km<sup>2</sup>, located in the north of the European part of Russia. Despite its relatively small size, the sea has a complex configuration. It extends deep into the land with large bays (gubas): the Dvina Bay, the Onega Bay, the Mezen Bay, and the Kandalaksha Bay. A large water area, the Basin, is distinguished in the center of the sea. To the east, the Basin connects with a narrowed section called the Gorlo (Throat). East of the Gorlo, it transitions into the Voronka – a vast water area connected to the Barents Sea (Gidrometeorologiya i gidrokimiya..., 1991). The shores are predominantly abrasion-accumulative. In the west, fjord coast are distinguished, with pronounced sediment accumulation along the coasts of narrow bays – fiards (Kaplin et al., 1991). Accumulative shores are represented by extensive beaches, while in river mouths, lagoons, and bays protected from wave action, wadden-marsh shores are formed (Kaplin et al., 1991; Safyanov and Repkina, 2013).

Tides occur throughout the sea's water area. The influence of the tidal wave arriving from the Barents Sea water area varies across different sections, reflected in the tidal range. The highest tides are observed in the Mezen Bay – 6 m; in the Basin and Dvina Bay, the average tidal range is 1 m. The average sea salinity is 26.7‰, but it varies significantly throughout the water area and depends on many factors: tides, the influence of numerous inflowing rivers, ice formation, etc. Significant diurnal fluctuations in tidal range, salinity, and hydrochemical parameters are observed in the coastal parts of the sea and in river mouths (Leshchev et al., 2015, 2017; Miskevich, 2004; Miskevich et al., 2018a, b).

The climate of the White Sea is transitional from moderately continental to subarctic maritime. The short summer lasts 1–1.5 months (July–August); winter lasts from November to April, extending until mid-May in the Voronka (Grishchenko, 2024). The average January water surface temperature across the entire water area is  $-0.3\text{ }^{\circ}\text{C}$ , and in July it is  $+13.4\text{ }^{\circ}\text{C}$ . The shallow southern part of the sea warms up more strongly. For example, in the south of the Onega Bay, the average water temperature in July is  $+18.1\text{ }^{\circ}\text{C}$ , while in January the sea surface cools down to  $-2.2\text{ }^{\circ}\text{C}$ . According to a number of terrestrial weather stations, the average air temperature varies significantly along the entire coast. In Kandalaksha, the average air temperature is  $-11.4\text{ }^{\circ}\text{C}$  in January and  $+14.9\text{ }^{\circ}\text{C}$  in July; in Onega,  $-10.9\text{ }^{\circ}\text{C}$  and  $+17.1\text{ }^{\circ}\text{C}$ , respectively; in Arkhangelsk,  $-11.6\text{ }^{\circ}\text{C}$  and  $+16.5\text{ }^{\circ}\text{C}$ ; in Mezen,  $-14.9\text{ }^{\circ}\text{C}$  and  $+14.5\text{ }^{\circ}\text{C}$  (Nauchno-prikladnoi..., 1989). Ice formation begins in November; by the end of May – beginning of June, the entire sea water area is free of ice (Grishchenko, 2024).

The natural conditions in the river mouths and lagoons within the study area are presented in Table 1. Marshes and beaches form in the coastal zone of all river mouths and lagoons.

The Sukhoye More Bay, with a water area of  $27\text{ km}^2$ , is located in the southeastern part of the Dvina Bay. It is freshened by the waters of the small rivers Mudyuga, Kad, Ulmitsa, Bolshaya Nitsa, and the large Severnaya Dvina River. The width of tidal flats in the bay is 0.5–3.0 km, facilitated by shallowness. The average tidal range is 1.0 m. In the northern part of the bay, salinity reaches 10–15‰; near the river mouths, it is about 8‰; and in the Zheleznye Vorota Strait, it is 14‰ (Miskevich and Miskevich, 2017; Miskevich et al., 2018b). On the western coast of the Dvina Bay, there is a large shallow lagoon – the Unskaya Bay, with a water area of 17 thousand  $\text{km}^2$ . The width of the tidal flats in the bay is 0.2–1.0 km. The average tidal range is 1 m. Salinity varies from 11–14‰ at the head of the bay (Moseev et al., 2022) to 24‰ at its mouth. The mouths of the Kyanda, Tamitsa, and Tapshenga rivers, flowing into the Onega Bay of the White Sea, are represented by estuaries where the average tidal range is 2.0–3.0 m. Salinity at high water at the marine boundary of the mouths is 19–25‰ (Leshchev et al., 2015; Miskevich et al., 2018a). The mouth of the Keret River, flowing into the Kandalaksha Bay, is represented by a wide estuary with an average tidal range of 1.7 m (Smagin, 2017). Salinity at high water during the tidal cycle reaches 23–25‰ (Moseev et al., 2022; Smagin, 2017). The mouth of the Kuloy River, flowing into the Mezen Bay, is represented by a wide funnel-shaped estuary. The tidal range at the marine boundary of the estuary is 3–4 m, and salinity at high water is 23‰. The Kargovka River flows into the sea near the mouth of the Kuloy River, where the tidal range is 4 m and salinity at high water is 23‰.

## Results

Currently, *P. australis* is actively colonizing various coastal ecotopes in the river mouths and bays of the White Sea: brackish coastal-water and near-water marshes, salt marshes, beaches, and tidal flats in the upper reaches of estuaries (Fig. 2). Reed communities form under the influence of various factors: the impact of tides and storm surges on shores, floods, and the mechanical composition of the substrate. At the same time, *P. australis* itself influences habitat formation. For instance, decaying reed litter forms a layer of humus on tidal shores.

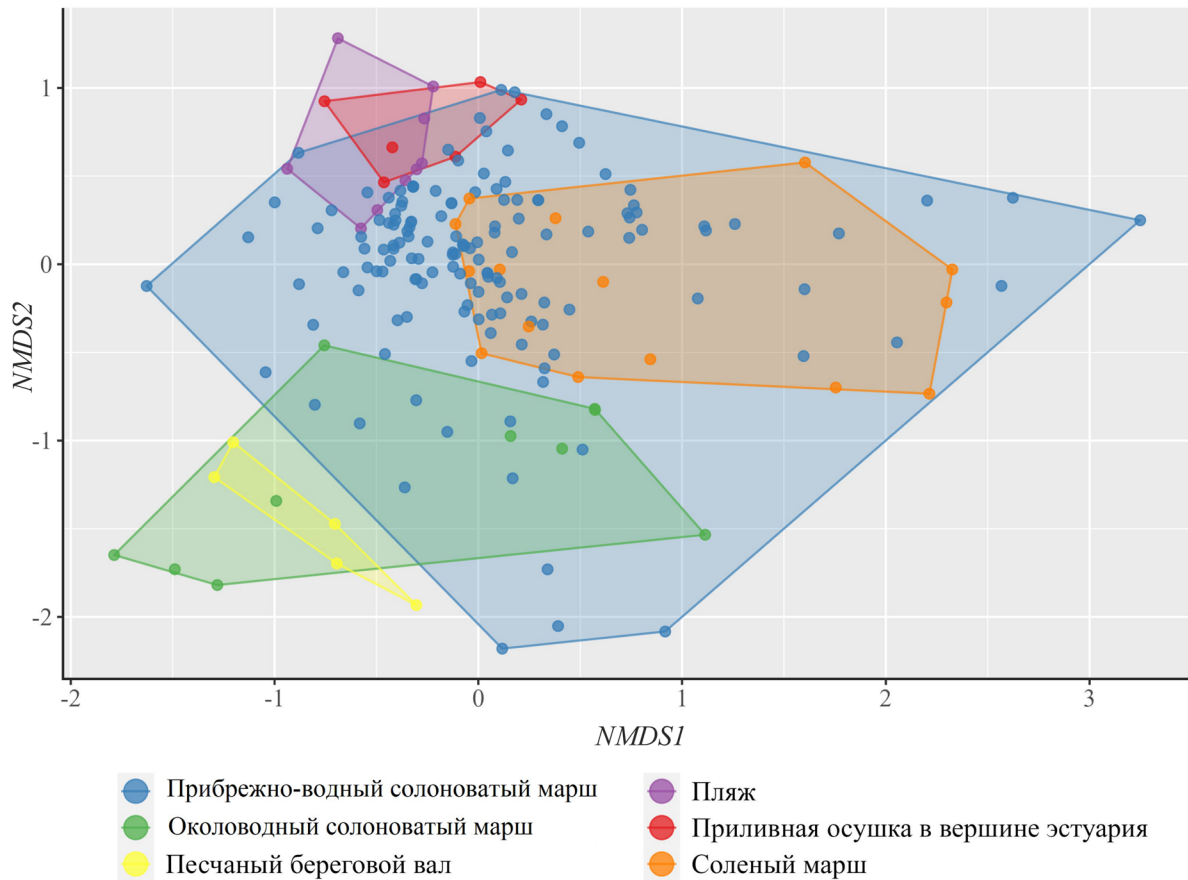
The predominantly freshwater species *P. australis* forms communities in lakes and rivers, covering almost the entire catchment area of the White Sea. As research shows, it is one of the leading coenosis-formers of the emergent aquatic vegetation formation in lakes of the taiga zone in the north of the East European Plain (Moseev and Drovina, 2017; Vekhov, 1994, etc.). Among the coastal ecotopes containing reed, only the tidal flats in the upper reaches of estuaries are freshwater, where saline water penetrates only during storm surges.

In the coastal zone of the White Sea, *P. australis* forms extensive mono- and oligodominant communities, which are grouped into associations and subassociations of various ecotopes of coastal halophytic vegetation.

**Table 1.** Natural conditions of the estuaries of rivers and lagoons of the White Sea. In most mouths, measurements were taken during the summer low water period, in Mokraya Guba, and at the mouths of the Shidrovka and Kotova rivers at the beginning of the autumn flood.

Water body	Main forms of mesorelief	Geomorphological type of water body or estuary	Mean tidal range, m	Salinity, psu
The mouth of the Keret' River	Marshes, sloping native shores, tidal flat	Estuary	1.6	23.0–25.0
The mouth of the Tapshen'ga River	Marshes, tidal flat	Estuary	2.5	21.0
The mouth of the Tamitsa River	Marshes, sandy beaches, tidal flat	Estuary	2.5	21.0
The mouth of the Onega River	Marshes, tidal flat	Estuary		
The mouth of the Kyanda River	Marshes, sandy beaches	Estuary	2.5	25.0
The mouth of the Shidrovka River	Marshes, sandy beaches, sea spit	Estuary	2.5	2.4–4.8
The mouth of the Kotova River	Marshes, sandy beaches, sea spit	Simple mouth	2.5	7.12–7.17
The mouth of the Veyga River	Marshes	Estuary	3.0	19.51–22.61
The mouth of the Una River in Unskaya Guba	Marshes	Estuary	1.0	9.91–13.8
The mouth of the Kuya River	Sandy beaches, marshes, slopes of the indigenous coast	Estuary	0.8	10.1
The mouth of the Kuloy River	Marshes, sandy beaches, slopes of the indigenous coast	Estuary	3.0	13.3–19.0
The mouth of the Kargovka River	Marshes, sandy beaches	Estuary	3.0	20.0–22.0
The mouth of the Bolshaya Nitsa River	Marshes	Simple mouth	0.8	9.1
The mouth of the Kad River	Marshes	Delta	0.8	7.2
The mouth of the Mud'yuga River	Marshes	Delta	1.0	5.1

Water body	Main forms of mesorelief	Geomorphological type of water body or estuary	Mean tidal range, m	Salinity, psu
Guba Sukhoye More (the northern part)	Marshes, sandy beaches	Lagoon	1.0	8.0–14.2
Unskaya Guba	Marshes, sandy beaches	Lagoon	1.0	13.8–22.3
Kinzhuskaya Guba and the mouth of the Kinzhuga River of the Unskaya Guba	Marshes	Bay	1.0	19.34–22.14
The northern shore of the Unskaya Guba near the Kholodny Stream	Marshes	Lagoon	1.0	19.5–20.1
The mouth of the Unskaya Guba near Cape Sosnovy	Marshes	Lagoon	1.0	22.0–23.0
Bay near Cape Chesmensky	Marshes	Bay	2.0	16.8–23.0
Mokraya Guba and the bays near Cape Letny Orlov	Marshes, sandy beaches	Bay	2.0	3.0–7.6
Guba Pushlacha	Marshes, beaches	Bay	2.0	21.0



**Fig. 2.** Graphical interpretation of the distribution of phytocenoses with *Phragmites australis* in the coastal zone habitats of the White Sea.

### ***Tidal flats in the upper reaches of estuaries***

Communities of tidal flats in the upper reaches of estuaries dominated by or containing *P. australis* are grouped into the associations **Phragmitetum australis petasitosum radiati**, **Phragmitetum australis scirposum lacustris**, **Caricetum aquatilis**, and **Caricetum acutae**. The formation of these communities is primarily influenced by tides, silty bottom sediments, and the impact of floodwaters that bring suspended sediments and biogenic compounds. In the graphical representation of ordination, they form a cluster close to the ecotopes of brackish coastal-water marshes due to the similarity in the structure of their phytocoenoses (Fig. 2).

In the association **Phragmitetum australis petasitosum radiati**, *P. australis* with a projective cover (PC) of 15–40% forms the upper layer up to 1.5 m high, while the lower layer with a PC of 10–60% is formed by *Petasites radiatus* (J.F. Gmel.) J. Toman. Such communities in the ecotope of tidal flats in the upper reaches of estuaries occupy areas near bedrock shores on sandy substrates in the pool of the Kuya River mouth. During low water of the tidal cycle, salinity in the reed stands reached 1‰.

In the association **Phragmitetum australis scirposum lacustris**, communities are formed by *P. australis* (PC 50%) and *Schoenoplectus lacustris* L. (Palla) (PC 15–20%). *Sparganium erectum* L. is abundant (PC 15%). These phytocoenoses occupy silty-sandy shoals located in the upper part of the Kuya River estuary. Mineralization during low water did not exceed 250 mg/l.

In the formation of phytocoenoses of the **Caricetum aquatilis** association, *P. australis* participates with low projective cover – 1–10%. The dominant species, *Carex aquatilis* Wahlenb., grows with a PC of 70–80%. These phytocoenoses occupy silty tidal flats in the upper reaches of the Kyanda River estuary (Onega Bay) and the Bolshaya Nitsa River estuary (Dvina Bay). Mineralization during low water was 250–300 mg/l.

### **Coastal-water brackish marshes**

Ordination of phytocoenoses dominated by *P. australis* indicates that its most characteristic ecotope on the White Sea shores is brackish coastal-water marshes (Moseev, 2024), where water salinity is generally low: ranging from 1 to 20‰ (Fig. 2). At such salinity levels, these coenoses can occupy extensive coastal areas with low- and mid-level marshes (Miskevich et al., 2018a; Moseev and Sergienko, 2017). The main factors in their formation are the influence of brackish tidal and storm surge waters, and additionally, in river mouths and lagoons, the impact of spring floods.

This ecotope is also characterized by waterlogged conditions, a thick peat layer within reed stands on marshes inundated during spring tides, silt accumulation on marshes flooded twice daily by tides, significant diurnal and seasonal variability in salinity (compared to the stable values on salt marshes), and large diurnal tidal fluctuations.

Within the **Phragmiteta australis** formation, various associations can be distinguished, differing significantly in species composition and the ecological growth conditions of the edificator species, *P. australis*. The most extensive and diverse association on the White Sea coast is **Phragmitetum australis maritimae**. It is distinguished based on significant species richness, and sometimes also the abundance of halophyte species within communities dominated by *P. australis* on saline soils of brackish coastal-water marshes. In all communities of river mouths, the reed forms a layer 2.0–2.5 m high. A total of 125 descriptions were made in phytocoenoses with TPC (Total Projective Cover) of 20–100% to delineate the subassociation. Based on differences in species composition, we subdivide this association into several subassociations.

The subassociation **Phragmitetum australis maritimae** subass. **purum** comprises pure or nearly pure reed communities of brackish marshes with a minor admixture of hygrophilous species (PC of all species 1%) – *Archangelica officinalis* Hoffm., *Cenolophium fischeri* (Spreng.) W.D.J. Koch, *Ranunculus repens* L., *Triglochin maritima* L. Projective cover of *P. australis* is 20–90%. A total of 23 descriptions were made for this subassociation in communities with TPC (Total Projective Cover) of 50–90%. These communities occupy the flats of low-level marshes and are the first in the ecological succession series from the littoral zone towards the supralittoral. The substrate contains a large amount of reed litter, but a peaty horizon is not developed, which is likely associated with the influence of tides and floods. In the mouths of the Kyanda and Tapshenga rivers, the communities form the background vegetation, spreading along the water's edge from the head of the estuaries to their marine boundary.

In the communities of the subassociation **Phragmitetum australis maritimae** subass. **subpurum**, *P. australis* dominates, forming PC from 30 to 90%. Facultative halophytes are common: *Alopecurus arundinaceus* Poir. (PC 1–10%), *Agrostis straminea* Hartm. (PC 1–10%). In the formation of some communities, halophytes participate with low projective cover (PC 1–10%): *Blysmus rufus* (Huds.) Link (PC 5–15%), *Carex mackenziei* V.I. Krecz. (PC 13%), *Cenolophium fischeri* (PC < 1–3%), *Juncus gerardii* Loisel. (PC < 1–10%), *Eleocharis uniglumis* (Link) Schult. (PC 5–10%), *Plantago maritima* L. (PC 5%), *Potentilla egedei* (L.) Raeusch. (PC 1–10%), *Stellaria humifusa* Rottb. (PC < 1%), *Triglochin maritima* (PC < 1–5%), *Tripolium vulgare* (Jacq.) Dobrocz. (PC 10%). Alongside halophytes, glycophytes are common in the association, becoming more abundant in the upper part of the coastal zone near the forest: *Archangelica officinalis* (PC 1–10%), *Artemisia vulgaris* L. (PC 5–10%), *Calamagrostis neglecta* (Ehrh.) Gaertn., B. Mey. & Schreb. (PC < 1–10%), *Calamagrostis langsдорffii* (Link) Trin. (PC < 5%), *Callitriche hermaphroditica* L. (PC 1–5%), *Eriophorum angustifolium* Honck. (PC 5%), *Elytrigia repens* (L.) Nevski (PC < 1), *Heracleum sibiricum* L. (PC 10%), *Parnassia palustris* L. (PC 5%), *Ranunculus acris* L. (PC < 1–3%), *Rorippa amphibia* (L.) Besser (PC < 5–10%), *Vicia cracca* L. (PC 1–5%). A total of 31 descriptions were made for this subassociation in communities with TPC of 15–95%. Such communities can occupy areas of brackish coastal-water marshes from the level of spring tide influence to the level of surge influence near the bedrock shore. A peat horizon up to nearly 1.0 m thick forms beneath the reed litter.

The subassociation **Phragmitetum australis maritimae** subass. **ligusticosum scoticae** is formed by communities in whose lower layer, under the reed canopy, *Ligusticum scoticum* L. (PC 15–20%) dominates. This species is common on sandy substrates in ecotonal zones located between marshes and forests, and on beach ridges. The upper layer is composed of reed shoots up to 1.5 m tall, growing with a PC of 50–60%. *Cenolophium fischeri* (PC 5–10%) is a constant species of this subassociation. A total of 3 descriptions were made for this subassociation in communities with TPC of 90%. Such

communities are rare on the White Sea coast and have been described by us only on the upper-level marshes of the Kinzhugskaya Bay in the southeastern part of the Unskaya Bay. They form on sandy loam soils near the forest.

The subassociation **Phragmitetum australis maritimae** subass. **aloppecurosum arundinacei** is formed by communities of tall grasses: *P. australis* (PC 50–90%) and *Alopecurus arundinaceus* (PC 5–30%). *Agrostis straminea*, *Juncus gerardii*, *Potentilla egedei*, *Sonchus humilis* N.I. Orlova, and *Triglochin maritime* are included in the community composition with a PC of 10% or less. A total of 5 descriptions were made for this subassociation in communities with TPC of 90–100%. These communities occupy areas in the tidal zone with peaty soil on marshes from low to mid-level, where they form under conditions of brackish water ranging from 10 to 15‰.

The subassociation **Phragmitetum australis maritimae** subass. **bolboschoenosum maritimi** unites communities dominated by *P. australis* (PC 5–50%), forming the upper layer up to 1.5 m high, and *Bolboschoenus maritimus* (L.) Palla (PC 10–40%), which predominates in the lower layer up to 1.0 m high. Halophytes participate in community formation with low projective cover of 1–5%: *Agrostis straminea*, *Juncus gerardii*, *Stellaria humifusa*, *Triglochin maritima*, *Triglochin palustris* L., *Tripolium vulgare* Nees. These phytocoenoses appear to be transitional between communities dominated by *B. maritimus* and those dominated by the larger salt-tolerant species *P. australis*. The communities have been described in the mouth of the Kyanda River, where at the same level of marsh succession, monodominant communities of the **Bolboschoenetum maritimi** association without reed participation are common. A total of 19 descriptions were made for this subassociation in communities with TPC of 40–95%. They occupy silty flats of low-level marshes, forming in the mid-littoral zone under conditions of brackish water ranging from 15.0 to 23.0‰. They differ from the previous communities by a significantly smaller amount of reed litter in the substrate.

In river mouths, nearly pure coenoses of *Bolboschoenus maritimus* are also found, typically forming a well-defined belt 3–10 m wide (Babina, 2002; Moseev, 2016a; Moseev et al., 2023b). The invasion and development of reed within them disrupts the zonation of halophytic vegetation in river estuaries.

During the colonization of shores by reed, a shift is observed from communities of the **Juncetum gerardii** and **Juncetum gerardii glaucosum maritimae** associations to communities transitional to brackish coastal-water marshes. These transitional communities are grouped into the subassociation **Phragmitetum australis maritimae** subass. **juncosum gerardii**. Their lower layer is formed by the hygrophilous species *Juncus gerardii* (PC 20–60%). In areas of marshes flooded daily by the tide, halophytes are abundant: *Agrostis straminea* (PC 3–15%), *Alopecurus arundinaceus* (PC 10–30%), *Eleocharis uniglumis* (PC 10–20%), *Glaux maritima* L. (PC 3–10%). In less saline areas of marshes within the influence zone of spring tides, mesophytes are common: *Festuca rubra* L. (PC 3–20%), *Calamagrostis neglecta* (PC 15%), *Potentilla egedei* (PC 1–10%), *Sonchus humilis* (PC 1%). A total of 26 descriptions were made for this subassociation in communities with TPC of 80–100%. These phytocoenoses occupy areas of mid-level brackish marshes with silty-sandy and peaty soils.

Within this association, based on the abundance of the obligate halophyte *Glaux maritima* (PC 10–50%), we distinguish an independent variant: **Phragmitetum australis maritimae** subass. **juncosum gerardii** var. **glaucosum maritimae**. These communities occupy areas of low-level marshes with clayey soils, and sometimes with a peat horizon 5–10 cm thick. A total of 7 descriptions were made for this variant in communities with TPC of 70–90%.

Communities dominated by *P. australis* in the upper layer and *Eleocharis uniglumis* in the lower layer are grouped into the subassociation **Phragmitetum australis maritimae** subass. **eleocharitosum uniglumis**. Most communities in this association are formed by only two species: *P. australis* in the upper layer and *Eleocharis uniglumis* in the lower. In the formation of some communities, the following species participate with low projective cover: *Blysmus rufus* (PC 5%), *Glaux maritima* (PC 10%), *Potentilla egedei* (PC < 1%). A total of 6 descriptions were made for this subassociation in communities with TPC of 70–90%. Phytocoenoses of this association have been described on the shores of Unskaya Bay and in the estuaries of the Keret and Veiga rivers, where they form under the same ecological conditions as the previous association. Similar to communities of **Phragmitetum australis maritimae** subass. **bolboschoenosum maritimi**, such communities are the result of the succession of monodominant communities dominated by *Eleocharis uniglumis* towards communities dominated by *P. australis* forming the upper layer, indicating a shift from salt marshes to brackish coastal-water marshes.

### **Near-water brackish marshes**

The reed also colonizes habitats of high-level brackish marshes, where it participates in the formation of communities of two associations: **Festucetum rubrae** and **Elytrigietum repentis**. The penetration of reed into these communities may indicate increased influence of floods and surges in river mouths, weak soil salinity, and increased soil moisture. In Fig. 2, communities from such habitats are represented by a cluster near coastal-water marshes.

In communities of the **Festucetum rubrae** association from the Onega Bay coast, *P. australis* grows with a PC of 10%, forming a sparse upper layer while *Festuca rubra* dominates the lower layer with a cover of 50–60%. A total of 2 descriptions were made for this association in communities with TPC of 70–90%.

The succession from *Festuca rubra* to *P. australis* is reflected in the community type **Phragmites australis + Festuca rubra**, which we recorded on peaty soils occupying an area of a high-level marsh on the coast of Unskaya Bay. In this community, the glycophyte *Festuca rubra* dominates the lower layer, which is 20–25 cm high (PC 50–60%), while *P. australis* dominates the upper layer, which is 1.7–2.0 m high (PC 10%). In communities of the **Elytrigietum repentis** association from the mouth of the Kyanda River, *P. australis* grows with a PC of 1–15%, while the grass *Elytrigia repens* dominates, growing in communities with a projective cover of 30–80%. *Sonchus humilis* and *Alopecurus arundinaceus* are also abundant in these communities. A total of 4 descriptions were made for this association in communities with TPC of 80–90%.

Communities of the **Juncetum gerardii glaucosum maritimae** association were described by us in the mouth of the Kyanda River and Unskaya Bay, where *P. australis* grows with low projective cover – 1–5%, unlike the dominant species *Juncus gerardii* (PC 50–70%) and *Glaux maritime* (PC 15–20%). A total of 4 descriptions were made for this association in communities with TPC of 80–90%.

In addition to the fairly characteristic ecotopes of brackish coastal-water marshes and tidal flats in the upper reaches of estuaries, the common reed colonizes atypical habitats for it on the shores of the White Sea: salt marshes and beaches.

### **Salt marshes**

In this ecotope on the White Sea shores, diverse communities with the participation and dominance of the common reed have been described, which also indicates ongoing successions within halophytic communities. However, according to descriptions of coastal vegetation, as of 2017–2023, the area colonized by reed in this ecotope is not extensive. In Fig. 2, such communities are represented by a large cluster within the conditional boundaries of brackish coastal-water marshes. These communities form under the influence of saline tidal waters on salinized substrates of varied mechanical composition.

In communities of the **Eleocharitetum uniglumis** association from the mouth of the Shidrovka River (Onega Bay), *P. australis* grows with a PC of 10%, which may indicate the beginning of its colonization of communities of this association. The dominant species forms the lower layer with a projective cover of 60–70%. Halophytes also participate in the formation of this association's communities: *Juncus gerardii* (PC 20%), *Glaux maritime* (PC 5%), *Plantago maritime* (PC < 10%). A total of 1 description was made for this association in a community with TPC of 90%.

In communities of the **Caricetum subspathaceae** association from the mouth of the Kuloy River, *P. australis* was recorded with a projective cover of 5% together with the dominant halophytic sedge *Carex subspathacea* Wormsk. ex Hornem. (PC 70%). A total of 1 description was made for this association in a community with TPC of 70%.

In communities of the **Caricetum rectae** association from Kinzhugskaya Bay, *P. australis* grows (PC 5%) together with the halophyte *Hippuris tetraphylla* L. f. (PC 10%). The latter possibly dominated here previously and is currently being replaced by the halophytic sedge *Carex recta* (PC 30%). A total of 1 description was made for this association in a community with TPC of 50%.

In communities of the **Caricetum glareosae** association from the mouth of the Kuloy River, *P. australis* grows with a PC of 20% together with the dominant halophytic sedge *Carex glareosa* Wahlenb. (PC 70%). A total of 1 description was made for this association in a community with TPC of 100%.

Within the **Phragmiteta australis** formation, some typical communities can be distinguished, the formation of which is associated with the colonization by *P. australis* of the salt marsh ecotope, which is uncharacteristic for it.

Communities of the **Phragmites australis + Atriplex nudicaulis** type occupy eroding sandy beach ridges in the mouth of the Veiga River (Onega Bay). They are formed by the nitrophilous species *Atriplex nudicaulis* Boguslaw (PC 20%) dominating the lower layer, which is most likely associated with a high concentration of soil nitrogen generated by the decay of algal wrack. A total of 2 descriptions were made for this community type with TPC of 80–90%.

The **Phragmites australis + Glaux maritime** community type is formed by the codominance of the obligate halophyte *Glaux maritime* (PC 30%) in the lower layer up to 10–20 cm high and *P. australis* (PC 70%) in the upper layer 1.5 m high, and is the result of the replacement of *Glaux maritime* by reed. The community occupies an area of low-level salt marsh in Unskaya Bay, where it is influenced by tidal waters with a salinity of about 22‰. A total of 1 description was made for this community type with TPC of 90%.

The **Phragmites australis + Plantago maritime** community type is formed by the codominance of the obligate halophyte *Plantago maritime* (PC 20%) in the lower layer, 20–25 cm high, and *P. australis* (PC 70%) in the upper layer, 1.6 m high, and is the result of the replacement of *Plantago maritime* by reed. The phytocoenosis occupies an area of low-level salt marsh with clayey-silty soils in Unskaya Bay, where it is influenced by tidal waters with a salinity of about 22‰. A total of 1 description was made for this community type with TPC of 90%.

The **Phragmites australis + Carex subspathacea** community type is formed by the codominance of the obligate halophyte *Carex subspathacea* (PC 20%) in the lower layer, 15 cm high, and *P. australis* (PC 30%) in the upper layer, 1.5 m high, and is the result of the replacement of *Carex subspathacea* by reed. *Atriplex littoralis* L., *Potentilla egedei*, and *Triglochin maritime* were recorded in the community with a PC of 10%. The phytocoenosis occupies an area of low-level salt marsh on silty soils in the mouth of the Kuloy River, where it is influenced by tidal waters with a salinity of about 15‰. A total of 1 description was made for this community type with TPC of 90%.

### **Sandy beaches and beach ridges**

Beaches represent another not entirely characteristic ecotope for common reed communities. The formation of these communities can be explained by the increasing influence of marine waters on beaches. Usually, reed does not grow on sea coast beaches or occurs only sporadically. However, the beach strip on the eastern shore of Unskaya Bay is actively eroded by wave action (Safyanov and Repkina, 2013), which facilitates the formation of a waterlogged sandy soil horizon at a shallow depth on the beach, freshened by terrigenous runoff from the slopes of the bedrock shores. The powerful root system of *P. australis* penetrates to the groundwater, enabling the reed to develop and form communities. Additionally, its development is supported by the influx of biogenic elements with the tides.

In Fig. 2, beach communities with reed are represented by a cluster intersecting with the ecotope of brackish coastal-water marshes.

In the mentioned habitats, a new association, **Phragmitetum australis honckeniosum peploidis**, can be distinguished within the **Phragmiteta australis** formation. Its communities, unlike marsh ecotopes, occupy a narrow strip of sandy beaches in the mouth of Unskaya Bay, which is also a result of the reed's colonization of White Sea coast ecotopes. A succession is occurring from communities of the psammophyton (among which *Leymus arenarius* (L.) Hochst., *Honckenia peploides* (L.) Ehrh., and *Lathyrus japonicus* Willd. are common) to communities dominated by *P. australis*. In such phytocoenoses, the lower layer is formed by the prostrate shoots of the halophyte *Honckenia peploides* (PC < 1–20%). *Sonchus humilis* is abundant on some beach sections. The upper layer is formed by *P. australis* (PC 15–80%). *Festuca rubra* (PC 10%) and *Sonchus humilis* (PC 1–10%) are also found in this layer. A total of 8 descriptions were made for this association in communities with TPC of 25–80%.

In the phytocoenoses of one of the **Honckenyetum peploidis** associations on the beaches of Unskaya Bay, *P. australis*, alongside the psammophilous grass *Leymus arenarius*, grows with a PC of 5%. The prostrate shoots of the cenosis-forming species *Honckenia peploides* form the lower layer with a PC of 30%. The community was delineated based on 1 description with TPC of 40%.

On beaches, as on salt marshes, several community types can be distinguished which, due to insufficient descriptions, cannot yet be assigned association rank. Like the communities of **Phragmitetum australis honckeniosum peploidis**, they represent successional series in the shift towards *P. australis*.

Communities of the **Phragmites australis + Leymus arenarius** type have been identified on the sandy beaches of the southern shore of Unskaya Bay. Here, two large grasses, *P. australis* (PC 20–

70%) and *Leymus arenarius* (PC 10–40%), combine in a single layer 1.2 m high. We believe that in the future, the reed will displace the sand ryegrass (*L. arenarius*), which is also observed in other areas of the bay's coast with active colonization of beaches by reed and changes in phytocoenoses along the shoreline. The community was delineated based on 2 descriptions with TPC of 60–80%.

The community type **Phragmites australis + Sonchus humilis** formed on a section of beach in Unskaya Bay with algal wrack, the decomposition of which releases nutrients. Its lower layer is formed by the nitrophile *Sonchus humilis* (PC 20%) with minor participation of *Atriplex littoralis* (PC 1%) and *Honckenya peploides* (PC 1%). The upper layer is formed by *P. australis* (PC 80%). The community was delineated based on 1 description with TPC of 80%.

In the community type **Calamagrostis arundinacea + Elytrigia repens + Phragmites australis** on the beach ridges near Cape Chesmensky, the reed grows with a PC of 10%, unlike the main dominant *Calamagrostis arundinacea* (L.) Roth (PC 60%). The other grass, *Elytrigia repens*, grows with a PC of 10%. The community was delineated based on 1 description with TPC of 70%.

The community type **Leymotrigia bergrothii + Phragmites australis + Festuca rubra**, recorded by us near Cape Chesmensky, is represented in the upper layer by *Leymotrigia bergrothii* (H. Lindb.) Tzvelev (PC 25%) and *P. australis* (PC 10%), while the lower sublayer is formed by *Festuca rubra* (PC 15%). In the lower layer, algal wrack facilitates the development of nitrophilous species: *Sonchus humilis* (PC 1%) and *Tripleurospermum hookeri* Sch. Bip. (PC 10%). The community was delineated based on 1 description with TPC of 60%.

In communities of the **Alopecurus arundinaceus + Leymotrigia bergrothii** type on beach ridges at the mouth of the Kotova River and on shores near Cape Chesmensky (Onega Bay), the projective cover of *P. australis* reaches 5%, unlike the species dominating it: *Alopecurus arundinaceus* (PC 15–30%) and *Leymotrigia bergrothii* (PC 10%). The community was delineated based on 2 descriptions with TPC of 70–80%.

The replacement of psammophyton communities on White Sea beaches by reed may be a result of the initial stage in the formation of a marsh shore dominated by reed communities.

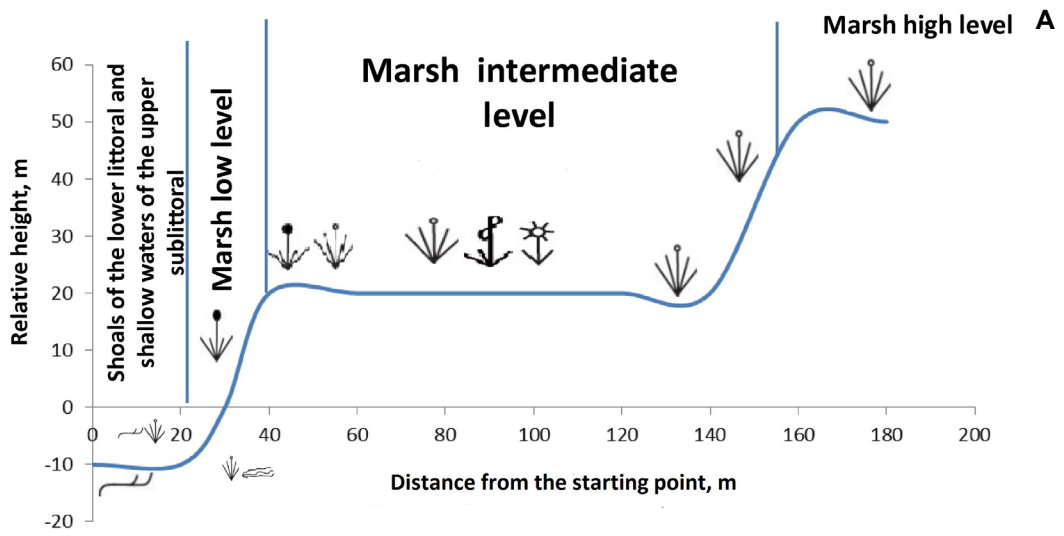
### **Shoals of the lower littoral**

In addition to salt marshes and beaches, *P. australis* also colonizes habitats uncharacteristic for it: wadden (tidal flat) silty flats of the middle littoral horizon. This ecotope is typical for marine hydrophytes *Zostera marina* L. and *Ruppia maritima* L.

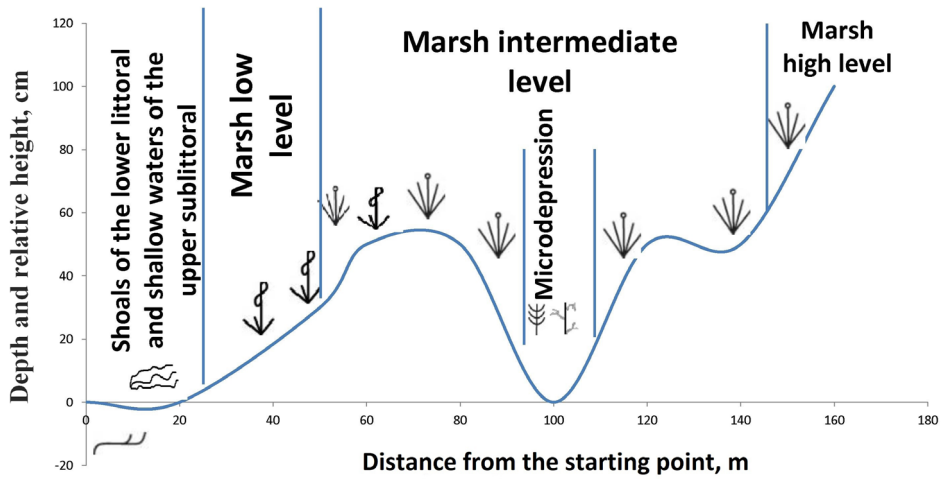
In communities of the **Phragmites australis + Zostera marina** type on the silty-sandy littoral of Kinzhugskaya Bay in the southeastern part of Unskaya Bay, *P. australis* with a PC of 5–15% forms the upper layer, and the dominant *Zostera marina* grows with a PC of 20–30%. The community was delineated based on 2 descriptions with TPC of 20–50%.

*P. australis* is more abundant (PC 10–30%) in communities with *Ruppia maritima* (PC 10%) of the **Phragmites australis + Ruppia maritima** type identified in the head of Unskaya Bay. In these communities, marine euryhaline algae grow with low abundance: *Fucus vesiculosus* (PC 10%) and *Ulva prolifera* O.F. Müller (PC 10%). The community was delineated based on 2 descriptions with TPC of 20–40%.

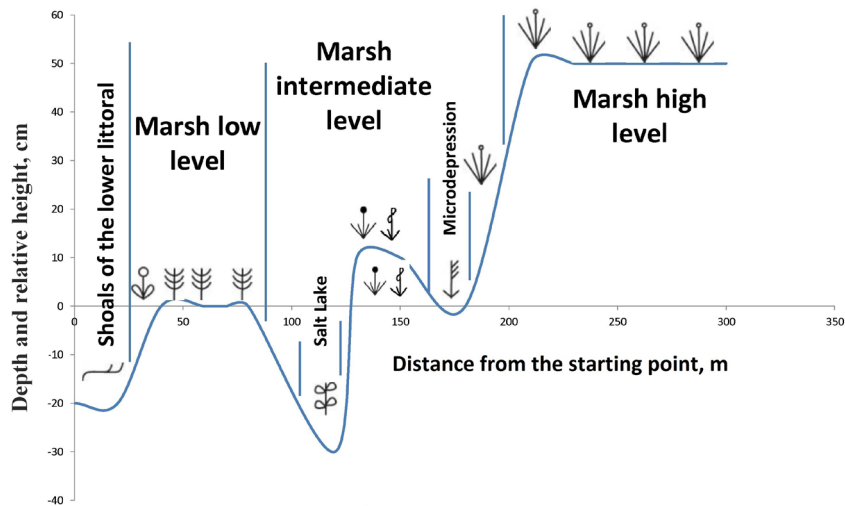
In the spatial structure of the coastal zone vegetation cover from sea to land, the phytocoenoses of *P. australis* replace the coastal aquatic phytocoenoses of *Zostera marina*, *Ruppia maritima*, and *Bolboschoenus maritimus*, and typically conclude the ecological-dynamic series of coastal vegetation (Fig. 3). Thus, *P. australis* spreads and can form communities on marshes of any level (from low to high). However, as our research shows, its communities are most characteristic of mid-level marshes. On the salt marshes of Kinzhugskaya Bay, halophytes dominate in communities with *P. australis*: *Plantago maritima*, *Juncus gerardii*, and *Glaux maritime* (Fig. 3A). In the mouths of the Una and Veiga rivers, at Cape Chesmensky, and in Mokraya Bay, communities dominated by *P. australis* form strips 3–10 m wide, concluding the ecological-dynamic series along the forest edge (Figs. 3D, 3G, 3H). In the mouths of the Kyanda and Shidrovka rivers, throughout almost the entire Unskaya Bay (including Kinzhugskaya Bay) and in Sukhoye More Bay, they form the background vegetation, prevailing over other phytocoenoses, and thereby have greater significance for shaping their ecosystems, demonstrating ongoing changes in the spatial structure of vegetation (Figs. 3A, 3B, 3C, 3F, 3I, 3J). The colonization by reed is beginning in the mouth of Unskaya Bay (Fig. 3E).



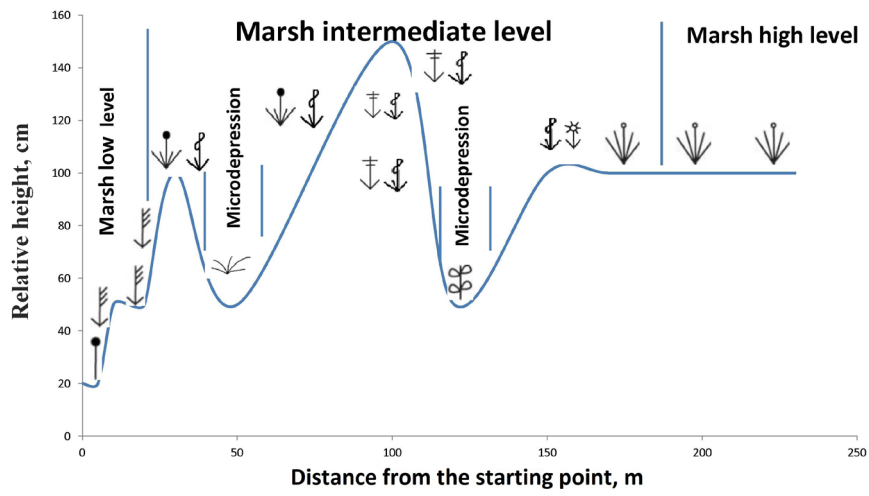
**B**



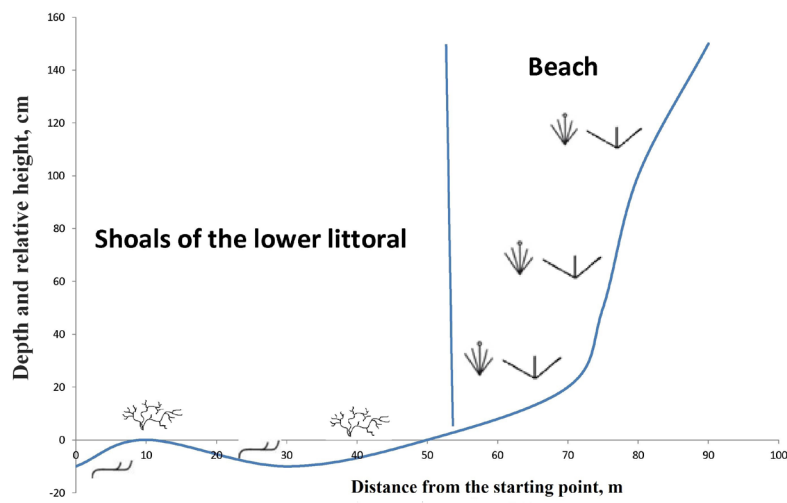
**C**



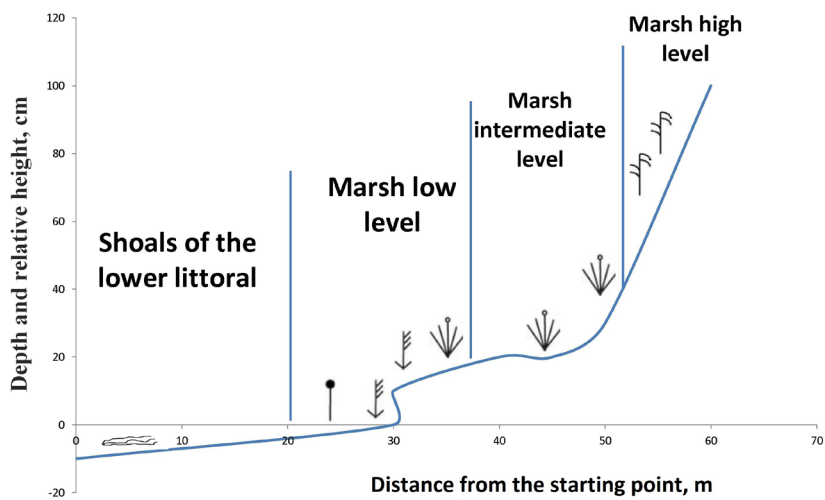
D



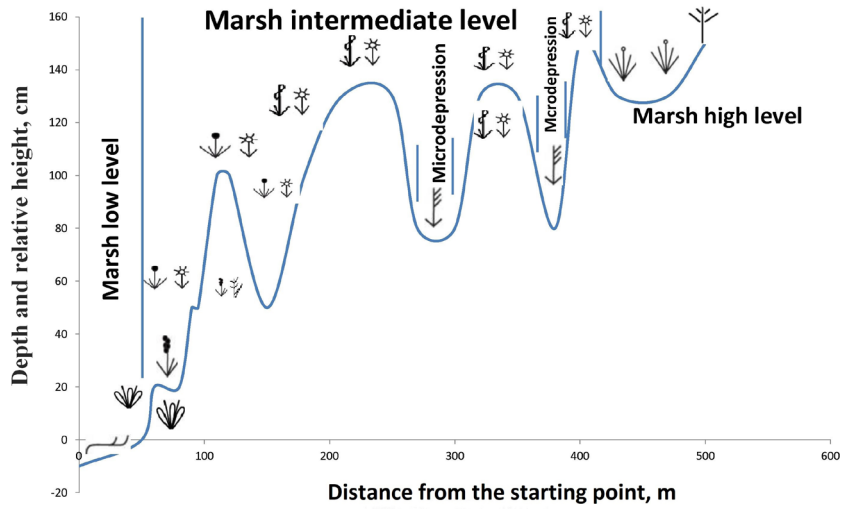
E



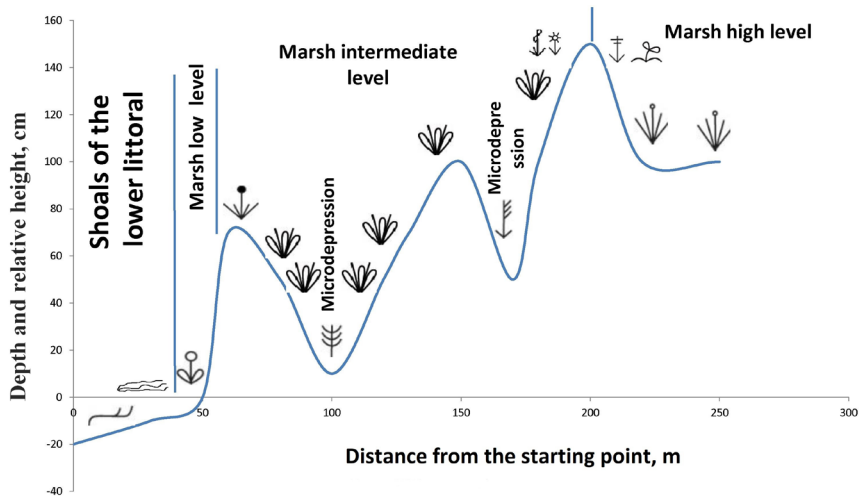
F



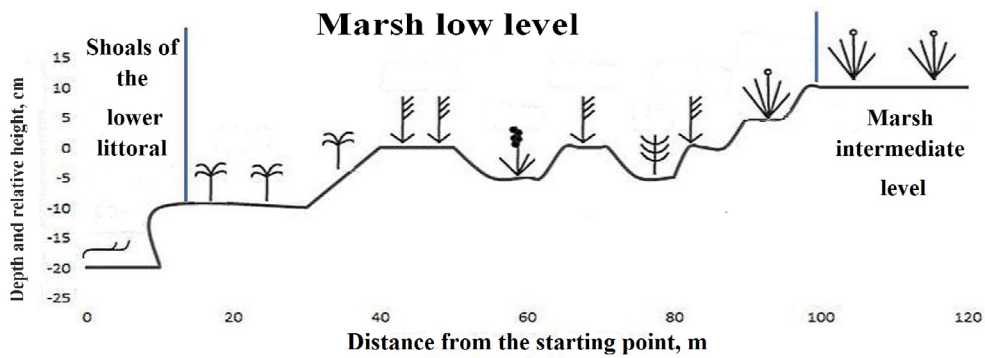
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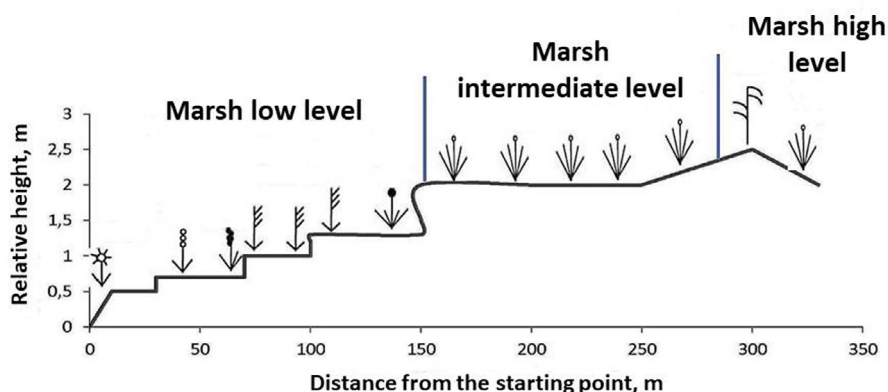
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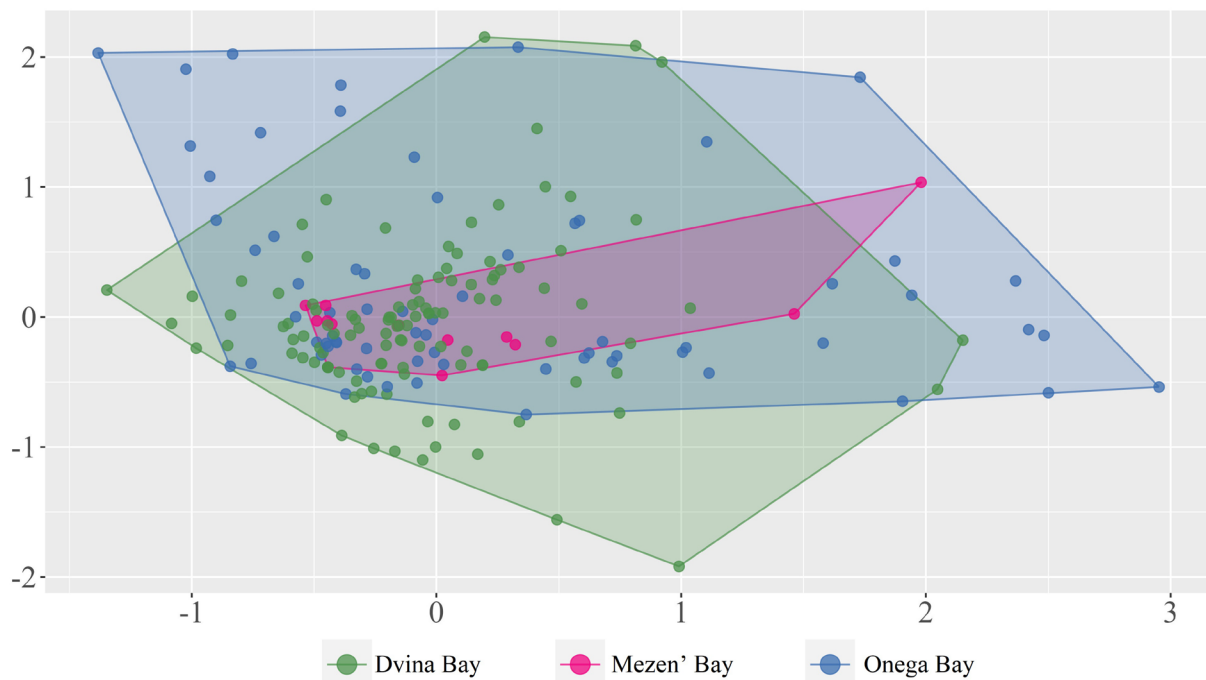
**Fig. 3.** Ecological-dynamic series of seaside phytocenoses in estuaries and lagoons of the White Sea. The letters denote ecological zones: **A** – in the saline marsh at Kinzhuga Bay, **B** – at the mouth of the Kinzhuga River, **C** – on the northern shore of Unskaya Bay, **D** – at the mouth of the Una River, **E** – at the mouth of Unskaya Bay, **F** – at the mouth of the Shidrovka River, **G** – at the mouth of the Veiga River, **H** – at Cape Cheshmensky, **I** – in Sukhoye More Bay, **J** – at the mouth of the Kynda River in Onega Bay.

Symbols: – *Phragmites australis*, – *Bolboschoenus maritimus*, – *Schoenoplectus tabernaemontani*, – *Juncus gerardii*, – *Eleocharis uniglumis*, – *Plantago maritima*, – *Carex subspathacea*, – *Carex glareosa*, – *Carex mackenziei*, – *Tripolium vulgare*, – *Puccinellia phryganodes*, – *Hippuris tetraphylla*, – *Spergularia marina*, – *Salicornia europaea*, – *Glaux maritima*, – *Elytrigia repens*, – *Festuca rubra*, – *Calamagrostis neglecta*, – *Ruppia maritima*, – *Zostera marina*, – *Fucus vesiculosus*, – *Honckenya peploides*, – *Zostera marina* + *Phragmites australis*, – *P. australis* + *Ruppia maritima*, – *P. australis* + *Plantago maritima*, – *P. australis* + *Juncus gerardii* + *Glaux maritima*, – *Salicornia europaea* + *Spergularia marina*, – *Festuca rubra* + *Juncus gerardii*, – *Juncus gerardii* + *Glaux maritima*, – *Plantago maritima* + *Glaux maritima*, – *Triglochin maritima* + *Puccinellia phryganodes*, – *Festuca rubra* + *Carex glareosa*, – *Phragmites australis* + *Honckenya peploides*.

## Discussion

On the White Sea coast, *P. australis* forms extensive communities in the ecotopes of the Onega Bay (the entire Onega shore, including the mouths of the Kyanda, Tapshenga, and Veiga rivers) and in the southern part of the Dvina Bay (the mouths of rivers flowing into Sukhoye More Bay) (Fig. 4). They were previously described along almost the entire western coast of the White Sea's Onega Bay in the mouths of the Nyukhcha, Kolezhma, Shuya, and Kemi rivers (Zaslavskaya, 2007), and were also identified by us in the mouth of the Keret River in Kandalaksha Bay (Moseev et al., 2022). At the same time, the species is less widespread on the shores of the northern Mezen Bay, which is limited by climatic conditions (Fig. 4), although in the southern part of Mezen Bay it forms extensive communities in the mouth of the Kuloy River. On the Mezen Bay coast, reed phytocenoses were studied as early as by A.A. Korchagin (1935) in the mouths of the Mglá and Nes' rivers; these are apparently the northernmost communities at the species' distribution limit. The reed has achieved its widest distribution on brackish coastal-water marshes in river mouths, where the species co-occurs with *Bolboschoenus maritimus*, *Schoenoplectus tabernaemontani* (C.C. Gmel.) Palla, *Alopecurus arundinaceus*, and *Juncus gerardii*. However, it and *Bolboschoenus maritimus* are likely competing species with similar ecological preferences. This is also characteristic of the American *Spartina alterniflora* (Chambers et al., 1998). *Bolboschoenus maritimus*, *Spartina alterniflora*, and *P. australis* are characterized by powerful root systems and form specific vegetation belts in river mouths (Moseev et al., 2023b). Although, as we have shown, *P. australis* forms communities with *Bolboschoenus maritimus*, which is most likely associated with the reed's invasion onto low-level marshes, the primary habitat of *Bolboschoenus maritimus*. On salt marshes, it establishes itself in communities with halophytes *Carex subspathacea*, *Carex glareosa*, and *Plantago maritima*.

Extensive reed stands have currently formed in White Sea bays sheltered from storms and freshened by rivers: throughout the Unskaya Bay coast of the Dvina Bay, in the mouths of the Kyanda, Veiga, and Tapshenga rivers in Onega Bay, and in Sukhoye More Bay (Fig. 4, Table 2). Here, the stands of this species not only actively develop but also play an ecosystem-engineering role, forming a phytogenic type of shore referred to as "reed coasts."



**Fig. 4.** Graphical interpretation of phytocenosis distribution with *Phragmites australis* in the White Sea bays.

For example, in Sukhoye More Bay, *P. australis* stands occupy 1612 hectares and form the vegetation background (Table 2). Extending into the bay, they promote sediment accumulation and waterlogging, which we have also observed in other White Sea bays (Moseev and Sergienko, 2016). Having spread throughout the mouths of small rivers in Sukhoye More Bay, reed stands, together with communities of other macrophytes, have begun to influence the formation of a marginal filter, slowing the mixing processes of river and marine waters (Miskevich et al., 2021).

Its phytocoenoses occupy significant areas in the mouths of the Kyanda, Tapshenga, Veiga, Onega, and Una rivers, in Kinzhugskaya Bay (east of Unskaya Bay), and in Pushlakhta Bay. Smaller coastal areas are currently occupied by reed communities in the mouths of small semi-mountainous rivers: Tamitsa, Kotova, and Shidrovka. Reed also occupies small areas on salt marshes near Cape Chesmensky and in Mokraya Bay. In the studied river mouths and lagoons, phytocoenoses dominated by *P. australis* occupy marshes from low to high levels of tidal influence, or from the upper littoral (rarely the mid-littoral) to the supralittoral. On the shores of the Mezen Bay at the northern distribution limit, the reed phytocoenoses thin out and become less distinct in the overall ordination of reed phytocoenoses in White Sea bays (Fig. 4). Large reed communities exist in the river mouths of the White Sea's western coast (Babina, 2002).

Kinzhugskaya Bay, the mouth of the Kyanda River, and the marshes near Cape Chesmensky are distinguished by significant phytocoenotic diversity of *P. australis* communities (Table 2). At the same time, in Sukhoye More Bay, where the largest reed areas are observed, its communities are represented by only two associations (Table 2). The largest colonized areas there are occupied by communities grouped in the association **Phragmitetum australis maritimae** subass. **subpurum**.

Reed communities occupy large areas on the tombolos of the White Sea and the more southerly Baltic Sea, facilitated by the species' broad ecological valence (Bagdasaryan et al., 2023), also demonstrated in our research.

Currently, extensive reed stands are forming on the Atlantic coast of North America (Burdick and Konisky, 2003; Chambers et al., 1998; Lissner and Schierup, 1997; Smith, 2013). Here, reed colonization is linked to anthropogenic influence (Burdick and Konisky, 2003) and even to sea-level rise (Smith, 2013).

According to some researchers, the spread of reed on the Atlantic coast of North America indicates the development of marsh shores (Smith, 2013). For instance, the expansion of marshes in estuaries bordering the states of New Jersey and Delaware is linked to increased marine influence on the shore and

**Table 2.** Representation of syntaxa with *Phragmites australis* on the White Sea coast.

Legend: I – *Phragmitetum australis maritimae*: Ia – *Phragmitetum australis maritimae* subass. *purum*, Ib – *Phragmitetum australis maritimae* subass. *subpurum*, Ic – *Phragmitetum australis maritimae* subass. *bolboschoenosum maritimi*, Id – *Phragmitetum australis maritimae* subass. *eleocharitosum uniglumis*, Ie – *Phragmitetum australis maritimae* subass. *juncosum gerardii*, If – *Phragmitetum australis maritimae* subass. *alopecurosus arundinacei*, Ig – *Phragmitetum australis maritimae* subass. *ligusticosum scoticae*, Ih – *Phragmitetum australis maritimae* subass. *juncosum gerardii* var. *glaucosum maritimae*, II – *Festucetum rubrae*, III – *Elytrigietum repentis*, IV – *Caricetum rectae*, V – *Caricetum subspathaceae*, VI – *Caricetum glareosae*, VII – *Eleocharitetum uniglumis*, VIII – *Phragmitetum australis petasitosum radiati*, IX – *Phragmitetum australis scirposum lacustris*, X – *Caricetum aquatilis*, XI – *Juncetum gerardii glaucosum maritimi*, XII – *Phragmitetum australis honckeniosum peploidis*, XIII – *Honckenietum peploidis*, XIV – *Phragmites australis* + *Plantago maritima*, XV – *Phragmites australis* + *Glaux maritimus*, XVI – *Phragmites australis* + *Carex subspathacea*, XVII – *Phragmites australis* + *Festuca rubra*, XVIII – *Phragmites australis* + *Leymus arenarius*, XIX – *Phragmites australis* + *Sonchus humilis*, XX – *Alopecurus arundinaceus* + *Leymotrigia bergrothii*, XXI – *Calamagrostis arundinaceus* + *Elytrigia repens* + *Phragmites australis*, XXII – *Leymotrigia bergrothii* + *Phragmites australis* + *Festuca rubra*, XXIII – *Phragmites australis* + *Zostera marina*, XXIV – *Phragmites australis* + *Ruppia maritima*, XXV – *Phragmites australis* + *Atriplex nudicaulis*.  
Dash – no area measurement data available.

Water body	Area occupied by reeds, ha	Association and subassociation numbers
Mokraya Guba and the bays near Cape Letniy Orlov	1.51	Ib
Pushlachta Guba	10.21	Ib
Bay near Cape Chesmensky	5.6	Ib, II, XX, XXV, XXI, XXII
Mouth of the Kotova River	2.5	Ib, II, XX
Mouth of the Shidrovka River	2.0	Ia, Ib, VII
Mouth of the Veyga River	11.0	Ia, Ib, Ie
Mouth of the Kyanda River	32.7	Ib, Ic, Ih, III, XI
Mouth of the Tamitsa River	1.0	Ib
Mouth of the Tapshen'ga River	0.02	Ib
Mouth of the Onega River	29.06	Ib
Mouth of the Una River, Unskaya Guba	34.49	Ia, Ib, Ic, XXIV
Northwestern shore of Unskaya Guba near the Kholodny Stream	7.77	Ia, Ib, Id, Ie
The mouth of the Unskaya Guba near Cape Sosnovy	–	XII, XIII
Kinzhuskaya Bay with the mouth of the Kinzhuga River of Unskaya Guba	262.49	Ia, Ib, Id, Ie, If, Ig, Ih, XVII, IV, XIV, XV, XVI, XVIII, XIX, XI, XXIII, XXIV
Mouth of the Kuya River	2.76	Ib, VIII, IX
Sukhoje More Guba (entirely, including the mouths of the Bolshaya Nitsa, Mud'yuga, and Kad' rivers)	1612.5	Ib, X
Mouth of the Kuloy River	–	Ia, Ib, If
Mouth of the Kargovka River	–	Ia, Ib, V, VI
Mouth of the Keret' River	0.0004	Id

soil salinization, which prevents the development of forest vegetation (Engelhart et al., 2009; Hussein, 2009). These phenomena on the North American coast are also explained by climate warming (Smith, 2013). Moreover, eyewitness accounts of the reduction of terrestrial ecotopes and their replacement by marine and transitional ecotopes on the Atlantic coast have been known since the mid-19th century (Kitchell, 1857). On the Onega Peninsula, reed often forms narrow strips of communities near the forest in the mouths of the Veiga and Una rivers, and on marshes near Cape Cheshmensky. However, in the mouth of the Una River, active colonization of the entire marsh strip by reed is already locally observed, which is occurring not only due to natural causes but also against the backdrop of the recent decline in agricultural intensity. For example, coastal meadows in the Una River mouth formerly dominated by reedgrasses, fescues, and saltmarsh rush (previously used as hayfields) are now being colonized by reed.

Communities dominated by *P. australis* on the shores of the Sea of Azov adjoin a belt of *Bolboschoenus maritimus* (Grechushkina et al., 2011); thus, a zonation of brackish marsh vegetation is formed here, which is also characteristic of the shores of the Onega River mouth (Moseev et al., 2023b), the Veiga and Kyanda rivers, Sukhoye More Bay, and Unskaya Bay. A similar zonation is observed on the Baltic Sea coast (Rebassoo, 1975).

The article by D.M. Burdick and R.A. Konisky (2003) presents a study on the establishment of reed in marsh areas with different salinity. According to the classification of wetlands by water salinity, mesohaline, polyhaline, and mesopolyhaline wetlands are distinguished in river mouths (Cowardin et al., 1979; Odum et al., 1984). It turned out that reed established well in areas with salinity up to 18‰, but its growth slowed in polyhaline marsh waters with higher salinity (Burdick and Konisky, 2003). There are known studies indicating reed development in saltwater of 30‰ (Hellings and Gallagher, 1992). Under White Sea conditions, it has been shown that *P. australis* growing in the littoral zone tolerates saline waters up to 22‰ well but is suppressed at higher salinity, forming stunted shoots (Moseev and Sergienko, 2018). The most saline waters (22‰) affect communities of the **Phragmitetum australis maritimae** association, which promotes the development of halophytes within them.

Thus, it can be said that the reed is quite tolerant to saline waters. Its growth on saline sea coasts is associated with a developed root system that reaches low-salinity or fresh water (Babina, 2002).

## Conclusion

The common reed *Phragmites australis* has spread widely on the White Sea coast. Ordination of vegetation with reed phytocoenoses in different coastal ecotopes indicates the reed's colonization of diverse habitats: brackish coastal-water marshes, near-water brackish marshes, beaches, wadden shoals of the mid-littoral zone, salt marshes, and tidal flats in the upper reaches of estuaries.

When colonizing beaches, the reed forms communities with plant species characteristic of sea coast beaches, such as the psammophiles *Honckenya peploides* and *Leymus arenarius*. This development of its communities likely indicates increased influence of estuarine waters on the shores and the development of marshes. In the coastal zone, suspended matter and nutrients brought by tides accumulate, which is favorable for reed development. The formation of reed communities on the beaches of Unskaya Bay may indicate shoreline deformation and the proximity of the groundwater level to the soil surface.

Apparently, *P. australis* will continue to replace halophyte communities under favorable growing conditions. Such predictions were made 20 years ago for the western coast of the White Sea (Babina, 2002), but these processes may intensify with current climate warming, leading to a shorter ice cover period in the river mouths and bays of the White Sea. To prove the colonization of different habitats by reed on the White Sea coast and to find its causes, monitoring studies of the reed community on the coast are necessary.

According to observations made in July 2025, an invasion of *P. australis* into shoreline areas with communities dominated by *Bolboschoenus maritimus* is indeed observed in the Onega River mouth, where reed was not growing according to 2022 data. In the coming years, monitoring of coastal vegetation communities in the mouths of the Onega and Kyanda rivers, and possibly in other coastal areas, is planned, which will serve as a scientific database to prove the colonization of White Sea coast ecotopes by reed.

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