Article

Boreal (Eemian) Transgression in the Northeastern White Sea Region: Multiproxy Evidence from Bychye-2 Section

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Abstract: Reconstructing interglacial marine environments helps us understand the climate change mechanisms of the past. To contribute to this body of knowledge, we studied a high-resolution 455 cm-thick sediment sequence of the Boreal (Eemian) marine beds directly overlying Moscovian (Saalian) moraine in the Bychye-2 section on the Pyoza River. We analyzed lithological and microfossil (foraminifers, ostracods, pollen, aquatic palynomorphs) variations at the studied site. Stratigraphical zonation is based on the local and well-established regional pollen zones, correlated with the western European pollen zones. The studied marine beds accumulated from the end of the Moscovian glacial (>131 ka) until ca. 119.5 ka. We distinguished three successive phases: a seasonally sea-ice-covered, relatively deep, freshened basin in the initial rapid flooding stage (>131–130.5 ka); a deep basin in the maximum flooding phase with less extensive sea ice cover (130.5–130.25 ka); and a shallow basin with reduced sea ice cover (130.25–119.5 ka). According to a pollen zone comparison with other sites, the regional glacioisostatic rebound started ca. 130 ka. The diverse warm-water assemblages of benthic foraminifers and ostracods containing typical Baltic Sea species occurred during the regression, mainly 128–124 ka, thus giving evidence for a relatively long-lasting connection between the White and Baltic Seas.

1. Introduction

The climate changes observed in recent decades are particularly well pronounced in the high northern latitudes and are responsible for the growing interest in climatically induced paleoenvironmental reconstructions of the previous (pre-industrial) interglacial and deglacial epochs. This primarily concerns the last interglacial of marine isotope stage (MIS) 5e and the preceding glacial termination II at the end of MIS 6, which coincide in time with the end of the Saalian glaciation, the Eemian interglacial of Western Europe, the end of the Moscovian glaciation, and the beginning of the Mikulinian interglacial in European Russia, from approximately 130–131 to 115–116 thousand years ago (ka) [1,2]. This warming phase is partially overlapping with the Boreal (Eemian) transgression, well known for its stratigraphic reference sediment sequence in the European north of Russia, northern Europe, and Scandinavia [2–18].

Many aspects of the paleogeography of the Boreal (Eemian) paleobasins remain controversial. One of the most important aspects in the course of the transgression is the relationship between the Arctic and the North Atlantic, namely, the timing and duration of warm and salty Atlantic waters' penetration into the Barents and White Seas and the character and duration of the marine connection between the White and Baltic Seas. The estimates

of the latter vary from 2–2.5 thousand years, according to mollusc fossil assemblages [8] to 6–7 thousand years, according to fossil diatom associations [6,15]. The question of whether the advection of warm Atlantic waters into the Arctic was actually more powerful compared to the Holocene remains unresolved [15,19–21]. On the one hand, the rapid advance in boreal vegetation, including broad-leaved trees to the north during the last interglacial [22,23], indicates significant warming, unlike during the Holocene. Similarly, the appearance of thermophilic species of marine macro- and microfauna in the White Sea and Karelia at the beginning of the interglacial is explained by the inflow of Atlantic waters [6,8,11]. On the other hand, paleoceanographic records from coeval sediments of the Norwegian Sea and the Fram Strait indicate the opposite trend, i.e., colder surface water temperatures in the Eemian compared to the Holocene and a significant weakening of the inflow of surface Atlantic waters due to the presence of a large surface meltwater plume until the middle (127 ka) or the final (118–116 ka) stage of the Eemian [19,20,24–27]. In this regard, detailed and comprehensive studies of regional marine sediment sequences become important, making it possible to reconstruct the evolution of transgression in the context of paleoclimatic and paleoceanographic changes. Here, we report our results of a high-resolution study of the Bychye-2 section exposed on the Pyoza River in the northeastern coastal area of the White Sea (Figure 1). The lithological and fossil evidence indicate that the section represents the whole transgressive–regressive postglacial cycle from the end of the Moscovian glacial until the end of the warmest interglacial stage related to the disappearance of thermophilic plant species, which makes the Bychye-2 section a reference section for reconstructing past environmental changes on the eastern White Sea coast during the Boreal transgression.
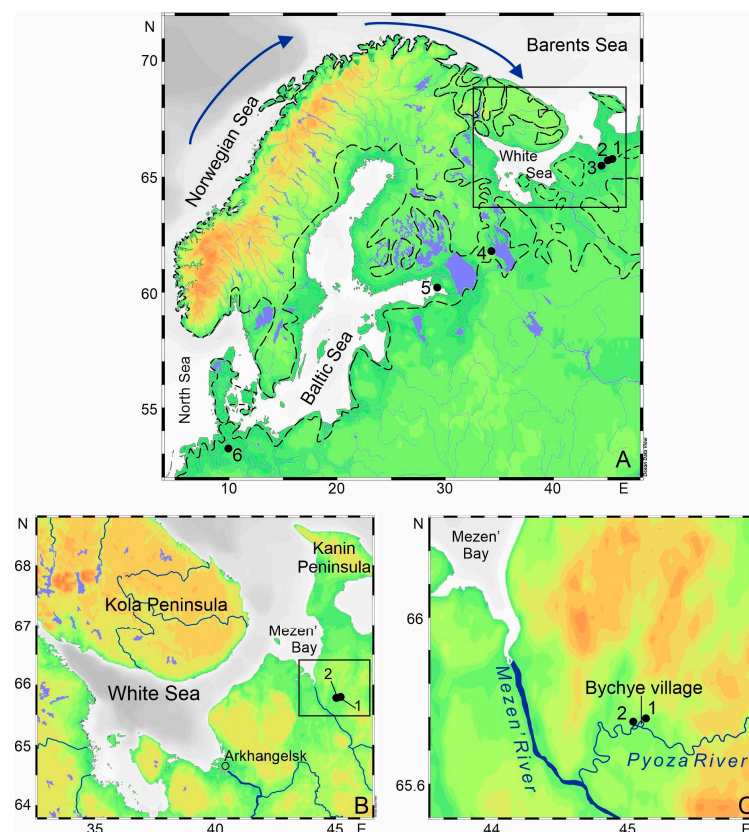
Figure 1. (**A**) Overview map with possible Eemian coastline (dashed line) after [8,15] and sites with Eemian (Boreal) marine beds mentioned in the text: 1—Bychye-1, 2—Bychye-2, 3—Zaton, 4—Petrozavodsk, 5—Peski, and 6—Bispingen. Arrows mark subsurface Atlantic water inflow. (**B**) Regional overview of the site locations of the previously studied [5,7,11] Bychye-1 section and Bychye-2 section (this study). (**C**) Enlarged view of the area marked by the rectangle in (**B**). Coloring in the plots highlights topography.

2. Materials and Methods

The studied site, the Byche-2 section, is located on the right bank of the Pyoza river, approximately 5 km downstream from the previously studied Bychye-1 section near Bychye village [5,11] (Figure 1). It is located on the westernmost downstream side of a 500 m-long exposed high bank of a river meander. The 455 cm-thick marine sediment sequence directly overlies the red-colored moraine of the Moscovian glaciation exposed at the river line at an absolute height of about 12 m and is overlain by fossil-barren sands of unknown (foreshore marine, fluvial?) origin (Figure 2).
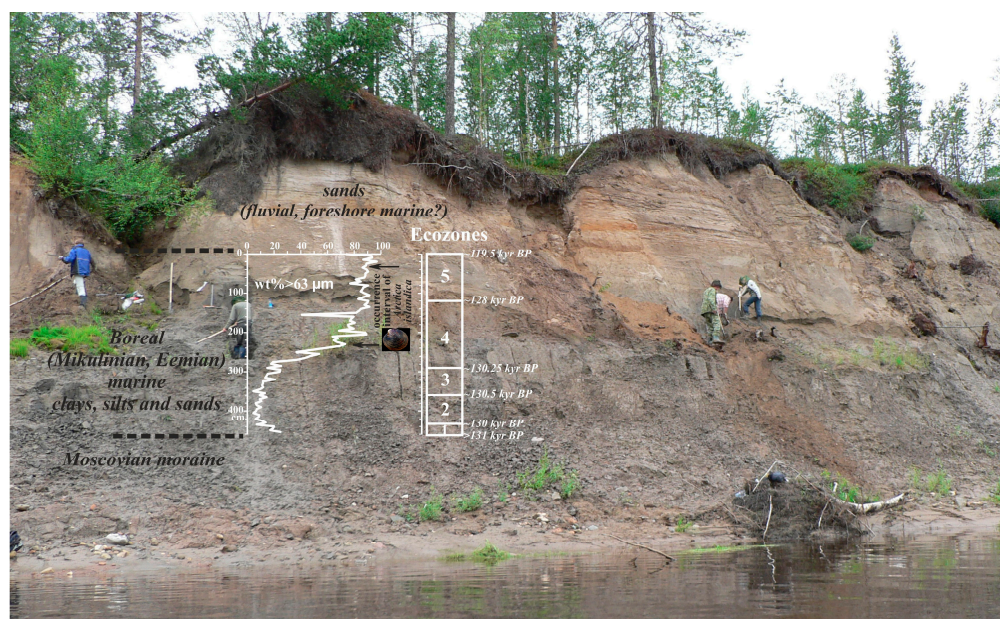
Figure 2. A photo and the lithology (wt% >63 μm fraction) of the studied Bychye-2 section. Additionally shown are the established ecozones 1–5 with their age assignments and the occurrence of the mollusc *Arctica islandica*.

We collected 2 cm-thick samples with 5 cm intervals throughout the section, which ensured a sufficient amount for high-resolution multiproxy analyses; for comparison, the previously studied Bychye-1 section was sampled at 50 cm intervals [11]. The multiproxy study of the Bychye-2 section consists of the following analyses: lithological, microfaunal (foraminifers, ostracods), and palynological (spores, pollen, aquatic non-pollen palynomorphs).

For the lithological and microfaunal analyses, the sediment was washed over a 63 μm mesh-size sieve. As a result, the weight percentage of the fraction >63 μm was determined. The taxonomic compositions of fossil benthic foraminifers and ostracods were studied under binocular in the >63 μm fraction. Their total abundance was determined relative to the dry bulk sediment weight, per 1 g for more abundant benthic foraminifers and per 100 g for relatively rare ostracods. The species diversity is presented as the number of species per sample. For benthic foraminifers, the relative species abundance was calculated, while for ostracods, the species abundance is given as the number of valves per 100 g of dry bulk sediment. No special study of fossil molluscs was carried out, but during sampling, the species composition of the shells was noted, and the range of the occurrence of the shallow-water subarctic species *Arctica islandica* was established (Figure 2).

The main task of the palynological part of the study was the pollen-based stratigraphic subdivision of sediments based on a spore and pollen diagram and the establishment of local pollen zones (LPZs) [28]. An age assessment of LPZs is described in Section 3.1 and shown in Figure 3. During the pollen analysis, it was noted that the slides repeatedly contained a few non-pollen aquatic palynomorphs—marine dinoflagellate cysts and freshwater colonial green algae, which carry important paleoecological information. Their

composition was studied in addition to spores and pollen. At the same time, we took into account the fact that palynomorph associations could be incomplete due to the fact that the samples were subjected to a rather aggressive sample preparation using a standard separation method with heavy liquid (KJ + CdJ2) with a 2.2 g/cm^{-3} specific gravity [29]. Microfossils were identified under a light microscope at ×400 magnification using the electronic database of photographs of non-pollen palynomorphs [30]. Latin names are given according to [31–34]. Their relative concentrations were determined by adding tablets with a fixed number of *Lycopodium clavatum* (Batch 177745) spore markers to the sediment before treatment [35]. To calculate concentrations and percentages, the Tilia/TGView2.02 software package was used [36,37].

Based on the changes in lithology, the composition of the fossil assemblages of benthic microfauna, and the associations of aquatic palynomorphs, 5 specific sediment intervals called ecozones were established in the Bychye-2 section that reflect the main stages in the paleoenvironmental evolution of the region. The age boundaries of the ecozones were determined based on the pollen zone data shown in Figure 3 and discussed in the Section 3.1, with further interpolation between the age assignments of the LPZ boundaries assuming uniform sedimentation rates between the LPZ age tie points.
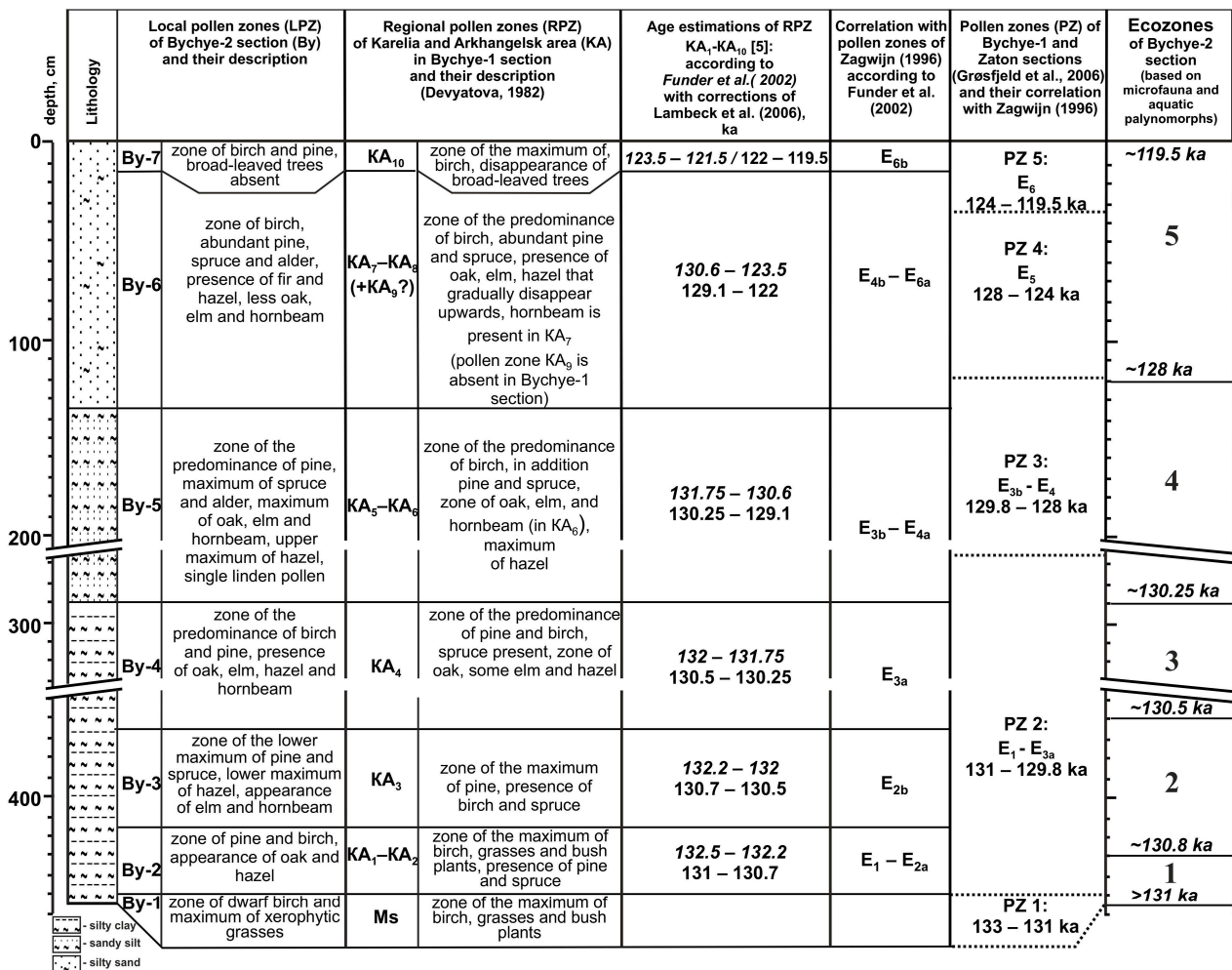
The source data are presented in Supplementary Tables S1–S4.

3. Results

3.1. Pollen-Based Stratigraphy

The age assessment of the ecozones and the LPZs identified in the Bychye-2 section (By-1-By-7) [28] is primarily based on the correlation of the LPZs with the regional pollen zones of the Karelia and Arkhangelsk regions (Ms, KA$_1$–KA$_{10}$) established in the Bychye-1 section [5], as shown in Figure 3. The latter were previously correlated by Funder et al. [8] and Lambeck et al. [12] with pollen zones in Western Europe (E$_1$–E$_6$) and Russia [22,23,38]. Also, Figure 3 shows the age boundaries of the pollen zones of the Zaton and Bychye-1 sections on the Pyoza River adopted in a paper by Grøsfjeld et al. [11]. The high accuracy of the pollen zone age boundaries in the lower part of the studied section, with ages ranging from >131 to 130.25 ka, is supported by an initial evaluation of these early Eemian pollen zones through direct counting of annual layers in the lacustrine varve clays of the sediment core from Bispingen (northern Germany) [38]. Zagwijn [23] linked the Eemian sea-level highstand in the North Sea area to the first half of the E$_5$ pollen zone. Based on the absolute dating of corals, the global sea-level highstand corresponds to 128 ± 1 ka [39] (although there are different age definitions; e.g., see the overview in [15]). Given the accepted duration of the Eemian pollen zones in Western Europe, the beginning of the Eemian interglacial is proposed to be from 131 ka [8,12,40]. In addition, we used the age markers of the appearance/disappearance of certain species determined by Miettinen et al. [15] in the Peski section on the Karelian Isthmus for the LPZs of the Bychye-2 section [28]. An important feature of Bychye-2 is the disappearance of the pollen of broad-leaved trees in the uppermost part of the marine sediment sequence (Figure 3). This event was dated by Miettinen et al. [15] to 119.5 ka. In the Bychye-2 section, this event was not recorded. Therefore, the Bychye-2 section covers the time period from the end of the Moscovian (Saalian) glacial with periglacial vegetation (LPZ By-1, >131 ka) to the end of the last interglacial with the elimination of thermophilic taxa (LPZ By-7, 119.5 ka).

depth, cm	Lithology	Local pollen zones (LPZ) of Bychye-2 section (By) and their description		Regional pollen zones (RPZ) of Karelia and Arkhangelsk area (KA) in Bychye-1 section and their description (Devyatova, 1982)		Age estimations of RPZ KA1-KA10 [5]: according to *Funder et al.(2002)* with corrections of Lambeck et al. (2006), ka	Correlation with pollen zones of Zagwijn (1996) according to Funder et al. (2002)	Pollen zones (PZ) of Bychye-1 and Zaton sections (Grøsfjeld et al., 2006) and their correlation with Zagwijn (1996)	Ecozones of Bychye-2 section (based on microfauna and aquatic palynomorphs)
0		By-7	zone of birch and pine, broad-leaved trees absent	KA_{10}	zone of the maximum of, birch, disappearance of broad-leaved trees	*123.5 – 121.5 / 122 – 119.5*	E_{6b}	PZ 5: E_6 124 – 119.5 ka	~119.5 ka
100		By-6	zone of birch, abundant pine, spruce and alder, presence of fir and hazel, less oak, elm and hornbeam	KA_7–KA_8 (+KA_9?)	zone of the predominance of birch, abundant pine and spruce, presence of oak, elm, hazel that gradually disappear upwards, hornbeam is present in KA_7 (pollen zone KA_9 is absent in Bychye-1 section)	*130.6 – 123.5* *129.1 – 122*	$E_{4b} – E_{6a}$	PZ 4: E_5 128 – 124 ka	5 ; ~128 ka
200		By-5	zone of the predominance of pine, maximum of spruce and alder, maximum of oak, elm and hornbeam, upper maximum of hazel, single linden pollen	KA_5–KA_6	zone of the predominance of birch, in addition pine and spruce, zone of oak, elm, and hornbeam (in KA_6), maximum of hazel	*131.75 – 130.6* *130.25 – 129.1*	$E_{3b} – E_{4a}$	PZ 3: E_{3b} - E_4 129.8 – 128 ka	4 ; ~130.25 ka
300		By-4	zone of the predominance of birch and pine, presence of oak, elm, hazel and hornbeam	KA_4	zone of the predominance of pine and birch, spruce present, zone of oak, some elm and hazel	*132 – 131.75* *130.5 – 130.25*	E_{3a}		3 ; ~130.5 ka
400		By-3	zone of the lower maximum of pine and spruce, lower maximum of hazel, appearance of elm and hornbeam	KA_3	zone of the maximum of pine, presence of birch and spruce	*132.2 – 132* *130.7 – 130.5*	E_{2b}	PZ 2: E_1 - E_{3a} 131 – 129.8 ka	2 ; ~130.8 ka
		By-2	zone of pine and birch, appearance of oak and hazel	KA_1–KA_2	zone of the maximum of birch, grasses and bush plants, presence of pine and spruce	*132.5 – 132.2* *131 – 130.7*	$E_1 – E_{2a}$		1 ; >131 ka
		By-1	zone of dwarf birch and maximum of xerophytic grasses	Ms	zone of the maximum of birch, grasses and bush plants			PZ 1: 133 – 131 ka	

- silty clay
- sandy silt
- silty sand

Figure 3. Local pollen zones (LPZs) in the studied Bychye-2 section, their correlation with regional pollen zones (RPZs) [5], and related age estimations of the LPZs and ecological zones of the Bychye-2 section [11] based on the previously established correlations of the RPZs with Western European pollen zones [23,38] made by [8,12].

3.2. Lithology

The weight percentage (wt%) of the >63 μm fraction (Figure 2) demonstrates an upward coarsening trend from silty clays in the lower part of the section (300–455 cm), to silts and silty sands in the middle (135–300 cm), and to sands with an admixture of silt in the upper 135 cm of the section. No hiatus is recorded in the Bychye-2 marine sediment sequence, but the described Weichselian glacial–fluvial sediments [7] are present farther east and upstream of the river in our section and in the Bychye-1 section. The slight increase in the wt% >63 μm in the lower part of the section is likely due to inclusions of the clasts of moraine material >2 mm in size, together with abundant redeposited fossilized ostracod carapaces and Crinoidea remnants found during the study of microfossils under binocular. However, the entire section contains—independent of the upward grain-size change, which we interpret as shoaling due to isostatic uplift—larger angular rock fragments (up to 10 cm) that must have been transported by moving sea ice, likely due to ice break-up during summer.

3.3. Benthic Foraminifers

The total abundance of benthic foraminifers varies greatly across the section, with a maximum of 200–300 tests per 1 g of dry bulk sediment at 300–100 cm (Figure 4). Species diversity is more evenly distributed, with an average of 10–20 species per sample, decreas-

ing at depths of 430–370 cm and 0–20 cm. Planktonic foraminifers have not been recorded in Bychye-2 sediments.
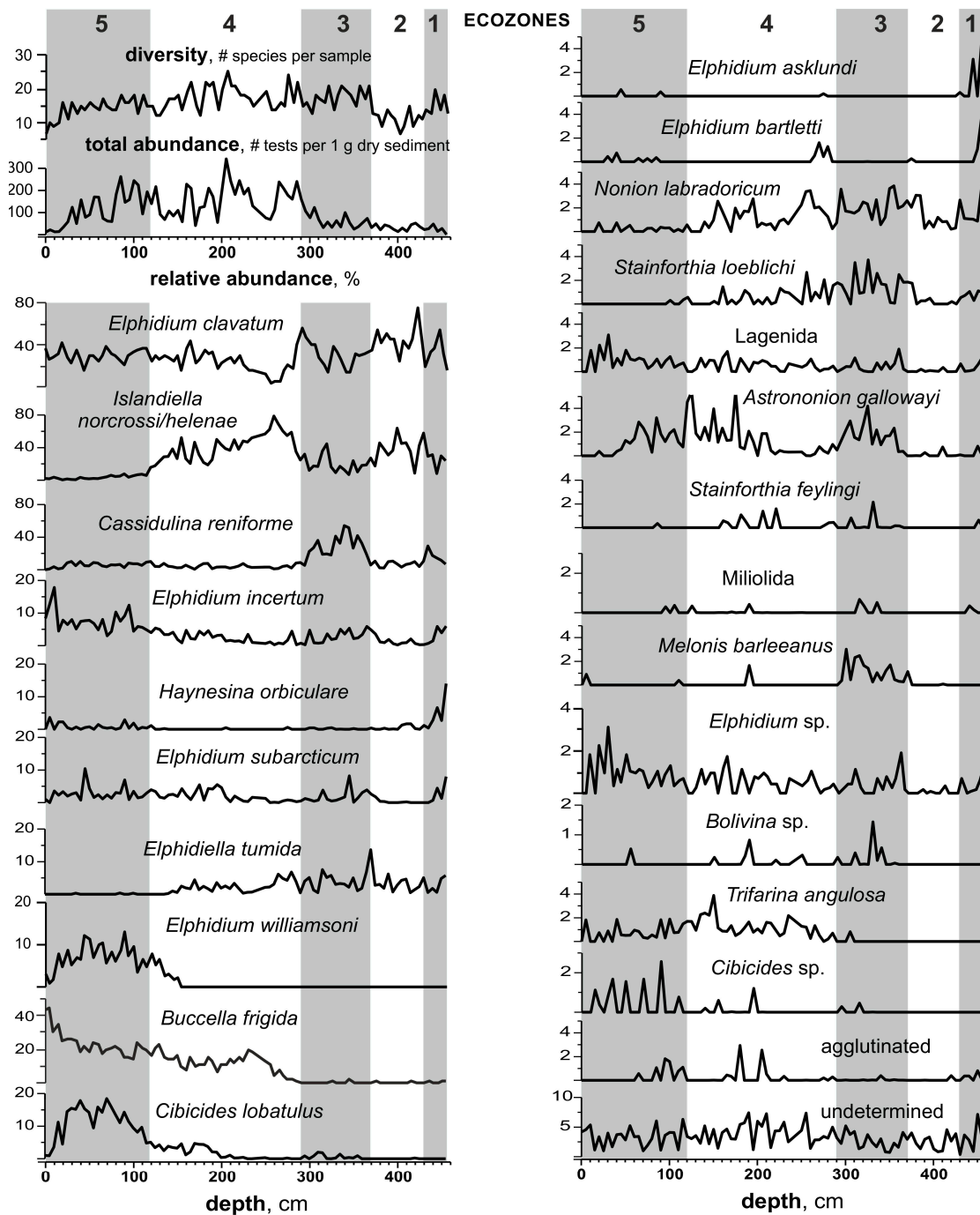
Figure 4. Downcore distribution of benthic foraminifers in the Bychye-2 section. The established ecozones are indicated with figures on the top and shading.

The changes in the species composition and abundance of benthic foraminifers, as the most numerous group of microfossils found in the Bychye-2 section, formed the basis for the identification of the ecozones (Figures 4 and 5). Most species of benthic foraminifers recorded in the section are typical inhabitants of the Arctic shelf seas [41,42]; only *Elphidium williamsoni* and *Trifarina angulosa*, which appear in its upper part, can be classified as warmer-water elements [43,44]. Polyak et al. [41] discriminated benthic foraminifers from the river-affected Arctic shelf seas into three groups: "river-proximal", "river-intermediate",

and "river-distal" ones. This succession of species from near-estuarine to distal open-sea locations was found to be controlled by a combination of bottom salinities and feeding conditions and appeared to be related to the riverine input of freshwater, organic matter, and sediments, as well as to sea ice cover characteristics.
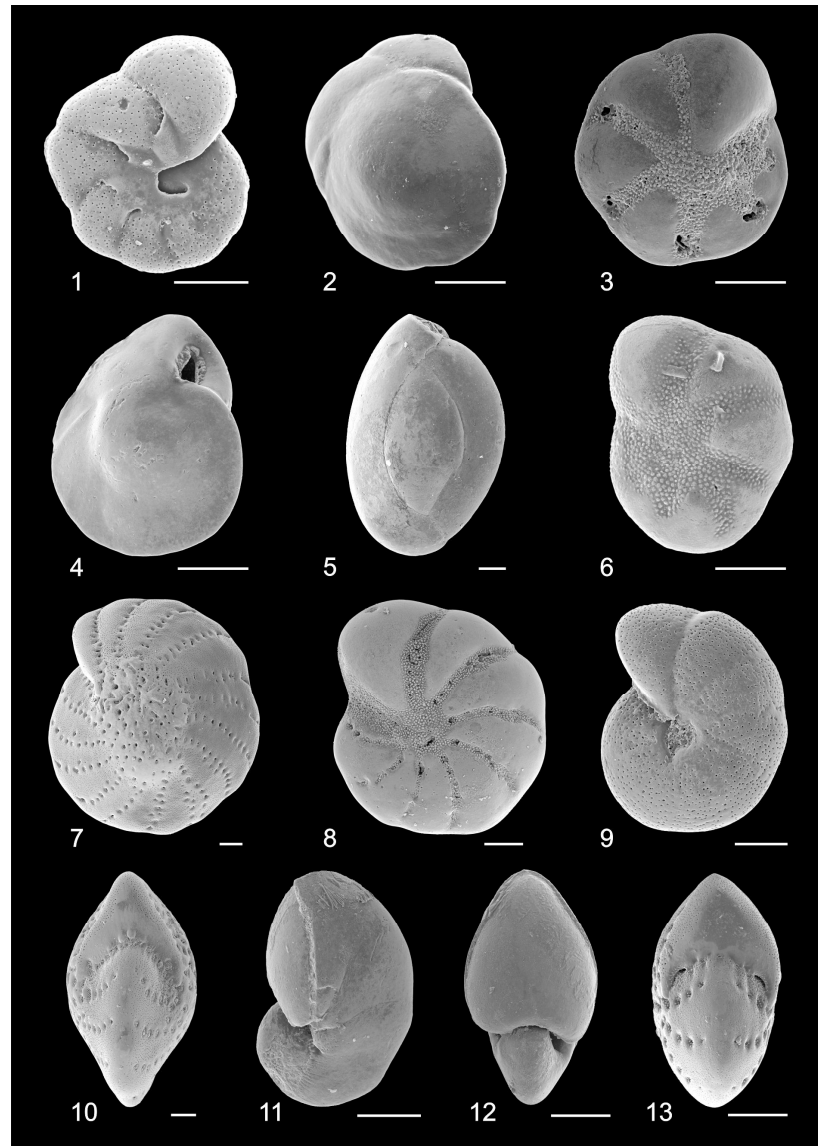
Figure 5. Phototable with SEM photos of some foraminifera species found in the Bychye-2 section (scale bar length: 50 μm): 1—***Astrononion gallowayi*** Loeblich and Tappan; 2, 3—***Buccella frigida*** (Cushman, 1922); 4—***Islandiella norcrossi/helenae***; 5—***Quinqueloculina seminulum*** (Linne, 1758); 6—***Elphidium subarcticum*** Cushman, 1944; 7, 10—***Elphidiella tumida*** Gudina, 1969; 8—***Haynesina orbiculare*** (Brady, 1881); 9—***Melonis barleeanus*** (Williamson, 1948); 11, 12—***Nonion labradoricum*** (Dawson, 1960); and 13—***Elphidium clavatum*** Cushman, 1930.

In the interval 455–430 cm (ecozone 1), the typical Arctic species *Elphidium clavatum*, *Cassidulina reniforme*, and *Islandiella norcrossi/helenae* predominate. These species form the basis of fossil foraminiferal assemblages throughout the section, especially in ecozones 1–4. *E. clavatum*, regarded as an opportunistic species [41,42], predominates in the lower 15 cm of the section, where *Haynesina orbiculare*, *Elphidium incertum*, *E. asklundi*, and *E. bartletti*, which belong to the group of Arctic river-proximal species [41], reach high representation. Further up the section, the Arctic river-intermediate species *C. reniforme* and the river-distal species *I. norcrossi/helenae* become more abundant. At the same time, it should be noted

that even at the very base of the section, the fossil assemblage contains such river-distal species as *Nonion labradoricum* and *Astrononion gallowayi*.

In the interval 430–370 cm (ecozone 2), two species predominate, *E. clavatum* and *I. norcrossi/helenae*, against the background of a significant reduction in biodiversity. *E. clavatum* is a widespread opportunistic Arctic species that reaches its highest abundance in coastal river-affected environments that are unfavorable for most species with surface water freshening by river runoff, fast ice cover, and high water turbidity. *I. norcrossi* and *I. helenae* largely occur in river-distal regions close to the seasonal sea–ice margin, which is associated with increased productivity during the spring diatom bloom [41].

The interval 370–290 cm (ecozone 3) is characterized by the predominance of the Arctic river-intermediate species *C. reniforme*, which prefers the cold and salty bottom waters of the middle shelf [41,42]. The relative abundance of *E. clavatum* decreases. The percentage of the species *A. gallowayi* and *Elphidium subarcticum*, characteristic of active near-bottom environments, slightly increases in this ecozone. The species *N. labradoricum* is usually associated with high seasonal productivity at the sea–ice margin [41]. An important feature of this complex is the presence of the species *Melonis barleeanus*, which is usually restricted to the most river-distal areas with bottom salinities above 34.5‰ [41]. In the Eurasian Arctic seas, it is often associated with shelf troughs, and its feeding strategy is the consumption of altered organic matter delivered to sea-floor depressions from shallow areas [41].

The interval 370–120 cm (ecozone 4) is characterized by an increase in the total abundance and species diversity. The percentages of *E. clavatum* and *C. reniforme* decrease, *I. norcrossi/helenae* predominates, and the relatively warm-water species *E. williamsoni* and *T. angulosa* appear in the sediments for the first time. The latter species, along with *A. gallowayi*, *E. subarcticum*, and *Cibicides lobatulus*, are characteristic of hydrodynamically active bottom environments and relatively coarse-grained sediments [42–44]. The percentage of the shallow-water species *Buccella frigida* [41] increases.

The uppermost interval of 120 cm (ecozone 5) demonstrates a decreasing total abundance and species diversity of foraminifers, a predominance of *E. clavatum*, *B. frigida*, and *C. lobatulus*, and an increasing relative abundance of the Arctic river-proximal species that were present at the base of the section, as well as a fairly high representation of the relatively warm-water and shallow-water species *E. williamsoni*.

3.4. Ostracods

Despite their relative paucity compared to benthic foraminifers, ostracods also show significant changes in their total abundance and taxonomic composition across the section (Figures 6 and 7). In ecozone 1, they are represented by the marine species *Normanicythere leioderma*, characteristic of Arctic shelf seas at water depths down to 50 m, and in ecozone 2, ostracods are absent.

A more diverse Arctic assemblage is characteristic of ecozone 3. It is dominated by the marine species *Acanthocythereis dunelmensis* and *Elofsonella concinna*, as well as by the euryhaline species *Heterocyprideis sorbyana*. Similarly to benthic foraminifers, the relatively deep-water species *Krithe glacialis* and Rabilimis sp. are present in this ecozone.

In ecozones 4 and 5, the total abundance of ostracods increases, and fossil assemblages become more diverse due to the appearance of the marine species *Sarsicytheridea punctillata*, *S. bradii*, and *Robertsonites tuberculatus*, which are characteristic of the middle and outer-shelf regions of the Kara and Laptev seas [45,46]. Upward of the section, they are supplemented by the shallow and warmer-water boreal marine species *Cythere lutea*, *Hemicytherura clathrata*, and *Hemicythere villosa*, characteristic of the Baltic Sea [47,48], that are not found in the high Arctic shelf seas. Other common species include *Finmarchinella finmarchica*, *F. logani*, *Patagonacythere dubia*, and, which are not typically found on shallow-water Arctic shelves, such as in the Kara and Laptev seas [49–53]. In some samples from ecozone 5, warm-water and shallow-water species dominate over Arctic shelf species.
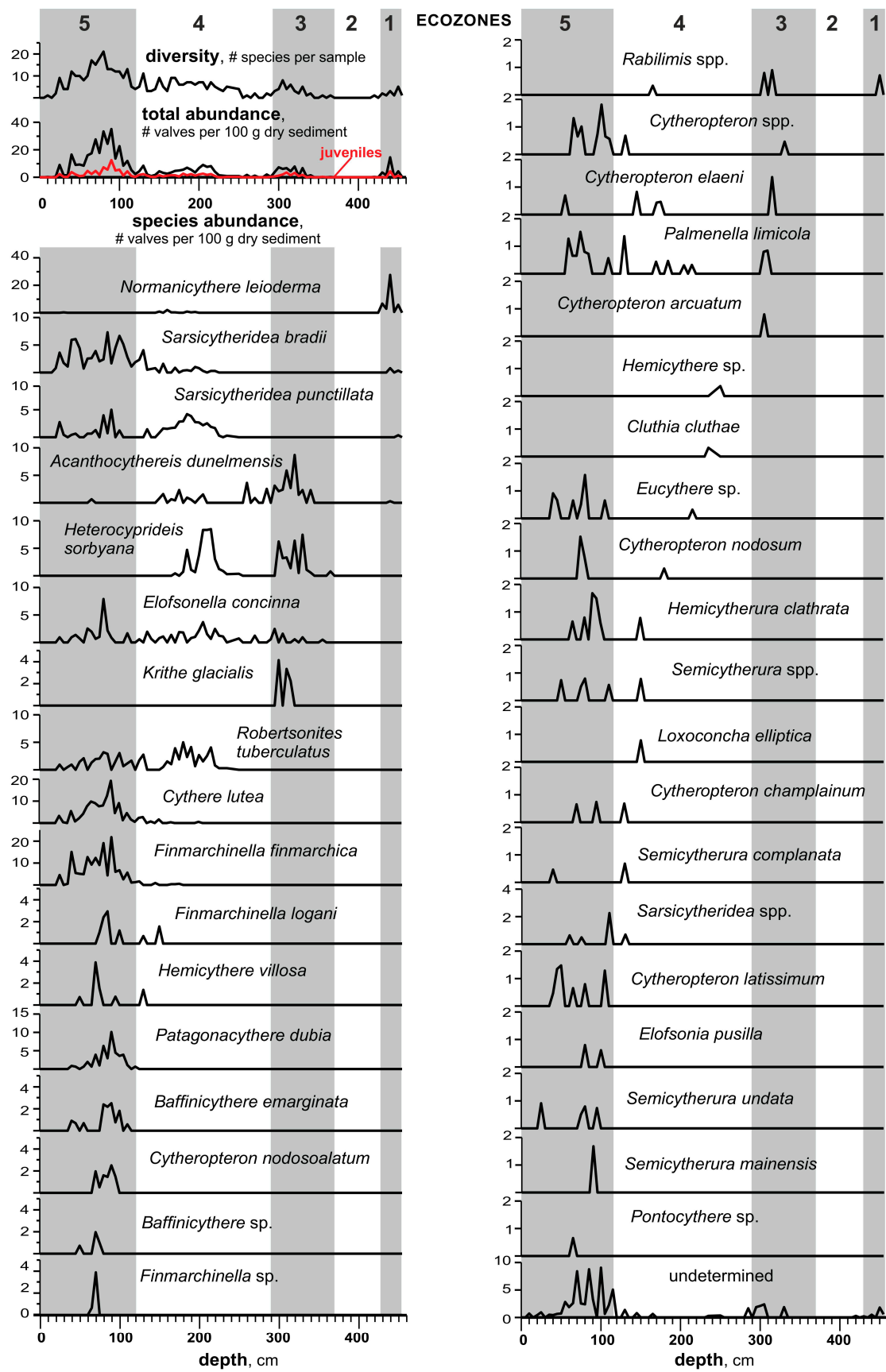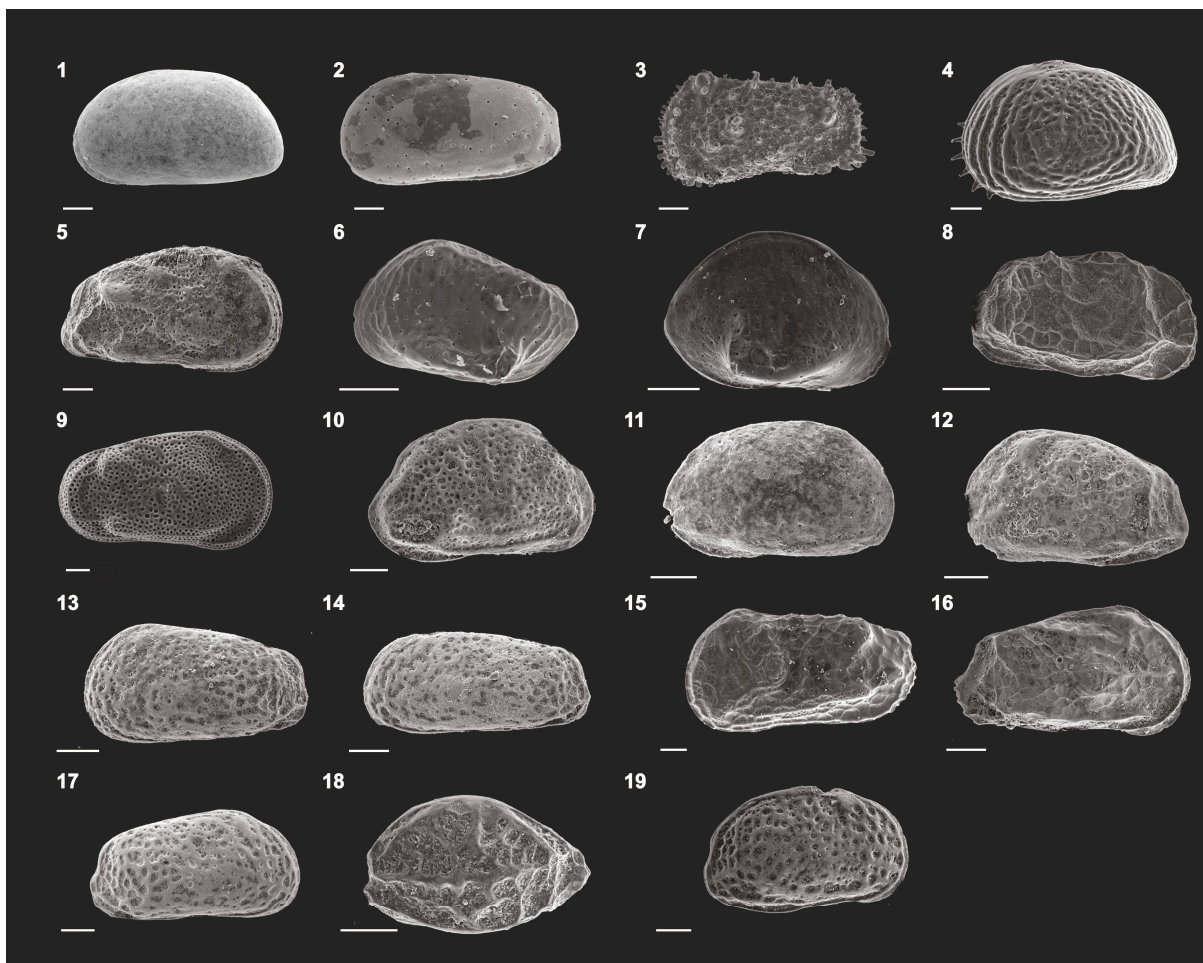
Figure 6. Downcore distribution of ostracods in the Bychye-2 section. The established ecozones are indicated with figures on the top and shading.

Figure 7. Phototable with SEM photos of some ostracod species found in the Bychye-2 section (scale bar length: 100 μm): 1—*Sarsicytheidea bradii* (Norman, 1864); 2—*Normanicythere leioderma* (Norman, 1869); 3—*Acanthocythereis dunelmensis* (Norman, 1865); 4—*Heterocyprideis sorbyana* (Jones, 1857); 5—*Elofsonella concinna* (Jones, 1857); 6—*Cytheropteron elaeni* Cronin, 1989; 7—*Cytheropteron arcuatum* Brady, Crosskey et Robertson, 1874; 8—*Palmenella limicola* (Norman, 1865); 9—*Cluthia cluthae* (Brady, Crosskey et Robertson, 1874); 10—*Cythere lutea* (O.F. Müller, 1785) sensu Frenzel et al., 2010; 11—*Cythere lutea* (O.F. Müller, 1785) smooth form; 12—*Baffinicythere emarginata* (Sars, 1865); 13, 14—*Finmarchinella finmarchica* (Sars, 1866); 15—*Finmarchinella logani* (Brady et Crosskey, 1871); 16—*Patagonacythere dubia* (Brady, 1868); 17—*Hemicythere villosa* (Sars, 1865); 18—*Hemicythere clathrata* (Sars, 1866); and 19—*Baffinicythere* sp.

3.5. Aquatic Palynomorphs

The concentration of marine dinoflagellate cysts is the highest in ecozone 2 (100–300 specimens/g), decreasing further up the section (Figure 8). Ecozone 1 is dominated by cysts of *Echinidinium karaense*, a heterotrophic species abundant in regions with prolonged sea ice cover and a short productive season, also characteristic of freshened estuarine areas and deltas [54,55]. Higher up the section, its concentration sharply decreases, and the heterotrophic cryophilic species *Islandinium minutum* and *Brigantedinium* spp. become dominant in ecozones 2–4. In the upper part of ecozone 4 and in ecozone 5, cysts of the autotrophic (photosynthetic) species *Nematosphaeropsis labyrinthus* appear, and the concentration of *Spiniferites* cf. *elongatus* increases, which can be considered a signal of surface water warming and a decrease in the extent of sea ice cover.
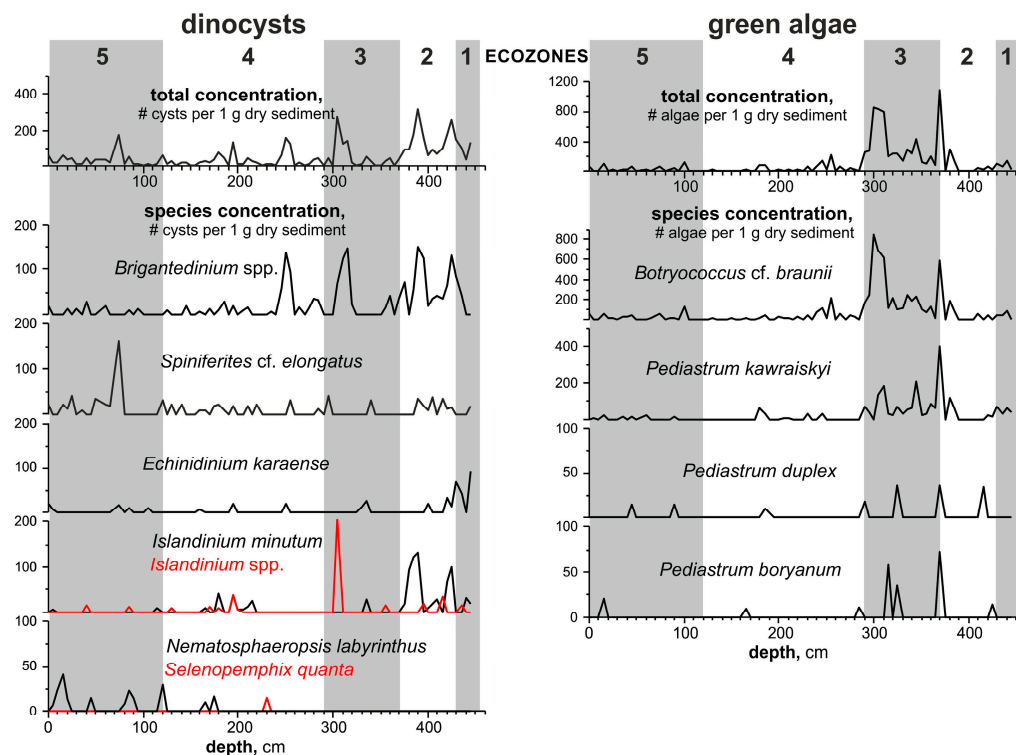
Figure 8. Downcore distribution of dinoflagellate cysts and green algae in the Bychye-2 section. The established ecozones are indicated with figures on the top and shading.

Green algae represented by *Botryococcus* cf. *braunii*, *Pediastrum kawraiskyi*, *P. duplex*, and *P. boryanum* are numerous only in ecozone 3 (Figure 8).

4. Discussion

The combination of lithological, microfaunal, and palynological data, together with pollen-based stratigraphy, made it possible to reconstruct the history of paleoenvironmental changes during the Boreal transgression in the northeastern White Sea area following the change in the ecozones of the Bychye-2 section.

Ecozone 1, >131–130.8 ka, corresponds to the end of the glacial epoch with periglacial vegetation (LPZ By-1) and the transition to interglacial conditions with forests (LPZ By-2). The flooding of this territory was rapid, as indicated by the clayey composition of marine sediments in combination with the species composition of benthic foraminifers and ostracods, with Arctic species typical of the middle and outer-shelf present even in the layers directly overlying the moraine. Their presence suggests that the paleobasin had water depths of at least 40–50 m and a bottom salinity of about 30‰. At the same time, the benthic foraminifers characteristic of the Arctic river-affected coastal areas indicate proximity to the paleocoast. In combination with the predominance of the opportunistic species *E. clavatum*, this signifies the freshening of surface waters, likely due to glacial meltwater input, whereas the high percentage of the river-distal species *I. norcrossi/helenae* occurring in bottom waters with normal salinity likely points to water stratification. The prolonged seasonal sea ice cover is confirmed by the dominance of the heterotrophic species *E. karaense* among dinocysts. This species lives in a narrow temperature range and can survive low salinity due to sea ice melt in areas with a short productive season, including Arctic estuaries [54]. According to Grøsfjeld et al. [11], the dominance of this heterotrophic species points to an increased concentration of nutrients in the water column that are supplied by rivers during spring and summer floods. To summarize, it was a deep coastal marine basin, with a freshened surface water layer and long-lasting seasonal sea ice cover.

Ecozone 2 corresponds to the time interval ~130.8–130.5 ka, which is associated with the spreading of coniferous forests and nemoral elements of the flora on land (LPZ By-3).

Paleobasin became deeper, as seen from the growing percentage of the outer-shelf species of benthic foraminifers dominated by *I. norcrossi/helenae*. The bottom water salinity was at least 30‰ or higher. The environmental conditions remained severe with extensive sea ice cover, as evidenced by the presence of *E. clavatum* among dominant species of benthic foraminifers, the absence of ostracods, and the predominance of the heterotrophic dinocyst species *I. minutum* and *Brigantedinium* spp. Being closely related in their life cycle to cryophilic diatoms of the genus *Chaetoceros* [56], these species occur in the surface water layer between melting ice floes and polynyas. Grøsfjeld et al. [11] link the abundance of *I. minutum* and *Brigantedinium* spp. in combination with *I. helenae* with a short productive period at the seasonal sea–ice edge.

Ecozone 3 corresponds to a short time period of 130.5–130.25 ka, when some broad-leaved trees penetrated the pine–birch forests (LPZ By-4). It was at this time that the Boreal paleobasin reached its maximum depth of more than 50–70 m, because only in this ecozone are the most deep-water species recorded, both among benthic foraminifers and among ostracods: the infaunal dweller *M. barleeanus* occurs on the outer-shelf and the upper continental slope of Arctic seas, often in troughs and depressions, where it feeds on buried organic matter [41]; *K. glacialis* and *Rabilimis* sp. are found on the outer-shelf and upper continental slope of the Arctic seas [45,46] as well as in the open Arctic basin [57]. The environmental conditions of ecozone 3 apparently resulted from rapid global eustatic sea-level rise in combination with a strong residual isostatic deepening of the territory that was covered by the ice sheet during MIS 6. The benthic microfauna of ecozones 1–3 has a distinctly Arctic appearance. For example, all species, except *Elphidiella tumida* among benthic foraminifera and *N. leioderma* among ostracods, were recorded by us in the surface sediments of the Laptev Sea [45,46,58]. Among dinocysts, the same heterotrophic arctic species predominate as in ecozone 2, indicating long-lasting seasonal sea ice cover. A distinctive feature of ecozone 3 is that it has the highest concentration of freshwater green algae. These are transported to the sea with river runoff [59], so we can assume an increase in the river runoff influence and its growing contribution to surface water freshening in comparison with ecozones 1 and 2. At the same time, it is also possible to assume that even during the phase of the maximum deepening of the basin, paleoenvironments could be rather similar to an outer Arctic fjord than to the open sea remote from the coast, given that even the above-mentioned relatively deep-water species of benthic foraminifers and ostracods are occasionally found in the fjords of Spitsbergen and Novaya Zemlya [60–62]. During the Boreal transgression, the indented paleocoastline was probably located relatively close to the Bychye-2 section, as evidenced by the Bychye-2 pollen spectra, which are different from the spectra of the open sea, which are usually dominated by buoyant fern spores and pine pollen [28].

Ecozone 4 corresponds to the time interval from ~130.25 to 128 ka and is compared with the LPZ By-5 and the lower part of the LPZ By-6, which characterize the most favorable interglacial conditions with pine, spruce, fir, and alder and the greatest diversity of broad-leaved trees. The distinct trend of sediment coarsening at the very beginning of this ecozone (~130 ka) reflects the onset of regression. Shells of the shallow-water mollusk *A. islandica* appear from approximately the middle of this ecozone. The shallowing and activation of bottom hydrodynamic conditions are also evidenced by the changes in species composition of benthic microfossils, with a high representation of *B. frigida* and *E. subarcticum*. Almost all species of benthic foraminifers and ostracods recorded in ecozone 4 presently occur in different parts of the Arctic shelf seas, from the inner to the outer-shelf [41,42,45,46]. Benthic foraminifers reach their maximum total abundance and species diversity in this ecozone, and the relatively warm-water species *T. angulosa* and *E. williamsoni* appear for the first time. Taken together, this allows us to conclude that the diversity of biotopes increased due to the development of vast shallow-water areas that were warmed and actively mixed in summer. The reduced sea ice cover is evidenced by a gradual increase in the proportion of autotrophic (photosynthetic) dinoflagellates.

Ecozone 5, 128–119.5 ka, corresponds to the upper part of LPZ By-6 and LPZ By-7. It is characterized by impoverished pollen spectra, a gradual reduction in the share of broad-leaved trees until their complete disappearance, and the spread of birch. These characteristic features signify the end of Eemian warming [15]. If ecozone 4 corresponds to the warmest climatic conditions on surrounding land, ecozone 5 reflects the warmest conditions in the paleobasin due to an increase in the area of shallow-water regions. The most warm-water and shallow-water species of benthic foraminifers and ostracods with a wide range of salinity adaptations flourish in this ecozone. The benthic foraminifera species *E. williamsoni* is characteristic of the Barents and White Seas. In the White Sea, it is found in the littoral zone and in salt marshes with a surface water salinity of 26–27‰ [63]; and in the Barents Sea, it is found on soft grounds of the littoral zone far from river mouths, where the salinity is close to normal marine salinity [60]. At the same time, in the Baltic and North Seas, as well as in the Skagerrak Strait, this species lives in shallow, freshened environments with a low salinity from 0 to 25‰ [44]. This is especially true for ostracods that include species that are not presently found in the Arctic, like *C. lutea*, *H. villosa*, and *H. clathrata*, but are characteristic of the Baltic Sea [47,48]. They are specifically abundant in the first half of ecozone 5 (~128–124 ka). Their occurrence in the White Sea paleobasin might be associated with a longer period of connection between these seas than proposed by Funder et al. [8]. Despite the fact that in ecozone 5, river-proximal benthic foraminifers that were abundant at the base of the section reappeared, the bottom salinity apparently remained close to normal marine, as indicated by the high percentages of the outer-shelf species (*C. lobatulus*, *A. gallowayi*). An increase in the number of autotrophic dinocysts suggests a decrease in the extent of sea ice cover and a growing marine influence. The decrease in the abundance of all the groups of microfossils in the upper 15–20 cm of the section coincides with the disappearance of broad-leaved trees on land and signifies the end of the Boreal transgression and interglacial conditions.

The reference Bychye-2 section records a complete sequence of paleoevents in the evolution of the Boreal transgression in the northeastern White Sea, which was covered by an ice sheet during MIS 6 before the onset of flooding. Ecozones 1–3 (>131–130.25 ka) correspond to a cold, Arctic basin with high sedimentation rates and a strongly stratified water column produced by surface water freshening due to glacial meltwater input and river runoff. From the very beginning of the flooding, the paleobasin was inhabited by Arctic benthic species that are typical of various shelf zones, including river-distal ones. This suggests the leading role of water salinity, and not temperature, in the dispersal of species when the sea penetrates the shelves after the removal of glacial loads [24]. Atlantic water indicative species like planktonic foraminifers or benthic foraminifer *Cassidulina (neo)teretis* [64] were not found in the Bychye-2 section. Our data confirm the idea of the predominantly subsurface nature of Atlantic water inflow in the eastern part of the Norwegian–Greenland basin until the middle or end of the Eemian [19,24–27]. Considering the large volume of glacial meltwater during termination II, it can be assumed that subsurface Atlantic water was flowing northward below 100–150 m and did not affect the northeastern White Sea, where water depths did not exceed 100 m. Information on the findings of planktonic foraminifers, including warm-water species, in the Petrozavodsk borehole [6] or benthic foraminifers *Cassidulina teretis* and *C. laevigata* on the Kola Peninsula [4,13,65] may, on the one hand, require taxonomic clarification, and on the other hand, may be evidence that subsurface Atlantic waters could spread south along the Kola Peninsula, where water depths were greater [8].

Ecozones 4 and 5 (130.25–119.5 ka) correspond to a long regressive stage coeval with interglacial climate warming. An increase in the area occupied by shallow-water regions that were warmed up in summer contributed to the settlement of shallow- and relatively warm-water species of benthic microfauna, including ostracods characteristic of the Baltic Sea that are presently absent in the Arctic seas. They are especially abundant between ~128 and 124 ka. Presumably, the connection between the White and Baltic seas existed until this

time and lasted about 6–7 thousand years, starting from >131 ka, which is consistent with the reconstructions of [6,15].

According to the pollen zone comparison with other sites, the regression due to the regional isostatic rebound started around 130 ka. This allows us to assume that the latter advanced the global eustatic sea-level highstand. The latter is usually dated at 128 ± 1 ka [39]; however, age estimates as well as global sea-level curves vary greatly (see the reviews in 24, 15). Our data differ from the age estimates of Grøsfjeld et al. [11], who believe that the regression began after 128 ka, in the middle of their ecozone 3, in which, however, they recorded a peak in the abundance of the relatively deep-water benthic foraminifer *M. barleeanus*. In the Bychye-2 section, the maximum content of this species coincides with the presence of the relatively deep-water ostracods *K. glacialis* and *Rabilimis* sp., which confirms, along with the fine-grained composition of sediments, the achievement of the maximum depth of the paleobasin in the studied area before the onset of the regression.

5. Conclusions

1. Based on the high-resolution, multiproxy study of the reference Bychye-2 section, we reconstructed the course of the Boreal transgression in the northeastern White Sea region, which includes three major successive phases of paleoenvironmental changes: (1) the relatively deep coastal basin in the initial phases of flooding, with extensive sea ice cover and strong stratification (ecozones 1–2, >131–130.5 ka); (2) the deepest basin in the maximum phase of flooding (ecozone 3, 130.5–130.25 ka); and (3) the shallow-water basin with reduced seasonal sea ice cover (ecozones 4–5, 130.25–119.5 ka).
2. The flooding by cold Arctic waters was rapid, and a relatively deep basin with high sedimentation rates existed for ~750 years, from >131 to 130.25 ka.
3. According to the pollen zone comparison with other sites, the regression due to the regional isostatic rebound started around 130 ka.
4. During the regressive stage, the occurrence of ostracods, which are characteristic of the Baltic Sea and presently absent in the Arctic seas, with the highest representation ~128–124 ka, allows us to assume that the connection between the White and Baltic seas existed for 6–7 thousand years, starting from >131 ka.
5. The absence of the Atlantic water indicative species among benthic microfossils suggests that the subsurface Atlantic waters did not reach the studied region, which represented a shelf with water depths of less than 100 m, even during the period of its maximum deepening.

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