



SHORT COMMUNICATION

Live autochthonous benthic diatoms on the lower depths of Arctic continental shelf. Preliminary results

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Summary An autochthonous community of benthic diatoms was discovered in June 2015 in the upper sediment layer at depths of 170, 205, and 245 m in the central Barents Sea. At least three benthic microalgae species (*Gyrosigma fasciola*, *Pleurosigma angulatum*, and *Pleurosigma* sp. 1) were detected in the sediment but not the upper water column. Analyses revealed that these benthic microalgae represent a depleted fragment of Arctic littoral microphytobenthos. Compared with the littoral flora, the deep-water assemblage is less diverse and displays low abundance. The data reported here challenge the generally accepted belief that the presence of certain microalgae at significant depths results from vertical or horizontal transfer.

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Microphytobenthos, together with phytoplankton and ice algae, are important components of the primary production potential in Arctic marine ecosystems. The importance of benthic microalgae in the littoral and sublittoral coastal

zones is well established (Cahoon and Laws, 1993). However, the entire current database of microphytobenthic production in Arctic waters comprises only 10 published studies, according to which the benthic production in Arctic coastal waters exceeds the pelagic production by a factor of ca. 1.5 (reviewed in Glud et al., 2009, see Fig. 1). An overview study conducted by Cahoon (1999) directly indicated that there is substantial underestimation of the benthic microalgal contribution to the productivity of marine ecosystems, especially for oligotrophic (including Arctic) waters. This underestimation results from the narrowness of the generally accepted approach to such investigations, which are often conducted at sites that presuppose the presence of the object under investigation. Consequently, an important unresolved issue is the depth distribution of benthic microalgae. According to the common point of view, sustainable existence of algal communities is governed by the availability

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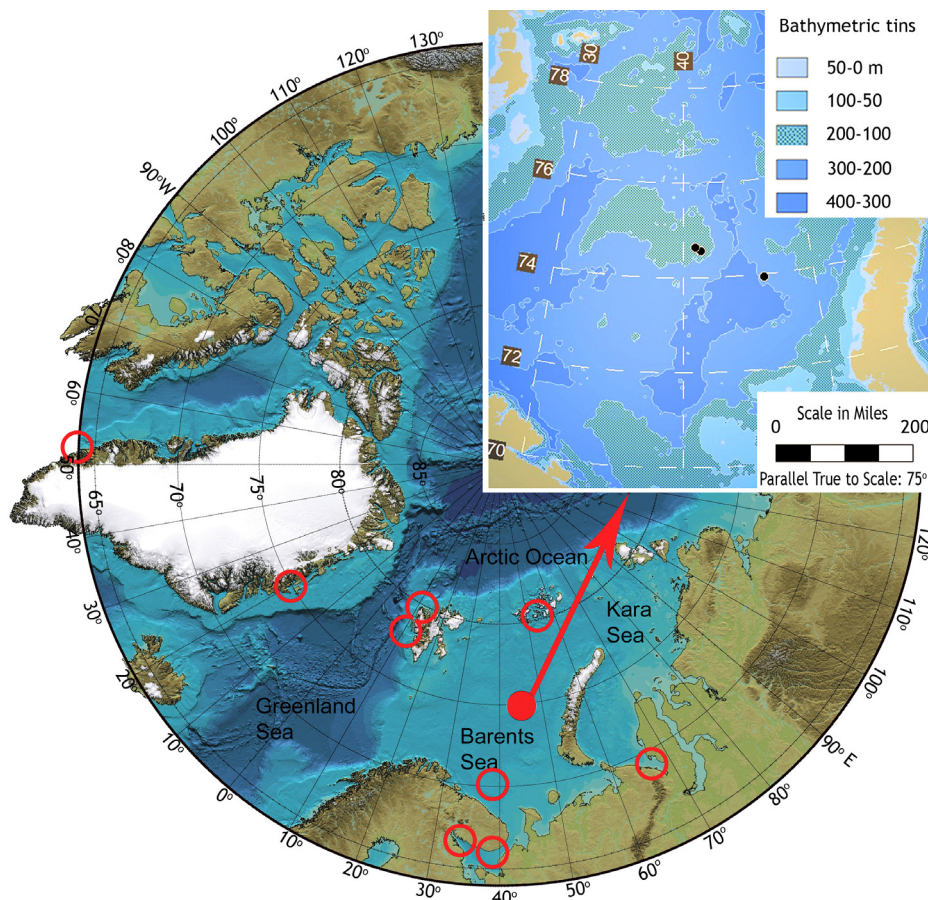


Figure 1 Locations of sampling stations in the Barents Sea, June 2015 (filled red dot). The figure of Arctic region is modified from Glud et al. (2009).

of photosynthetically active radiation and in aquatic habitats is limited by the compensation depth (i.e. the depth at which the energy of incoming light balances the metabolic costs), which constitutes the first tens of meters for continental shelf seas and 100–300 m for oceanic water areas (Raymont, 1980). The zone of the World Ocean below 200 m is considered to be free of floral organisms (Kiselev, 1969). However, there have been several studies indicating the presence of living microalgae at depths below 100 m (Cahoon, 1999), e.g. chlorophyll-*a* was reported from sediments of the continental shelf at depths down to 222 m (Cahoon et al., 1990; Cahoon and Cooke, 1992), and even to 2000 m (Cahoon et al., 1994), indicating that benthic microalgae may exist at significant depths. However, this hypothesis has not been verified, as previous investigations were conducted using indirect and/or calculation methods (Karsten et al., 2011). Although such data extend the lower distribution limits of live benthic microalgae, the lack of direct observations renders the conclusions questionable. We have found only one previous study in which indirect measurements of the biomass of deep-sea benthic microalgae using chlorophyll-*a* values were directly verified. In October 2003 in Onslow Bay, McGee et al. (2008) collected sediment samples at depths of 67–191 m and discovered 11 species of live benthic diatoms by direct microscopy. Moreover, that study indicated and substantiated an autochthonous origin for the species found.

The objective of this study was to investigate the surface sediments of the Barents Sea Continental Shelf to determine whether microphytobenthic assemblages are present at depth.

The study was conducted on the Central Plateau of the Barents Sea (Fig. 1) during a cruise by the Murmansk Marine Biological Institute on board the *r/v Dalnie Zelentsy* in June 2015. Samples were obtained at three stations (74.56°N, 41.41°E, depth 205 m; 74.64°N, 40.96°E, depth 174 m; 73.94°N, 46.15°E, depth 245 m) at a distance of 130–240 miles from the nearest shore.

The sediment consisted of red mud with some inequigranular sand. The depth of photic zone (45–75 m) was determined as 3 times the Secchi depth for case 2 water (Abakumov, 1983; Jerlov, 1968).

A Van Veen grab device was used to collect sediment from the surface layer in triplicate. Each subsample (ca. 30 ml volume and 1 cm depth) was obtained from a separate sediment sample. All three subsamples, taken from one station, were placed together into one sample cup (total volume ca. 100 ml) and preserved in 40% formaldehyde (final concentration of 2%). Water samples were gathered with a bathometer (“Hidro-bios”, 5l) from the surface water layer, the pycnocline (30 m), the intermediate layer (100 and 120 m water depths), and the near-bottom layer, and by a small-meshed plankton net with a mesh size of 29 $\mu\text{m} \times 29 \mu\text{m}$ from the 150–50 m water layer.

For cell count analyses sediment subsamples of 1–1.5 ml were taken from the mixed total sediment sample, then placed in a test tube and diluted with certain volume of water (V_{H_2O}) up to the mark of 10 ml ($V_{\Sigma} = 10$ ml). Exact volume of sediment subsample ($V_{sed} \pm 0.02$ ml) is a difference between V_{Σ} and V_{H_2O} . After resuspension of a subsample solid particles settled within 5 min were removed. Diluted in such a way subsample of the volume V'_{Σ} corresponds to the sediment of the volume V'_{sed} as

$$V'_{sed} = V_{sed} \times \left(\frac{V'_{\Sigma}}{V_{\Sigma}} \right).$$

Then cells were enumerated (n , cells ml^{-1}) in a Nageotte counting chamber using a generally accepted method and recalculated per volume of sediment (N , cells cm^{-3}):

$$N = \frac{n}{V'_{sed}}.$$

The number of cells per cm^2 (R) can be expressed as

$$R = N \times h,$$

where N is the number of cells per cm^3 , h is the height of sampled sediment layer (1 cm).

Enumeration of microalgae was conducted by direct light microscopy (at a magnification of 400 \times) using Nageotte counting chambers. Taxonomic identifications were based on descriptions in Proshkina-Lavrenko (1950) and Hendey (1964). Some small forms could not be identified to species level because of the limitations of the methods used. Division into dead and live cells was conducted by visual assessment of undamaged state of cell content (Woelfel et al., 2010).

Each cell was measured individually with an ocular micrometer. Best fitting geometric shape and matching equations were used to determine cell biomass in μg (Olenina et al., 2006).

Living cells of at least ten species of diatoms were detected in the sediment samples (Table 1), of which seven species were identified as mass forms of spring or summer plankton represented by spore-bearing or vegetative cells.

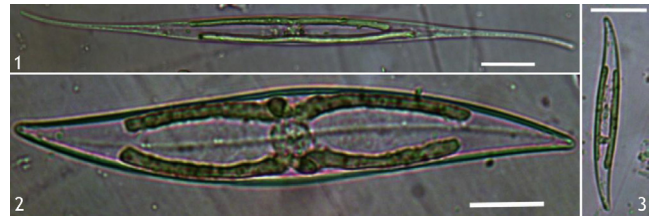


Figure 2 Typical species of microphytobenthos (1 – *Gyrosigma fasciola* Griffith & Henfrey, 2 – *Pleurosigma angulatum* Smith, 3 – *Pleurosigma* sp. 1) from sediment samples. Scale bar represents 20 μm .

Cells of all these planktonic species were abundant in the pelagic layer throughout the whole water area studied. In the benthic community under investigation, this assemblage of pelagic species is an allochthonous component introduced directly from the water column. However, three species of pennate diatoms, *Gyrosigma fasciola*, *Pleurosigma angulatum*, and *Pleurosigma* sp. 1 (Fig. 2), only occurred in the sediment samples.

Direct examination of the bathometric and net samples demonstrated the absence of these three species throughout the whole vertical profile of the pelagic zone at a lower threshold of detectability of 0.6–1.0 cells cm^{-2} , whereas in bottom sediments the average density (in total for cells of the three species) was ca. 600 cells cm^{-2} (Table 1), but empty frustules and damaged cells were rare. Therefore, the presence of these forms in the benthic zone cannot be explained by settling out from the water column, i.e. direct derivation from pelagic assemblages. Members of genus *Gyrosigma* and *Pleurosigma* are common in the Barents Sea coastal algal communities, where they co-occur with typical dominant microphytobenthic species such as *Melosira juergensii*, *Melosira moniliformis*, *Melosira nummuloides*, *Rhabdonema minutum*, *Synedra pulchella*, and *Synedra tabulata* (Kuznetsov and Shoshina, 2003; Makarevich and Druzhkova, 2010; Makarevich et al., 2015). If direct transport had occurred, for example with shore ice from the littoral

Table 1 Abundance and biomass of microalgae in surface sediments (average values for the three stations).

Taxon	Abundance [cells cm^{-2}]	Biomass [μg cm^{-2}]
<i>Amphiprora hyperborea</i> Grunow	99	0.99
<i>Chaetoceros contortus</i> Schütt (spores)	13	0.01
<i>Chaetoceros furcillatus</i> Bailey (spores)	5233	2.62
<i>Chaetoceros socialis</i> Lauder (spores)	60,333	6.03
<i>Fragilariopsis oceanica</i> Hasle	33	0.01
<i>Gyrosigma fasciola</i> Griffith & Henfrey	365	2.85
<i>Pleurosigma angulatum</i> W. Smith	67	0.53
<i>Pleurosigma</i> sp. 1	202	0.30
<i>Pseudo-nitzschia seriata</i> complex	13	0.01
<i>Thalassiosira gravida</i> Cleve (spores)	147	0.01
Centrales 15–20 μm	160	0.16
Pennales <30 μm	926	0.28
Pennales 30–50 μm	3890	1.95
Pennales 50–60 μm	186	0.19
Total	71,667	15.9

zones of neighboring archipelagoes, the bottom sediments under investigation would be expected to contain a microalgae diversity similar in composition to that of coastal waters. No such assemblage was detected. Hence, the horizontal transport hypothesis fails to explain the presence of single components of the littoral benthic microalgae assemblage in the sediments with a background of the absence of the majority of species. A similar pattern of a difference in taxonomic composition from the planktonic microalgae community and a similarity with the littoral one was reported for deep-sea microphytobenthos on the North Carolina Continental Shelf (Cahoon and Laws, 1993).

This presence of viable microalgae cells much deeper than the location of the possible compensation depth, where photosynthesis cannot be the main source of energy, does not contradict existing knowledge of the physiology of these organisms. The possible mechanism of life support in such conditions is the capability for heterotrophic metabolism, which is widespread among diatoms (Hellebust and Lewin, 1977; Lewin, 1953; Tuchman et al., 2006; Veuger and van Oevelen, 2011), and/or storage and utilization of energy reserves at a reduced metabolic rate (Zhang et al., 1995).

Finally, the occurrence of a considerable number of cells of small pennate diatoms, which were not identified to species level during study of the sediment samples, suggests that *G. fasciola*, *P. angulatum*, and *Pleurosigma* sp. 1 represent only part of a specific algal community inhabiting the lower depths of the Barents Sea Continental Shelf.

This discovery of an autochthonous microalgal community in the benthic zone of the central Barents Sea represents a depleted fragment of Arctic littoral assemblages of benthic microalgae. At present, a depth of at least 245 m may be regarded as the lower habitat limit of the microphytobenthic community on the Barents Sea Continental Shelf. The formation of such a deep-sea algal community may be considered to result from loss of species incapable of adopting heterotrophic feeding from the microphytobenthos during transport from the littoral zone to below the compensation depth.

Findings of live autochthonous algal communities in bottom habitats suggests that the occurrence of viable microalgae at similar depths in the pelagic zone (Agusti et al., 2015) (optionally as Deep Chlorophyll Maxima/Deep Biomass Maxima; Fennel and Boss, 2003) in some cases might not be directly related to the overlying surface waters.

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