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EXPERIMENTAL ARTICLES

# Abundance and Activity of Microorganisms at the Water–Sediment Interface and Their Effect on the Carbon Isotopic Composition of Suspended Organic Matter and Sediments of the Kara Sea

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**Abstract**—At ten stations of the meridian profile in the eastern Kara Sea from the Yenisei estuary through the shallow shelf and further through the St. Anna trough, total microbial numbers (TMN) determined by direct counting, total activity of the microbial community determined by dark $CO_2$ assimilation (DCA), and the carbon isotopic composition of organic matter in suspension and upper sediment horizons ($\delta^{13}C$, ‰) were investigated. Three horizons were studied in detail: (1) the near-bottom water layer (20–30 cm above the sediment); (2) the uppermost, strongly hydrated sediment horizon, further termed fluffy layer (5–10 mm); and (3) the upper sediment horizon (1–5 cm). Due to a decrease in the amount of isotopically light carbon of terrigenous origin with increasing distance from the Yenisei estuary, the TMN and DCA values decreased, and the $\delta^{13}C$ changed gradually from –29.7 to –23.9‰. At most stations, a noticeable decrease in TMN and DCA values with depth was observed in the water column, while the carbon isotopic composition of suspended organic matter did not change significantly. Considerable changes of all parameters were detected in the interface zone: TMN and DCA increased in the sediments compared to their values in near-bottom water, while the $^{13}C$ content increased significantly, with $\delta^{13}C$ of organic matter in the sediments being at some stations 3.5–4.0‰ higher than in the near-bottom water. Due to insufficient illumination in the near-bottom zone, newly formed isotopically heavy organic matter ($\delta^{13}C \sim -20$‰) could not be formed by photosynthesis; active growth of chemoautotrophic microorganisms in this zone is suggested, which may use reduced sulfur, nitrogen, and carbon compounds diffusing from anaerobic sediments. High DCA values for the interface zone samples confirm this hypothesis. Moreover, neutrophilic sulfur-oxidizing bacteria were retrieved from the samples of this zone.

*Keywords*: microbial number, carbon isotopic composition of organic matter, water–sediment interface, Kara Sea

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Integrated oceanographic, microbiological, and biogeochemical studies of the Russian Arctic shelf seas were initiated by our institutions during the cruise of the *Akademik Mstislav Keldysh* research vessel in September 1993 to the Kara Sea. One of the objectives of the microbial biogeochemistry group was to study the stable carbon isotope composition of suspended and sedimental organic matter (OM) and to reveal the role of microorganisms in its change in the course of mineralization and OM synthesis.

In the first expedition of 1993 we found that $\delta^{13}C$ content for OM in suspension and in the upper sediment carbon differed significantly [1]. This was confirmed by an extensive data set during the second expedition to the Kara Sea and during the voyages to the Chukchi and the East Siberian Seas [2–5]. During the 2006 expedition to the White Sea, we succeeded in using the Niemiste tubes to sample the undisturbed cores of the upper sediment layers and near-bottom water from the 20–30 cm layer, which directly contacted with the upper liquid sludge. Comparison of the $\delta^{13}C$ values for suspended OM from the bottom and near-bottom water, as well as of sediments, showed that OM carbon isotopic composition in the water/sediment boundary zone gradually became heavier [5, 6]. This phenomenon may result from additional OM production by chemoautotrophic bacteria in the boundary zone, which was stimulated by the up-flow of reduced nitrogen and sulfur compounds, formed during anaerobic OM mineralization in the underlying bottom sediments. Presently, however, there is relatively little direct evidence for this hypothesis. Therefore, during our third expedition to the Kara Sea, the

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detailed studies of $\delta^{13}C$ in the boundary zone were complemented with the total microbial count (TMC) and measurements of the microbial community activity by radioisotope analysis of dark carbon dioxide assimilation (DCA).

In this paper we present and discuss the results of our investigation.

## MATERIALS AND METHODS

Samples of water and bottom sediments were taken during the cruise of the *Akademik Mstislav Keldysh* research vessel in August–September 2011 to the Kara Sea. Water samples were taken with Niskin bathometer fixed on a Rosette explorative complex. For sampling the water–bottom sediments boundary zone, a multicore sampler was used. The near-bottom water samples were taken from the top 20–30 cm of the sampler tubes directly above the topmost sediment layer. The second sampling horizon was the upper 5–10 mm of water-saturated sediment (fluffy layer), and the third sampling horizon was the upper 1–2 cm layer of the sediment. If the sampling tubes contained enough sediment, deeper horizons, down to 30 cm from the surface, were collected as well (Tables 1, 2).

Immediately after sampling, the experiments on the rate of the dark $CO_2$ assimilation were performed, using $^{14}C$-bicarbonate. To stimulate the activity of nitrifying bacteria and neutrophilic sulfur-oxidizing bacteria, the samples were supplemented with $NH_4Cl$ and $Na_2S_2O_3$, respectively.

Samples for the total microbial count (TMC), for determination of carbon isotopic composition of organic matter in suspensions and sediments, and for determination of the content of the compounds and biogenic elements dissolved in sea- and silt water were taken immediately after heaving on board the vessel. Samples of water suspension were obtained by filtering several liters of water through GF/F glass-fiber filters.

Total microbial count (TMC) was determined by direct cell counting on black polycarbonate membrane filters (Osmonix) with 0.2 μm pore diameter. The filters were stained with acridine orange and observed under a 1000× oil immersion system in an Olympus BX41 fluorescence microscope equipped with image analysis software (Image Scope M).

The OM carbon isotopic composition (OM IC) was determined in carbon dioxide obtained by incineration of suspended and sedimental OM pretreated with hydrochloric acid to remove the mineral carbon compounds (carbonates). The isotopic analysis was performed with the mass spectrometer Delta Plus (Germany) using the standard calibrated against PDB. The analysis accuracy was ±0.1‰. Analyses of alkalinity, total nitrogen and $PO_4^{2-}$ were performed using the standard hydrochemical methods.

## RESULTS AND DISCUSSION

The main results of this work are presented in Fig. 1 and Tables 1 and 2. At three shallow stations of the Yenisei River profile (stations 5013, 5018, and 5011-2, Table 1), the total microbial count in the water column surface layers was $1.3–1.6 \times 10^6$ cells $mL^{-1}$. In the deep-water sea areas the number of bacteria in the surface horizons was significantly lower, $0.14–0.44 \times 10^6$ cells $mL^{-1}$ (Table 2, stations 5032, 5033, 5039, 5042, and 5044). The distribution of DCA values varied significantly in different parts of the sea. At 3 shallow stations the DCA was more than 1 μg C per liter per day (Table 1), while in all deep stations it was almost two orders of magnitude lower (Table 2). Intermediate TMC and DCA values were found at station 5026 located at the northern end of the shallow Yenisei profile (Fig. 1 and Table 1).

The isotopic composition of suspended OM carbon (OM IC) from surface waters in two contrasting areas of the sea was also markedly different. At shallow coastal stations which receive high quantity of isotopically light terrigenous OM, the $\delta^{13}C$ value ranged from −29.58 to −29.73‰ (Table 1). At the deep stations (Table 2) and station 5026, which receive less terrigenous OM, the $\delta^{13}C$ value varied from −23.58 to −24.59‰, indicating an increased share of the $^{13}C$ isotope, compared to the coastal stations.

The bottom water samples at all stations, except for station 5013, located in the deepening of the Yenisei River bed (Fig. 1), demonstrated a decrease in TMC and DCA (Tables 1 and 2). A noticeable decrease in TMC, down to $4.4–4.9 \times 10^4$ cells $mL^{-1}$ of water, was detected at the deepest stations (stations 5039, 5042 and 5044, Table 2). The carbon isotopic composition of the suspension of the near-bottom waters remained unchanged, compared to the OM IC of the surface waters (stations 5013, 5026, 5039, and 5044), or had higher $\delta^{13}C$ values (stations 5018, 5011-2, 5039, and 5042). In the water column, the number of microorganisms and their activity decreased significantly with depth. Thus, the observed increase of the OM $^{13}C$ isotope content may be only explained by additional synthesis by phytoplankton which uses the seawater bicarbonate with $\delta^{13}C = 0...-2$‰.

A significantly different pattern of OM IC changes was observed in the boundary zone, samples from which demonstrated an increase of microbial number and activity, especially noticeable at the deep stations 5039, 5042, and 5044, where TMC in the near-bottom water increased by orders of magnitude (Table 2). At all the stations, except for 5011-2, we detected a noticeable increase in OM IC $^{13}C$ share in near-bottom waters compared to the bottom waters (Tables 1, 2).

Increase of TMC and DCA rate was also observed in the fluffy layer contacting with the near-bottom water. At the same time, increased $^{13}C$ content of OM

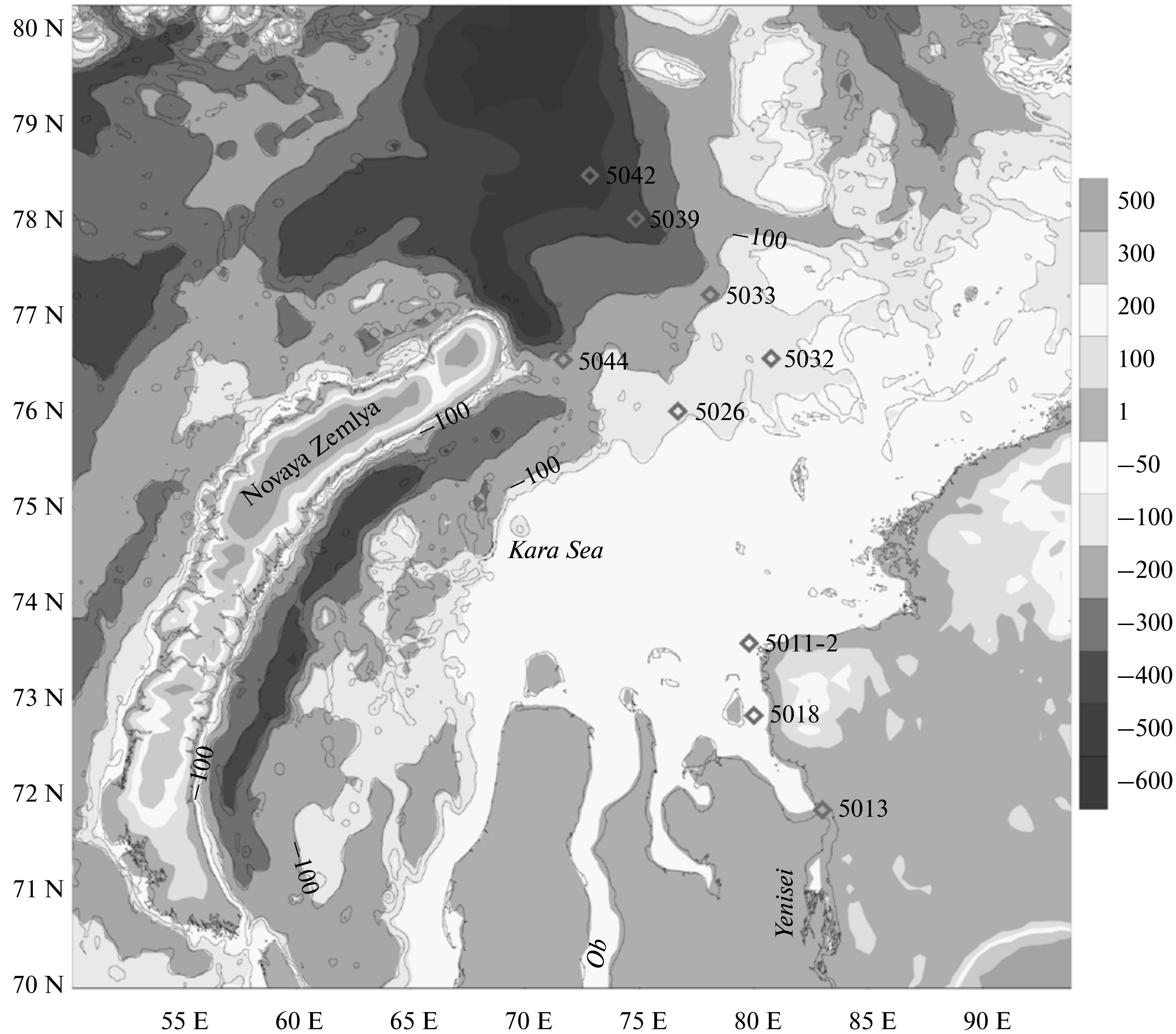


**Fig. 1.** Station location in the Kara Sea during the 59th cruise of the *Akademik Mstislav Keldysh* research vessel, August–September 2011.

was detected in the silt layer samples of all the stations. Maximum values of $\delta^{13}C$ were observed at stations 5013, 5039, and 5026; the difference between the OM $\delta^{13}C$ in the bottom water and the silt layer was 2.28, 2.039, and 1.71‰, respectively. Minimum $\delta^{13}C$ values of 0.02 to 0.26‰ were detected at deep stations, except for the station 5036 (Tables 1 and 2).

In the samples of the bottom sediment surface layer and 1–5 cm horizon, the DCA rate was significantly lower than in the fluffy layer, and the $\delta^{13}C$ value was becoming slightly more negative (Tables 1, 2). As demonstrated in our previous work on the seas of the Eastern Arctic [5], with lowering into reduced sediments, the balance of OM synthesis by aerobic autotrophic bacteria is replaced by OM consumption by heterotrophic, primarily sulfate-reducing, bacteria, which results in a decreased content of isotopically heavy OM. We also observed a decrease if the share of the carbon $^{13}C$ isotope in the residual organic matter, resulting in its lighter carbon isotopic composition [4].

At all the stations in a narrow (20–30 cm) boundary layer we found a significant change in the suspension OM IC from the near-bottom waters and in the fluffy layer organic carbon, with a shift of OM $\delta^{13}C$ towards the values reflecting higher quantities of the $^{13}C$ isotope. The lack of conditions for phytoplanktonic photosynthesis and a significant increase in TMC suggested that these changes were the result of microbial activity. Theoretically, two mechanisms are possible: (1) selective consumption of isotopically light terrigenous OM, which is a part of the suspension, precipitating from the water column, and (2) additional production of the newly formed isotopically heavy OM, a product of chemoautotrophic bacteria.

**Table 1.** Salinity distribution (S, ‰), TMC (thousand cells $cm^{-3}$), diurnal DCA rate (μg $dm^{-3}$) and OM $\delta^{13}C$ carbon (‰) in the water column, near-bottom water samples, fluffy layer, and the upper sediment horizon of the Yenisei profile of the Kara Sea

| Station 5013, depth 33 m | | | | | Station 5018, depth 22 m | | | | | Station 5011-2, depth 35 m | | | | | Station 5026, depth 66 m | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sampling depth, m | S, ‰ | TMC | DCA | $\delta^{13}C$, ‰ | Depth, m | S, ‰ | TMC | DCA | $\delta^{13}C$, ‰ | Depth, m | S, ‰ | TMC | DCA | $\delta^{13}C$, ‰ | Depth, m | S, ‰ | TMC | DCA | $\delta^{13}C$, ‰ |
| 1 | 0.07 | 1380 | 1.390 | –29.73 | 1 | 13.91 | 1920 | 1.040 | –27.58 | 5 | 14.50 | 1580 | 1.230 | –28.46 | 6 | 24.25 | 540 | 0.047 | –24.50 |
| 10 | 0.07 | | | – | 6 | 24.97 | | – | –25.74 | 12 | 29.68 | | | –24.33 | 20 | 32.82 | – | – | –23.58 |
| 31 | 0.07 | 1900 | 1.550 | –29.90 | 14 | 28.39 | 850 | 0.770 | –26.81 | 25 | 31.48 | 820 | 0.570 | –24.26 | 62 | 34.80 | 233 | 0.024 | –25.52 |
| Near-bottom water | | 1750 | 2.68 | –28.16 | | | | 0.600 | –26.13 | | | 1150 | 0.400 | –24.80 | | | 1000 | 0.210 | –23.66 |
| Swarp | | 11000 | 3.32 | –25.88 | | | 70000 | 2.700 | –25.55 | | | 25000 | 4.800 | –24.62 | | | 17500 | 2.200 | –21.95 |
| Sediment surface | | – | 22.00 | –26.26 | | | | 6.300 | –25.88 | | | | 12.600 | –25.12 | | | | 5.500 | –22.23 |
| Sediment 1–5 cm | | | | –27.12 | | | | 4.700 | –25.87 | | | | 6.300 | –25.08 | | | | 4.200 | –23.06 |

**Table 2.** Salinity distribution (S, ‰), TMC (thousand cells $cm^{-3}$), diurnal DCA rate (μg $dm^{-3}$) and OM $\delta^{13}C$ carbon (‰) in the water column, near-bottom water samples, fluffy layer, and the upper sediment horizon at the shelf stations and St. Anna trench

| | Station 5032, depth 58 m | | | | Station 5033, depth 124 m | | | | | Station 5039, depth 371 m | | | | | Station 5042, depth 476 m | | | | | Station 5044, depth 158 m | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sampling depth, m | S, ‰ | TMC | DCA | $\delta^{13}C$, ‰ | Depth, m | S, ‰ | TMC | DCA | $\delta^{13}C$, ‰ | Depth, m | S, ‰ | TMC | DCA | $\delta^{13}C$, ‰ | Depth, m | S, ‰ | TMC | DCA | $\delta^{13}C$, ‰ | Depth, m | S, ‰ | TMC | $\delta^{13}C$, ‰ |
| 1 | 28.64 | 310 | 0.027 | –24.59 | 1 | 27.27 | 444 | 0.025 | –23.88 | 1 | 31.70 | 322 | 0.020 | –23.58 | 1 | 32.01 | 145 | 0.030 | –24.02 | 2 | 30.89 | 253 | –23.90 |
| 16 | 31.00 | | | –24.73 | 9.6 | 27.56 | | – | –27.88 | 150 | 34.85 | | | | 200 | 34.85 | | – | | 25 | 34.01 | | |
| 57 | 34.05 | 280 | 0.020 | –25.61 | 115 | 34.41 | 233 | 0.016 | –23.94 | 355 | 34.95 | 49 | 0.020 | –23.29 | 460 | 34.95 | 44 | 0.010 | –23.36 | 147 | 34.80 | 47 | –23.02 |
| Near-bottom water | | 950 | 0.700 | –23.47 | | | 600 | 0.140 | –22.94 | | | 400 | 0.020 | –20.85 | | | 360 | 0.075 | –20.53 | | | 320 | –20.48 |
| Swarp | | 12400 | 3.600 | –23.21 | | | 6100 | 0.880 | –22.81 | | | 9600 | 0.025 | –20.82 | | | 9700 | 0.270 | –20.51 | | | 17800 | –20.48 |
| Sediment surface | | – | 12.400 | –21.75 | | | | 12.900 | | | | | 7.600 | –21.84 | | | | 21.15 | | | | | –22.10 |
| Sediment 1–5 cm | | | 4.900 | –22.73 | | | | 6.120 | | | | | 3.400 | –22.08 | | | | 19.430 | –21.17 | | | | |

**Table 3.** Results of the experiments on enhancement of DCA by sulfur-oxidizing and nitrifying bacteria in fluffy layer samples supplemented with sodium thiosulfate and ammonium chloride (DCA in μg C $dm^{-3}$ day)

| Experiment variant | Station number | | |
|---|---|---|---|
| | 5013 | 5032 | 5042 |
| No administration | 3.320 | 3.600 | 0.270 |
| $+NH_4Cl$ | 4.660 | 2.820 | 3.620 |
| $+Na_2S_2O_3$ | 4.550 | 4.240 | 3.590 |

As the isotopically light terrigenous OM is mainly represented by humic compounds, which are difficult to degrade for microorganisms, the first mechanism is hardly responsible for changing OM IC, and greatly increased DCA values in the samples from the boundary zone favor the second explanation.

Favorable conditions for the development of autotrophic bacteria exist in the boundary zone, where the diffusion flow of OM mineralization products from the anaerobic sediments is directed. This flow contains reduced carbon, nitrogen, and sulfur compounds (Fig. 2). The development of autotrophic bacteria results in a ten- or hundredfold increase of DCA (Tables 1, 2), and to additional autotrophic bacterial OM.

The rate of carbon isotopes' fractionation in the process of biomass synthesis from carbon dioxide varies significantly in autotrophic bacteria, which use various ways of $CO_2$ fixation [7]. Most of the chemoautotrophic bacteria use the Calvin cycle for $CO_2$ fixation, which results in the difference in the isotopic composition of $CO_2$ and biomass from –19.7 to –22.5‰ [7–10]. Since the $\delta^{13}C$ composition of marine bicarbonate is approximately 0 to –2‰, we can assume that the chemoautotrophic biomass in natural communities has the $\delta^{13}C$ values of approximately –20‰.

The direct evidence of the autotrophic bacteria presence in the samples of near-bottom water, warp layer, and the surface sediment layers are the results of the total count of neutrophilic sulfur-oxidizing bacteria, cultivated on Beijerinck media with thiosulfate. The TMC in various samples from the boundary zone reached 1000 cells per 1 mL of water and wet bottom sediments.

Additional evidence of the presence of active chemoautotrophic bacteria in the samples of the boundary zone were the results of the experiments with fluffy layer samples from various stations, which were incubated with radioactive bicarbonate in three parallel versions: warp without additives, warp with sodium thiosulfate for sulfur-oxidizing, and warp with ammonium chloride for nitrifying bacteria as the energy substrates. Table 3 shows that in five cases of six, administration of the energy substrates resulted in a significant DCA increase, which may be explained by enhancement of the autotrophic bacterial community.

## CONCLUSIONS

1. Comparison of salinity, TMC, DCA and OM $\delta^{13}C$ composition of the surface water layers showed that these parameters regularly changed from almost freshwater of the coastal station 5013 to the deepest stations 5042 and 5044. The same trend had a considerable decrease in TMC and DCA, and the $\delta^{13}C$ values changed from –29.73 to –23.90‰, which could be explained by a relative decrease of the proportion of isotopically light terrigenous OM carbon in suspension.

2. In all the samples, except for station 5013, a noticeable decrease of TMC and DCA along the water column was observed. At certain stations the suspension carbon $\delta^{13}C$ content in the samples from different water column horizons almost did not differ from the $\delta^{13}C$ values in the upper horizons. However, in the water samples collected from the photosynthesis zone at the stations 5018, 5011-2, 5039, and 5042, a slight increase of heavier isotopes content in the suspension was detected, which was due to production of fresh organic matter by phytoplankton.

3. Significant changes in all the parameters studied at all stations were observed in a narrow 20–30 cm boundary layer. The number of microorganisms increased already in the near-bottom water and reached its maximum of 1.7–2.5 × $10^7$ cells $mL^{-1}$ in the fluffy layer. The same trend was observed for DCA, which increased from near-bottom water to the sediments, reaching its maximum in the fluffy layer or in the upper surface sediment layers. In the same boundary zone samples, an increase of organic carbon $\delta^{13}C$ share in the sediments over the near-bottom water was observed.

4. All the data obtained support the idea that the changes in the isotopic composition of organic carbon

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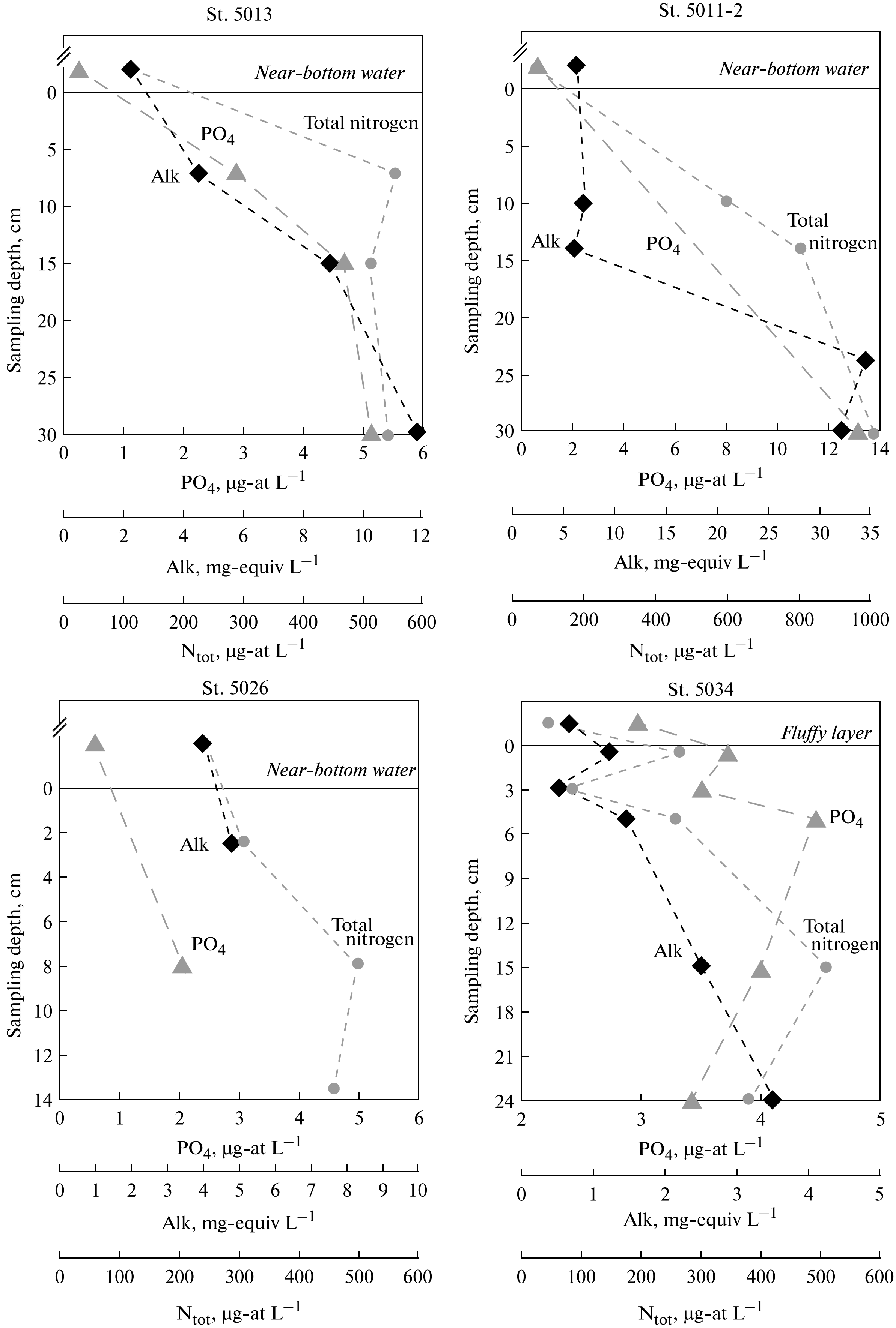
**Fig. 2.** Distribution of total alkalinity, total nitrogen, and $PO_4^{3-}$ in pore water and in water–sediment boundary zone at various stations during the 59th cruise of the *Akademik Mstislav Keldysh* research vessel in 2011 (data by P.N. Makkoveeva, Institute of Oceanography, Russian Academy of Sciences).


St. 5013
Near-bottom water
Total nitrogen
PO4
Alk
Sampling depth, cm
PO4, µg-at L−1
Alk, mg-equiv L−1
Ntot, µg-at L−1
St. 5011-2
Near-bottom water
Total nitrogen
PO4
Alk
Sampling depth, cm
PO4, µg-at L−1
Alk, mg-equiv L−1
Ntot, µg-at L−1
St. 5026
Near-bottom water
Alk
Total nitrogen
PO4
Sampling depth, cm
PO4, µg-at L−1
Alk, mg-equiv L−1
Ntot, µg-at L−1
St. 5034
Fluffy layer
PO4
Total nitrogen
Alk
Sampling depth, cm
PO4, µg-at L−1
Alk, mg-equiv L−1
Ntot, µg-at L−1

in the water-sediment boundary zone may be explained by an intense activity of chemoautotrophic microorganisms, which use as energy substrates the reduced compounds diffusing from the underlying sediments, producing the biomass with carbon isotopic composition of −20‰.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