Phototrophic and heterotrophic nano- and microorganisms of sea ice and sub-ice water in Guba Chupa (Chupa Inlet), White Sea, in April 2002

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Autotrophic and heterotrophic flagellates, microalgae and ciliates sampled at four stations in the White Sea in April 2002 were studied using epifluorescence microscopy. The concentrations of phototrophic 1.5 μm algae in the middle and lower part of the ice core were very high: up to 6.1×10^8 cells l^{-1} and 194 μg C l^{-1}. Heterotrophic algae made up the largest proportion of the nanoplankton (2 - 20 μm) and microplankton (20 - 200 μm) at depths 10 - 25 m below the ice. The proportion of ciliates ranged from about 0.01 % to 18 % at different stations and depths. Most of the ciliate biomass in the ice was made up of typical littoral zone species, whereas the water under the ice was dominated by phototrophic *Myrionecta rubra*. Ice algae, mainly flagellates in the upper ice layer and diatoms in the bottom ice layer, supported the proliferation of heterotrophs, algae and ciliates in early spring. Small heterotrophs and diatoms from the ice may provide food for early growth and development of pelagic copepods. Mass development of the ice algae in early spring appears typical for the seasonal ice of the White Sea. Ice algae differ in species composition from the spring pelagic community and develop independently in time and space from the spring phytoplankton bloom.

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Information about winter and early spring plankton in the White Sea is scarce and mainly consists of data on composition and abundance of net-collected meso-zooplankton. Little is known about pelagic unicellular organisms in this area, and there are few reports on winter phytoplankton. There are only three studies of winter phytoplankton in the White Sea (Khlebovich 1974; Zhitina & Mikhailovsky 1990; Krell et al. 2003), and only two studies on ice algae have been published (Mikhailovsky & Zhitina 1989; Krell et al. 2003). In these studies phytoplankton were concentrated by sedimentation and preserved with formaldehyde. This procedure destroys many small and fragile microalgae (Throndsen 1978). Moreover, autotrophic and heterotrophic cells could not be consistently distinguished with the light microscopy techniques used previously. This study aims to contribute to the knowledge of structure and distribution of the plankton and ice communities of the White Sea during the early spring.

Materials and methods

Samples of ice and sub-ice water were collected between 6 and 9 April 2002 at four stations in Guba Chupa (Chupa Inlet), Kandalaksha Bay, White Sea, near the White Sea Biological Station of the Zoology Institute, Russian Academy of Sciences. The stations were located along the section from the centre of the Guba Chupa towards Guba Krivoozerskaya (Fig. 1). The depths at stations 1 - 4 were 63, 40, 22 and 15 m, and the dis-

tance from shore was 1000, 950, 750 and 600 m, respectively.

Plankton samples were collected in 10 litre Niskin bottles at depths of 2, 10, 20 (25) and 40 m under the ice. Ice cores a maximum of 36 cm thick were obtained with a drill (cutting ring 14 cm in diameter) and cut into three parts: i) lower 2 - 5 cm (brownish) layer; ii) upper 10 cm layer; and iii) the remaining central part of the column. The ice was allowed to melt indoors for 24 h at air temperature 4 - 10 °C; sample temperature never exceeded 1 °C. Nano- and microplankton were counted and trophic status detected in water and ice samples. No major loss of flagellae was detected in the process of the ice melting (data not shown).

Organisms were studied using the epifluorescence method (Grebecki 1962; Hobbie et al. 1977; Caron 1983), as modified by Nejstgaard et al. (2001). The 10 - 50-ml subsamples were stained with primulin, fixed in 3.6 % glutaraldehyde solution with 10 % glycerol added for better preservation, and sedimented onto Nucleopore filters with 0.4 μm pore size. All filters were frozen at –18 °C before analysis. Cells were counted using a LUMAM-P8 epifluorescence microscope. Cell volumes for phototrophic and heterotrophic unicellular organisms were calculated by approximation to the 3D shapes. In our study the volume of diatoms was less than 3000 μm^3 so we were able to apply the Menden-Deuer & Lessard (2000) volume-to-carbon conversion formula for protist plankton: $pgC\ cell^{-1} = 0.216 \times volume^{0.939}$.

Results

Environment

Guba Chupa (Chupa Inlet) is an estuary about 37 km long with water circulation typical for a shallow-water fjord. From December to April (and during our study) most of the estuary is covered with thick (30 - 60 cm) ice. Winter convection does not reach the bottom of the basin; therefore the near-bottom waters are renewed only by advection. Ebb-tide currents are mainly of 0.05 - 0.30 m s^{-1}, sometimes reaching 0.40 m s^{-1} at 5 - 20 m depth. Total water transport is in general directed from the inner to the outer part of the estuary, both in the upper 5-m layer and in the near-bottom layers (20 - 65 m), and transport from the sea toward the inner estuary prevails in the intermediate 5 - 20-m layer (Howland et al. 1999). During our study, temperature and salinity in the deeper part of the inlet increased gradually from the ice–water boundary to the bottom. The lowest temperature and salinity values were –1.1 to –0.9 °C and 26.0 to 27.2 psu; the highest values were –0.3 °C and 28.0 psu (K. B. Kirpichev, pers. comm.). The intermediate layer (5 - 20 m), mainly formed by the open sea waters, showed a very slight decrease in temperature with depth; no decrease was observed at stations with less than 20 m depths (Fig. 2). The salinity recorded at the beginning of April indicated intensification of the ice melt, normally observed in Gupa Chupa at the end of April or in May (Gogorev 1998).

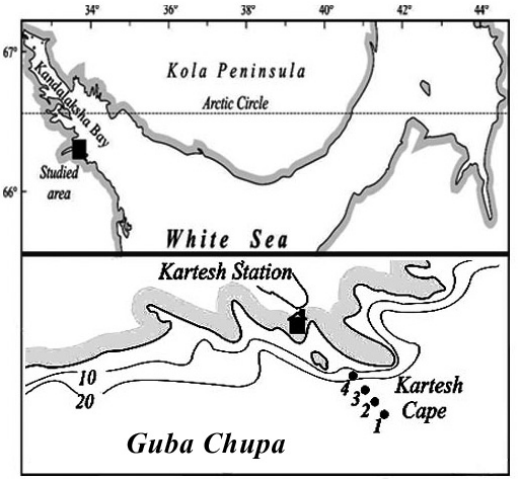

Fig. 1. Location of the stations in Guba Chupa (Chupa Inlet).

During our study the snow layer on the ice was about 5 cm thick at all stations. The ice was 34 - 36 cm thick, greyish, dull, half-soft, homogeneous along the whole core, with brine channels 3 - 5 mm in diameter. The undermost 2 - 4 cm of the core was brown, the bottom layer of congelation of columnar ice showed an actively growing skeletal layer and was most intensely coloured, reflecting the abundance of *Nitzschia frigida*, which was highest in this part of the core. Only in the coastal zone (station 4) was the ice less dense; signs of melting and brine drainage were evident.

Ice populations

At least 16 species of flagellates (not including dinoflagellates) and 13 species of ciliates were

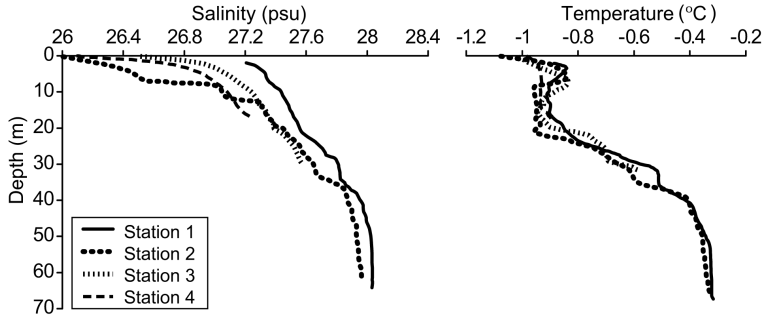

Fig 2. Temperature and salinity in the sub-ice water.

found in ice samples. Among phototrophic flagellates the most abundant were *Chlamydomonas* sp., *Dunaliella* sp., *D. tertiolecta, Teleaulax acuta, Pyramimonas grossii, P. orientalis, Euglena viridis, Euglena* sp., *Eutreptiella* sp. and *Heterosigma* sp. *Ochromonas* sp., *Chroomonas baltica* and *C. vectensis* were also rather common. Unidentified small (1.5 - 2.0 μm), round phototrophic cells without flagellae were also abundant. Heterotrophic algae were represented by a number of dinoflagellates: *Gyrodinium*, *Gymnodinium* and *Protoperidinium* spp. The relative number of unidentified heterotrophic cells of variable size was high. *Telonema* sp. and *Telonema subtilis* were common. Two ecological groups of ice ciliates were noted. The first group (low number) was comprised mainly of pelagic forms: *Strombidium stylifer*, *Strobilidium elegans*, *Didinium nasutum, Monodinium* sp., *Mesodinium pulex* and a phototrophic *Myrionecta rubra*. The second group, dominating in both total number and biomass, included common inhabitants of the White Sea littoral zone: *Lacrymaria* sp. (two species), *Euplotes* sp. (three species), *Dileptus* sp., *Litonotus* sp., *Uronema* sp., *Histiobalanthium* sp., *Stichotricha* sp. and *Trachelophyllum* sp. These genera ordinarily inhabit bottom sediments (Burkovsky 1970).

The vertical distribution of phototrophic flagellates in the ice layer varied strongly among stations and was different for the different core layers. In general, there was more biomass in middle and bottom ice layers; however, vertical differences were not statistically significant. Figure 3 shows averaged data for the four stations. *Chlamydomonas* and *Dunaliella* were dominant species in the upper ice layer; *T. acuta* and *Chlamydomonas* sp. were dominant in the middle part of the core. In the lower layer (the zone of the *N. frigida* bloom) there was no strong dominance of any species of autotrophic flagellate. The concentration of flagellated algae in different ice layers was: $217 - 684 \times 10^3$ cells l^{-1} (22.3 - 69.4 μg C l^{-1}) at station 1; $184 - 670 \times 10^3$ cells l^{-1} (7.1 - 42.9 μg C l^{-1}) at station 2; $498 - 2366 \times 10^3$ cells l^{-1} (33.9 - 62.7 μg C l^{-1}) at station 3; and $883 - 1243 \times 10^3$ cells l^{-1} (61.4 - 137.5 μg C l^{-1}) at station 4. Interestingly, very high concentrations of phototrophic eukaryotic algae 1.5 μm in diameter were recorded at station 3 (middle and lower core) and station 4 (upper and middle core). Their abundance at station 3 in the middle core layer was 1882×10^3 cells l^{-1} (0.59 μg C l^{-1}), while in the lower layer of that core it reached $610\,400 \times 10^3$ cells l^{-1} (194 μg C l^{-1}). At station 4 the concentration of these small cells was $426 - 716 \times 10^3$ cells l^{-1} (0.14 - 0.23 μg C l^{-1}), with the greatest abundance in the middle layer of the ice core.

The vertical distribution of heterotrophic flagellates was similar at all stations, though variations in their abundance and biomass were considerable. Numbers of heterotrophic flagellates were highest in the bottom section of the core and lowest in the middle section. No single species was dominant. Cell number in the upper ice layer at the four stations was $34 - 128 \times 10^3$ cells l^{-1}, with biomass 1.19 - 6.38 μg C l^{-1}. In the middle layer of the ice core the total number of heterotrophic flagellates was $24 - 123 \times 10^3$ cells l^{-1}, giving a biomass of 1.51 - 11.72 μg C l^{-1}, and in the bottom layer there were $92 - 319 \times 10^3$ cells l^{-1}, biomass 3.24 - 23.53 μg C l^{-1}. Vertical profiles averaged for stations 1 - 4 show a slight decrease in cell numbers from the upper to the middle part of the core and a considerable increase in the bottom ice layer (Fig. 3). Mean biomass of the heterotrophic flagellates gradually increased from the ice surface to its lower edge, because of the larger cell size in the middle ice layer and the increase in number in the lower layer (Fig. 3).

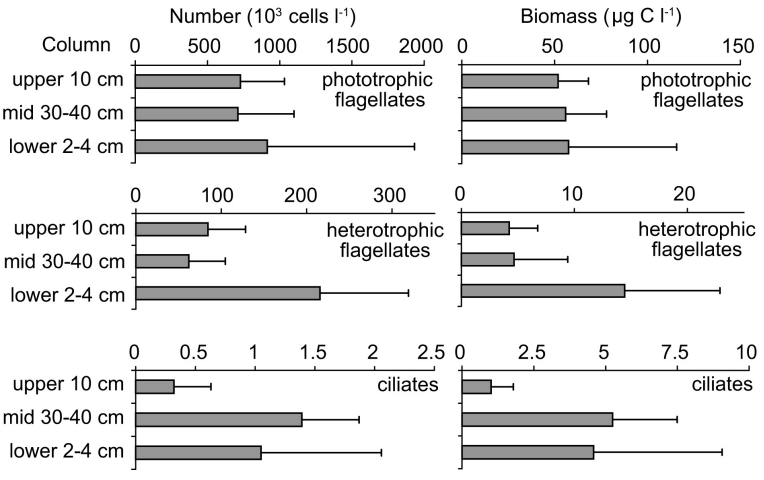

Fig. 3. Abundance and biomass of different groups of nano- and microorganisms in ice (average, stations 1 - 4). Error bars indicate standard deviation of the mean values.

There were few ciliates in the upper layer of the ice core. The middle layer contained more ciliates, and in the lower layer their number either increased further (stations 1, 4) or decreased (stations 2, 3). Most common were *Lacrymaria* spp. (two unidentified species) and *Euplotes* spp. (three unidentified species). These species stood for most of the total ciliate numbers and biomass. In upper layer of the core, ciliate number at different stations was $0.02 - 0.7 \times 10^3$ cells l^{-1}, giving a biomass of 0.15 - 1.83 μg C l^{-1}. Ciliate number and biomass in the middle layer of ice were $0.82 - 1.94 \times 10^3$ cells l^{-1} and 2.34 - 7.24 μg C l^{-1}. In the lower layer at stations 1 and 4 ciliate number and biomass were $1.38 - 2.3 \times 10^3$ cells l^{-1} and 5.67 - 10.34 μg C l^{-1}. At stations 2 and 3 the corresponding figures were $0.01 - 0.5 \times 10^3$ cells l^{-1} and 0.06 - 2.24 μg C l^{-1}. The vertical distribution of mean ciliate number and biomass followed similar patterns at all four stations, with lowest values in the upper layer (Fig. 3).

Population of the sub-ice water

Flagellated algae of the sub-ice water were represented by 34 species (not including dinoflagellates). The most common phototrophic forms included *Pyramimonas grossii*, *Teleaulax acuta*, *Plagioselmis prolonga*, *Eutreptiella braarudii*, *Rhodomonas marina* and *Chroomonas baltica*. Less frequent were *Phaeocystis pouchaetii* (motile stage), *Dinobryon baltica* and *Dunaliella* sp. Rare species included: *Apedinella spinifera*, *Pterosperma polygonum*, *Dictyocha speculum*, *Pyramimonas amylifera* and *P. octopus*. Heterotrophic flagellates were mainly represented by several small (< 10 - 15 μm in diameter) *Gyrodinium* species, *Monosiga marina* (cells with weakly developed collar) and *Telonema subtilis*. Less common were *Leucocryptos marina* and *Gyrodinium fusiforme*. Single records were obtained for *Pseudobodo* sp., *Bodo parvulus*, *Gyrodinium lachryma* and *G. aureolum*. The species *Amphidinium sphaenoides*, *Cochlodinium archimedes* and *Torodinium robustum* were also found. These phototrophic flagellates usually contain chlorophyll, but those in our sample did not. Ciliates of the sub-ice water were represented by 9 species; 7 of these were common inhabitants of the sea pelagic zone (*Strombidium conicum*, *S. wulfii*, *Strobilidium elegans*, *Monodinium balbianii*, *Lochmanniella spiralis*, *Halteria* sp. and *Myrionecta rubra*) and 2 more typical for the shallow coastal zone (*Lacrymaria coronatum* and *Dysteria monostyla*).

The vertical distribution pattern of phototrophic flagellates in the sub-ice water was the same from station to station, though cell concentrations varied. Algal abundance was maximal just below the ice and decreased considerably at greater depths (Fig. 4). The largest number of phototrophic algae at 2 m depth was found at station 2 (953×10^3 cells l^{-1}), and the biomass of these algae at 2 m was greatest at station 3 (14.49 μg C l^{-1}). Most of the phototrophic flagellates were small (2.5 - 3 μm in diameter) cells of the genus *Pyramimonas* (mainly *P. grossii*) with short flagella. Considerable contribution to the total biomass was provided by larger algae, mainly *P. prolonga*.

The vertical distribution of heterotrophic flagel-

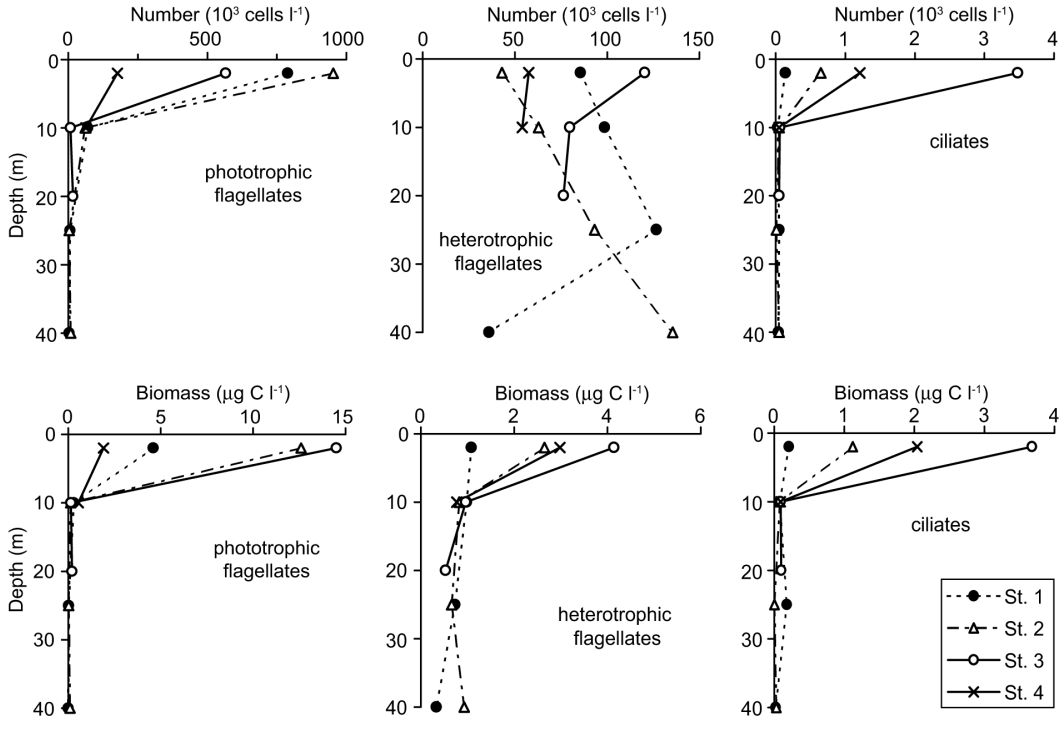

Fig. 4. Abundance and biomass of different groups of nano- and microplankton in sub-ice water (stations 1 - 4).

late numbers showed no obvious trends (Fig. 4). At station 1 these algae were most plentiful at 25 m (127×10^3 cells l^{-1}) and at station 2 they were most plentiful at 40 m (136×10^3 cells l^{-1})—the highest values at any station. Maximal numbers of heterotrophic flagellates at stations 3 and 4 were found at 2 m depth: numbers decreased in the deeper layers. The biomass of heterotrophic flagellates was maximal in the surface water due to large cells; it decreased sharply with depth. The total biomass of this group at 2 m was 1.08 - 4.14 µg C l^{-1}. Small (8 - 12 µm diameter) *Gyrodinium* species dominated in the sub-ice water. Some heterotrophic cells remained unidentified.

Ciliates were distributed similarly to phototrophic flagellates, being mainly concentrated in the upper layer of the sub-ice water with very low concentrations at depths >2 m (Fig. 4). Vertical patterns of number and biomass distribution were highly similar. The maximal number was 3.48×10^3 cells l^{-1} and the highest biomass density was 3.68 µg C l^{-1}. Phototrophic *M. rubra* formed the main part of the total ciliate abundance and biomass. *Strombidium* sp. also contributed to total ciliate biomass.

Discussion

This is the first study of species composition, distribution and quantitative parameters of phototrophic and heterotrophic populations of the ice and sub-ice water in the White Sea in early spring. The study has shown that ice and sub-ice populations of the White Sea in early spring include numerous phototrophic and heterotrophic flagellates as well as diatoms. The dominant flagellate species are common for the Arctic (Ikavalko & Gradinger 1997) in both winter and summer. Our estimates of the abundance of phototrophic and heterotrophic nano- and microorganisms are considerably higher than the flagellate numbers reported for the Barents Sea: $16 - 440 \times 10^3$ cells l^{-1} in ice and $166 - 319 \times 10^3$ cells l^{-1} in sub-ice water (Druzhkova & Druzhkov 2001). Very high concentrations of phototrophic picoalgae (eukaryotic cells of about 1.5 µm) should probably not be considered as unique to the White Sea. Similar cells, albeit at lower abundance (36×10^3 cells l^{-1} and 63×10^3 cells l^{-1}), were found in ice and in sub-ice water near the Canadian coast (Robineau et al. 1994) and in the Chukchi Sea ($10^3 - 10^4$ cells ml^{-1};

Sherr et al. 1997).

The upper layer of seasonal sea ice was mainly inhabited by species of *Chlamydomonas*; vertical stratification observed for the species of the flagellated algae is found throughout the seasonal ice of the Arctic Basin (Druzhkov et al. 2001). The dominance of *Chlamydomonas* spp. in the upper ice layer is a common feature of melting ice pools throughout the Arctic (Maykut 1985; Syvertsen 1991; Juterzenka et al. 1997; Okolodkov 1997; Gradinger 1999). As in other Arctic waters (Mel'nikov 1989; Gradinger 1999; Druzhkov et al. 2001), maxima for the main algae groups were found in the bottom layer of ice. Pennate diatoms were most abundant in the bottom ice layer, as in the Barents Sea (Syvertsen 1991; Hegseth 1992). Again similar to the Barents Sea, the planktonic population was mainly concentrated in the upper few metres of the water column. However, some groups of heterotrophic algae increase in number with depth. Common pelagic species were found in the sub-ice nano- and microplankton. Mass development of *Pyramimonas* sp. in the sub-ice water of the White Sea probably occurs in the entire Arctic Basin (Gradinger 1996).

No prior information was available about the ciliate population in White Sea ice. Among the pelagic forms, only *Tintinnoinea* have been studied, and then mainly during the warm season. As shown by this study, the phototrophic ciliate *M. rubra* was dominant in sub-ice water of the White Sea. Similar data were obtained for the inner bays of the Japanese coast that are covered with seasonal ice (Sime-Ngando, Juniper et al. 1997). During our study, almost all ciliates (including *M. rubra*) were concentrated at 2 m depth. The ciliates found in ice mainly inhabited the middle and lower ice layers. As in the Barents Sea, benthic ciliate species were the dominant forms in the ice core (Druzkov & Druzhkova 2001; Druzhkova & Druzhkov 2001)—all Arctic ice populations appear to share this characteristic (Agatha et al. 1993; Sime-Ngando, Gosselin et al. 1997). For the White Sea this is easy to explain. At the beginning of the winter period ice is formed in the littoral zone during low tide and then is washed together with bottom particles during high tide (personal observations). The resulting ice floes are transferred by tidal currents and form a part of the solid ice cover. Some benthic species are favoured by the ice biotope and grow successfully in ice. The same mechanism may also be acting on the algae; however, we have no experimental data to support this. Data on the occurrence of certain benthic algae in the ice of the White Sea can be found only in one study (Gogorev 1998).

The data reported here for all main groups of nano- and microorganisms forming the population of the White Sea ice (we do not consider bacteria and meiofauna) provide the first possibility to estimate the abundance of these groups in total biomass of the ice community and in its carbon flow system (Table 1). In early spring the contribution of heterotrophic ciliates to the total biomass was low (commonly about 0.1 %, maximum 5 % of the biomass of the total ice population). Total algal biomass increased considerably from the upper to the lower layers of ice. This is due to increasing biomass of the diatoms in lower layers. In contrast, the relative contribution of phototrophic flagellates to total biomass sharply decreases from upper to the lower ice levels. Phototrophic flagellate biomass was highest in the upper 10 cm of ice, up to 2.4 times higher than the biomass of the diatoms. The contribution of the heterotrophic flagellates in ice was rather small. Their greatest contribution (4 - 9 %) is usually found in the upper ice layer and the smallest in the bottom ice layer.

The contribution of different nano- and microplankton groups to the total algal biomass in sub-ice water changed with depth (Table 2). The number of algae was maximal at 2 m depth. The

Table 1. Biomass—in ice—of different algal groups expressed as % of the total algal biomass (measured as μg C l^{-1}). The total biomass of algae and biomass of the ciliates is given as μg C l^{-1}.

Station	Ice column (cm)	Diatoms (%)	Photo-trophic flagellates (%)	Hetero-trophic flagellates (%)	Total biomass of algae	Biomass of ciliates
1	0 - 10	48	48	4	145	0.57
	10 - 30	81	17	0.7	286	2.34
	30 - 34	97	0.9	0.1	2504	5.67
2	0 - 10	26	62	9	68	1.48
	10 - 30	67	30	1	143	7.24
	30 - 34	98	0.2	0.4	4320	2.24
3	0 - 10	36	58	5	59	0.15
	10 - 32	55	39	3	109	4.59
	32 - 34	99	0.7	0.07	35 682	0.06
4	0 - 10	36	59	1.1	105	1.83
	10 - 34	46	46	6	195	6.79
	34 - 36	96	3	0.3	4692	10.34

diatoms formed 13 - 35 % of the total phytoplankton biomass, almost always second after phototrophic flagellates (20 - 60 %). At 10 m depth the relative biomass of the diatoms increased to 40 - 71 %, and below 10 m it further increased (stations 1, 4), remained stable (station 2) or decreased (station 3). The proportion of phototrophic flagellates decreased with depth except at the shallow-water station 4, where it slightly increased near the bottom (10 m). The contribution of heterotrophic flagellates in the sub-ice water was high: 11 - 51 % of the phytoplankton biomass. The contribution of heterotrophic algae to the total biomass of nano- and microplankton was maximal at 10 - 25 m. The ciliate population was comprised mainly of phototrophic *M. rubra*. Biomass of the ciliates varied considerably at different stations and depths, ranging from about 0.01 to 18 % of the total biomass of nano- and microorganisms.

Earlier observations in the same region (Krell et al. 2003) show that mass development of the ice algae has not yet started in February. It seems that growing irradiance and the beginning of snow melting on the ice surface are essential factors for the start of mass development of the ice algae. The origin of these algae is probably pelagic; however, benthic species can also be important.

During our study (and in early spring 2001 [Rat'kova et al. 2002]) the dense bloom of *N. frigida* comprised a food source for the development of heterotrophic organisms in the sub-ice water. This bloom was studied further in the same region later in April 2002; it terminated during the last stage of the intense ice melting, and the community was nitrogen-limited (Krell et al. 2003).

To conclude, the ice algae—mainly flagellates in the upper ice layer and diatoms in the bottom ice layer—provide food for the intense proliferation of heterotroph, algae and ciliate populations in early spring. In turn, small heterotrophs provide for the early growth and development of pelagic copepods (Kosobokova et al. 2003). Mass development of the ice algae in early spring appears typical for the White Sea, and probably for other Arctic regions. Though Krell et al. (2003) believe that the year 2002 was an exception, there is evidence that mass development of the ice algae has occurred in other years as well. For example, the development of *N. frigida* in the bottom ice layer of the Chupa Inlet was observed in March 2001 (Rat'kova et al. 2002).

The ice algae population is quite different in composition from the algae involved in the spring plankton bloom (*Thalassiosira*, etc.) and therefore the spring development of ice algae and of pelagic phytoplankton are independent in time and space.

Table 2. Biomass—in sub-ice water—of different algal groups expressed as % of the total algal biomass (measured as μg C l^{-1}). The total biomass of algae and biomass of the ciliates is given as μg C l^{-1}.

Station	Sample depth (cm)	Diatoms (%)	Photo-trophic flagellates (%)	Hetero-trophic flagellates (%)	Total biomass of algae	Biomass of ciliates
1	2	22	53	22	8.71	0.21
	10	45	11	40	2.70	0.08
	25	52	0.7	39	2.48	0.18
	40	56	0.6	39	0.85	0.02
2	2	35	50	11	25.12	1.12
	10	71	2	22	6.86	0.08
	25	64	0.4	34	3.97	0.002
	40	76	2	18	5.14	0.03
3	2	13	60	25	24.21	3.68
	10	40	7	50	1.94	0.09
	20	25	17	51	1.21	0.10
4	2	35	20	42	9.45	2.04
	10	43	23	33	2.30	0.09

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