

# Phytoplankton in the south-western Kara Sea: composition and distribution



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The taxonomic composition and spatial distribution of pelagic algae were studied in the south-western Kara Sea in August–September 1981. In the north-western and easternmost regions of the study area the phytoplankton community, dominated by neritic diatoms and autotrophic dinoflagellates, was at the late spring bloom stage of the seasonal succession. In the central deep-water zone of the sea, there was a predominance of heterotrophic dinoflagellates from the genera *Protoberidinium* and *Dinophysis*, and the autotrophic compartment of the algal community was clearly in a stage of decline. The distribution of the phytoplankton assemblages followed closely the major routes of receding marginal ice zones. Three stages of the seasonal succession were established for the area of interest: (1) early spring (ice edge) bloom of arcto-boreal neritic diatoms; (2) late spring bloom of neritic diatoms and autotrophic dinoflagellates, fuelled by continental run-off; and (3) summer minimum with a predominance of heterotrophic dinoflagellates, followed by autumnal decline of the phytoplankton community.

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Phytoplankton studies in the Kara Sea started more than 100 years ago with Nordenskiöld's cruise of 1875–76 (R/V *Pröven*) to Enisei Bay. During the Swedish expedition of 1878–79 (R/V *Vega*), a substantial collection of planktonic diatoms was obtained, and many species were found to be new to science (Cleve & Grunow 1880; Cleve 1883). In 1903–07 the taxonomic composition of pelagic algae of the Kara Sea was investigated by Palibin & Linko (for a review, see Makarevich & Koltsova 1989) and Meunier (1910). Most extensive were phytoplankton studies carried out by Russian researchers in the 1920s and '30s. The most important contribution to these studies was done by Zabelina (1930, 1946); all materials from the pre-war period were summarized by Usachev (1968). Since then there have been only episodic plankton surveys in the

Kara Sea, all being of a local character (Koltsova & Ilyash 1982). This stagnant situation exploded in the 1990s when the Kara Sea became an arena of international industrial and scientific activities (Alexandrova & Shevchenko 1997; Vedernikov et al. 1997; Druzhkov & Druzhkova 1999).

In this context, results of the earlier phytoplankton studies in the Kara Sea are of special interest as they serve as a starting point for a thorough comparative analysis of the space–time variability of pelagic algal communities and for accurate assessments of any anthropogenic impacts on marine pelagic ecosystems. In this paper we present the results of a phytoplankton survey carried out by the Murmansk Marine Biological Institute (MMBI) in the south-western Kara Sea in 1981. This study is the most extensive one in the post-war period in this area. Special atten-

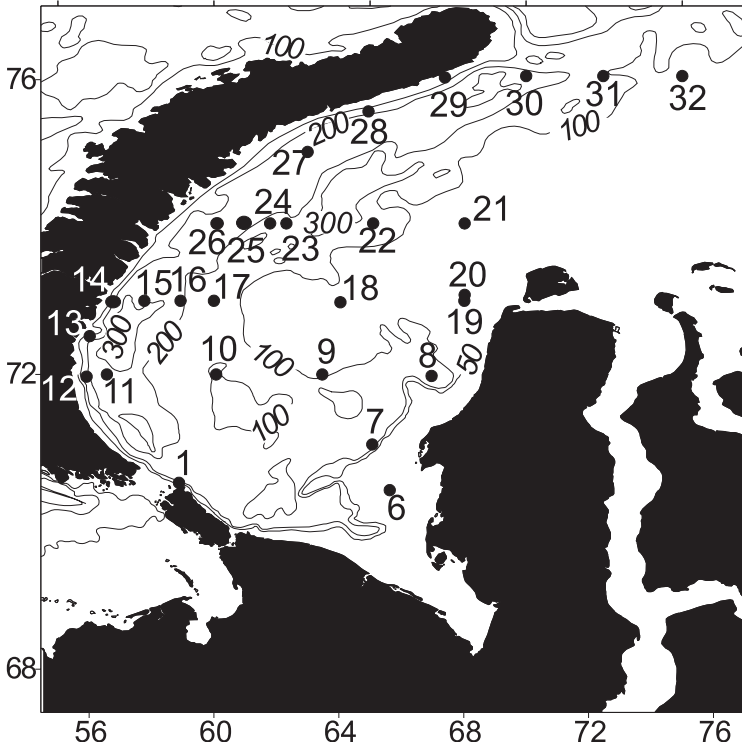


Fig. 1. Location of the sampling stations in the south-western Kara Sea in August–September 1981. Depth lines are shown in italics.

tion is focused on the taxonomic composition and distribution of the phytoplankton assemblages. Additionally, an attempt is made to reconstruct the structure of the phytoplankton seasonal succession.

## Materials and methods

The phytoplankton samples were collected during the ninth cruise of R/V *Pomor* (29 August–13 September 1981) in the south-western Kara Sea (Fig. 1), preserved with 4 % borax-buffered formaldehyde and deposited in the phytoplankton collection of MMBI. The 0.5-litre samples were taken from depths of 0, 5, 10, 25, 50, 75 and 100 m with a 5-litre sampling bottle. The samples were concentrated to volumes of 2 - 3 ml using the routine sedimentation method: after sedimentation of particulate material (Edler 1972), most of the seawater was decanted with a polychlorvinyl siphon supplied with a very thin curved glass capillary. Enumeration and taxonomic identification of algae were carried out in 0.05-ml counting chambers (5 replicates) according to

standard procedures (Fedorov 1978) under the Zeiss Amplival microscope (200 and 400× magnification). The whole volumes of the concentrated samples (2-3 ml) were then studied in 10-ml Bogorov (snake-channelled) counting chambers under the stereomicroscope MBS-10 (24 and 56× magnification) to determine the presence of larger and rarer forms. The linear dimensions of cells were measured with an ocular micrometer with a precision of 3 μm, and cell volumes were calculated using the recommended approximations to simpler geometric bodies (Edler 1972). In the case of some species with complex cell configurations, we used the standard biomass tables compiled by Makarevich et al. (1993). All biomass values are presented below as wet weight units calculated from cell volumes.

The problem of establishing adequate phyto-geographical and ecological diagnoses of planktonic algae is difficult because authors diverge somewhat on this subject. There are many approaches to the problem and many classification schemes, e.g. subdivision of polar diatoms into Arctic and arcto-boreal forms (Guillard & Kilham 1977; Heimdal 1989; Druzhkov & Makarevich 1999).

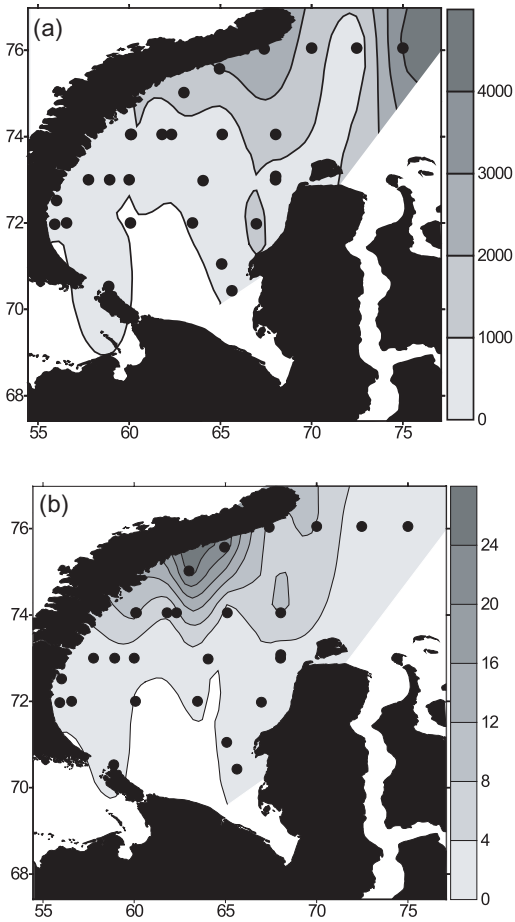


Fig. 2. Horizontal distribution of (a) the cell numbers (cells  $\times 10^3 \text{ m}^{-2}$ ) and (b) biomass (g wet weight  $\text{m}^{-2}$ ) of the total phytoplankton (top 100 m layer).

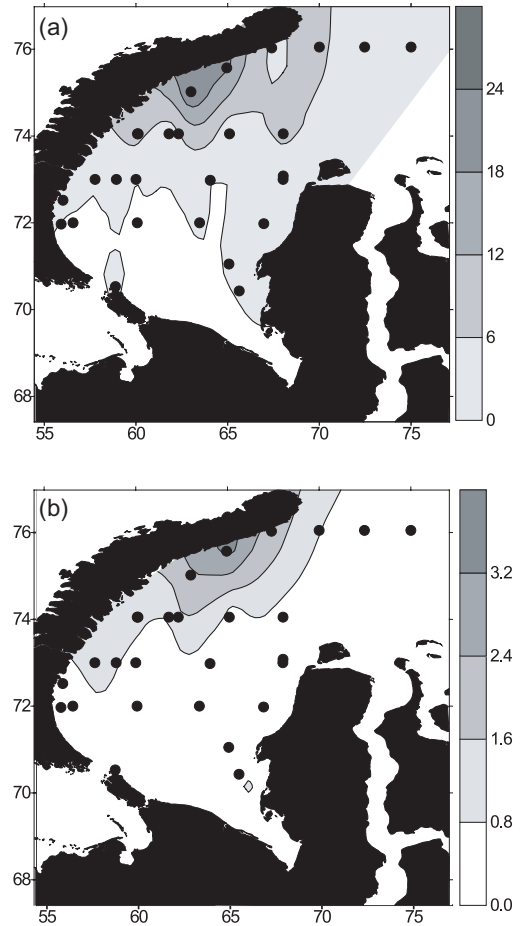


Fig. 3. Horizontal distribution of the biomass (g wet weight  $\text{m}^{-2}$ ) of (a) diatoms and (b) dinoflagellates (top 100 m layer).

The situation is aggravated by the vast lacunae in our knowledge of the geographical distributions of many northern species. Therefore, for the preliminary assessment undertaken in the present work we have used as few phytogeographical and ecological categories as possible (see Druzhkov & Makarevich 1999). For the phytogeographical analysis only three categories were applied (Table 1): (A) arcto-boreal species; (B) boreal species (including all species of boreal and tropical-boreal origin); and (C) cosmopolitan species (including some forms with bipolar distribution, such as *Chaetoceros concavicornis*, *Dinophysis arctica*, *Thalassiosira cf. gravida* and some others). The freshwater forms were not characterized phytogeographically. Five categories were introduced to

give the ecological characteristics of microalgae: (O) oceanic species; (P) panthalassic (oceanic-neritic) species; (N) neritic species; (M) microphytobenthic species; and (F) freshwater species.

For evaluating the floristic similarity between the stations (as well as for delimiting the microalgal assemblages) we used the Sørensen (Dice) similarity coefficient (Clarke & Warwick 1994):

$$\text{SCS} = 2C / (A + B)$$

where A and B are the numbers of the species recorded at compared stations (the numbers of two species' records at the stations in the study area), and C is the number of the species found in both areas (the number of records of both species at the stations). The cluster analysis was carried

Table 1. Taxonomic composition of the phytoplankton in the south-western Kara Sea in August–September 1981. PC = phyto-geographical characteristics, EC = ecological characteristics, RF = record frequency (% of stations), MB = maximum biomass ( $\mu\text{g dm}^{-3}$ ), MD = maximum cell density (cells  $\text{dm}^{-3} \times 10^3$ ), A = arcto-boreal species, B = boreal species, C = cosmopolitan species, O = oceanic species, P = panthalassic (oceanic–neritic) species, N = neritic species, M = microphytobenthic species, F = freshwater species.

Taxa	PC	EC	RF	MB (MD)
<b>Class Centrophyceae</b>				
<i>Attheya septentrionalis</i> (Østrup) Crawford	A	N	39.3	14.8 (39.0)
<i>Bacterosira bathyomphala</i> (Cleve) Syvertsen et Hasle	A	N	3.6	0.4 (0.1)
<i>Chaetoceros borealis</i> Bailey	A	O	25.0	29.3 (1.1)
<i>C. compressus</i> Lauder	C	N	17.9	21.3 (15.8)
<i>C. concavicornis</i> Mangin	A	O	17.9	1.8 (0.1)
<i>C. convolutus</i> Castracane	C	P	21.4	7.6 (0.4)
<i>C. danicus</i> Cleve	A	N	3.6	0.3 (0.2)
<i>C. debilis</i> Cleve	C	N	7.1	25.6 (13.2)
<i>C. decipiens</i> Cleve	C	P	75.0	222.3 (17.7)
<i>C. diadema</i> (Ehrenberg) Gran	A	N	39.3	31.2 (8.2)
<i>C. karianus</i> Grunow	A	N	7.1	0.2 (0.3)
<i>C. simplex</i> Ostenfeld	A	N	3.6	0.05 (0.1)
<i>C. socialis</i> Lauder	C	N	17.9	0.9 (2.4)
<i>C. teres</i> Cleve	B	N	3.6	3.3 (0.2)
<i>Coscinodiscus</i> sp.			3.6	0.3 (0.03)
<i>Cyclotella</i> sp.			7.1	2.0 (0.1)
<i>Eucampia groenlandica</i> Cleve	C	N	28.6	41.8 (8.7)
<i>Leptocylindrus danicus</i> Cleve	C	N	14.3	21.4 (9.4)
<i>L. minimus</i> Gran	B	N	10.7	0.2 (1.7)
<i>Melosira arctica</i> (Ehrenberg) Dickie	A	N	7.1	2.9 (0.3)
<i>M. varians</i> Agardh	-	F	7.1	7.0 (1.1)
<i>Porosira glacialis</i> (Grunow) Jørgensen	C	N	7.1	2.0 (0.2)
<i>Guinardia delicatula</i> (Cleve) Hasle	C	N	14.3	53.1 (8.2)
<i>R. hebetata</i> (Bailey) Gran	A	O	3.6	2.9 (0.1)
<i>R. setigera</i> Brightwell	C	N	7.1	18.7 (0.5)
<i>Skeletonema costatum</i> (Gréville) Cleve	C	N	17.9	0.3 (1.0)
<i>Thalassiosira bioculata</i> (Grunow) Ostenfeld	A	N	25.0	41.9 (1.1)
<i>T. eccentrica</i> (Ehrenberg) Cleve	C	N	3.6	3.8 (0.04)
<i>T. cf. gravida</i> Cleve	C	P	46.4	707.2 (24.3)
<i>T. pseudonana</i> Hasle et Heimdal	A	N	14.3	3.3 (4.9)
<i>T. nordenskiöldii</i> Cleve	A	N	21.4	16.7 (5.0)
<b>Class Pennatophyceae</b>				
<i>Achnanthes taeniata</i> Grunow	A	N	3.6	2.2 (0.2)
<i>Asterionella bleakeleyi</i> W. Smith	A	N	14.3	1.7 (1.1)
<i>Catacombas gaillonii</i> (Bory) Williams et Round	A	M	3.6	0.6 (0.1)
<i>Cylindrotheca closterium</i> (Ehrenberg) Reimann et Lewin	C	N	35.7	1.7 (8.5)
<i>Fragilariopsis oceanica</i> (Cleve) Hasle	A	N	17.9	1.0 (2.3)
<i>Grammatophora arctica</i> Cleve	C	M	3.6	0.3 (0.1)
<i>Licmophora abbreviata</i> Agardh	C	M	3.6	0.2 (0.03)
<i>L. gracilis</i> (Ehrenberg) Grunow	C	M	3.6	0.1 (0.02)
<i>Navicula vanhoeffenii</i> Gran	A	N	7.1	0.2 (0.3)
<i>N. frigida</i> Grunow	A	N	10.7	0.2 (0.1)
<i>N. laevissima</i> Grunow	A	N	7.1	0.03 (0.1)
<i>N. longissima</i> (Brébisson) Ralfs	C	P	14.3	0.2 (1.0)
<i>Pleurosigma angulatum</i> (Queckett) W. Smith	A	N	7.1	1.9 (0.03)
<i>Pseudo-nitzschia delicatissima</i> (Cleve) Heiden	A	N	39.3	370.0 (876.9)
<i>P. seriata</i> (Cleve) H. Peragallo	A	P	17.9	4.0 (9.6)
<i>Synedra acus</i> Kützing	-	F	3.6	0.2 (0.05)
<i>Tabularia fasciculata</i> (Agardh) Williams et Round	C	M	7.1	0.4 (1.0)
<i>Thalassionema nitzschioides</i> Grunow	C	P	10.7	2.7 (2.9)
<b>Class Dinophyceae</b>				
<i>Alexandrium ostenfeldii</i> (Paulsen) Balech et Tangen	A	N	10.7	0.2 (0.04)
<i>Amphidinium crassum</i> Lohmann	B	N	7.1	0.3 (0.2)
<i>A. extensum</i> Wulff	A	P	21.4	1.2 (0.5)
<i>A. lacustre</i> Stein	B	N	14.3	0.4 (0.2)
<i>A. sphenoides</i> Wulff	A	O	14.3	0.7 (0.3)

Table continued next page

<i>Amylax triacantha</i> (Jørgensen) Sournia	A	N	17.9	3.0 (0.3)
<i>Ceratium arcticum</i> (Ehrenberg) Cleve	A	P	64.3	46.8 (0.6)
<i>C. longipes</i> (Bailey) Gran	A	O	7.1	4.3 (0.04)
<i>C. tripos</i> (O.F. Müller) Nitzsch	C	O	3.6	2.3 (0.05)
<i>Dinophysis acuminata</i> Claparède et Lachman	C	N	28.6	7.2 (0.4)
<i>D. arctica</i> Mereschkowsky	C	N	57.1	3.4 (0.2)
<i>D. norvegica</i> Claparède et Lachman	A	N	25.0	2.1 (0.1)
<i>D. pulchella</i> (Lebour) Balech	B	N	17.9	1.7 (0.2)
<i>D. rotundata</i> Claparède et Lachman	C	O	21.4	1.8 (0.1)
<i>D. sphaerica</i> Stein	A	O	7.1	0.5 (0.04)
<i>Glenodinium danicum</i> Paulsen	B	N	3.6	0.2 (0.04)
<i>G. paululum</i> Lindemann	B	N	10.7	4.3 (0.2)
<i>Gonyaulax polygramma</i> Stein	C	P	3.6	2.2 (0.1)
<i>G. spinifera</i> (Claparède et Lachman) Diessing	C	N	7.1	0.1 (0.1)
<i>Gymnodinium arcticum</i> Wulff	A	N	17.9	1.4 (0.6)
<i>G. fusus</i> Schütt	A	N	28.6	2.2 (0.6)
<i>G. wulffii</i> Schiller	A	N	28.6	6.9 (5.0)
<i>Gyrodinium fusiforme</i> Kofoid et Swezy	C	N	7.1	12.8 (0.1)
<i>G. lachryma</i> (Meunier) Kofoid et Swezy	A	P	53.6	64.0 (1.0)
<i>G. pellucidum</i> (Wulff) Schiller	A	N	7.1	0.7 (0.3)
<i>G. pingue</i> (Schütt) Kofoid et Swezy	C	P	17.9	1.1 (0.6)
<i>G. prunus</i> (Wulff) Lebour	A	N	28.6	6.0 (0.5)
<i>G. varians</i> (Wulff) Schiller	?	N	7.1	0.8 (0.3)
<i>G. wulffii</i> Schiller	A	N	3.6	0.2 (0.1)
<i>Oxytoxum gladiolus</i> Stein	B	O	10.7	0.5 (0.2)
<i>O. milneri</i> Murray et Whitting	A	O	7.1	17.0 (0.3)
<i>Peridiniella catenata</i> (Levander) Balech	A	N	32.1	28.1 (1.7)
<i>Prorocentrum balticum</i> (Lohmann) Loeblich	C	N	7.1	0.4 (0.7)
<i>P. compressum</i> (Bailey) Dodge	A	N	10.7	1.2 (0.)
<i>Protoperidinium bipes</i> (Paulsen) Balech	A	N	46.4	4.2 (1.7)
<i>P. breve</i> (Paulsen) Balech	C	O	32.1	15.0 (0.1)
<i>P. brevipes</i> (Paulsen) Balech	C	N	85.7	9.1 (0.9)
<i>P. conicoides</i> (Paulsen) Balech	A	N	7.1	4.1 (0.05)
<i>P. crassipes</i> (Kofoid) Balech	C	O	3.6	1.0 (0.1)
<i>P. curvipes</i> (Ostenfeld) Balech	A	N	3.6	27.6 (0.2)
<i>P. decipiens</i> (Jørgensen) Balech	A	N	3.6	6.8 (0.1)
<i>P. depressum</i> (Bailey) Balech	C	O	3.6	17.6 (0.02)
<i>P. divergens</i> (Ehrenberg) Balech	C	N	3.6	30.1 (0.2)
<i>P. globulum</i> (Stein) Balech	C	O	17.2	28.0 (0.2)
<i>P. granii</i> (Ostenfeld) Balech	C	N	53.6	48.5 (3.1)
<i>P. groenlandicum</i> (Woloszynska) Balech	B	N	3.6	2.4 (0.04)
<i>P. islandicum</i> (Paulsen) Balech	A	N	7.1	28.9 (0.3)
<i>P. monacanthus</i> (Broch) Balech	A	O	42.9	14.7 (0.2)
<i>P. pallidum</i> (Ostenfeld) Balech	C	P	3.6	13.7 (0.2)
<i>P. pellucidum</i> Bergh	C	N	78.6	7.5 (0.4)
<i>P. pyriforme</i> (Paulsen) Balech	?	O	7.1	4.0 (0.04)
<i>P. thorianum</i> (Paulsen) Balech	C	N	10.7	5.8 (0.05)
<i>Scrippsiella trochoidea</i> (Stein) Loeblich III	A	N	46.4	3.1 (0.8)
<i>Spatulodinium pseudonoctiluca</i> (Pouchet) Cachon et Cachon	C	O	3.6	26.5 (0.03)
<i>Zygabikodinium lenticulatum</i> (Paulsen) Loeblich et Loeblich	C	O	21.4	73.7 (2.4)
Other classes				
<i>Dictyocha speculum</i> Ehrenberg	C	O	28.6	0.8 (0.1)
<i>Dinobryon balticum</i> (Schütt) Lemmermann	A	N	21.4	0.3 (7.0)
<i>Ebria tripartita</i> (Schumann) Lemmermann	B	N	3.6	0.4 (0.04)
<i>Halosphaera viridis</i> Schmitz	C	O	10.7	+

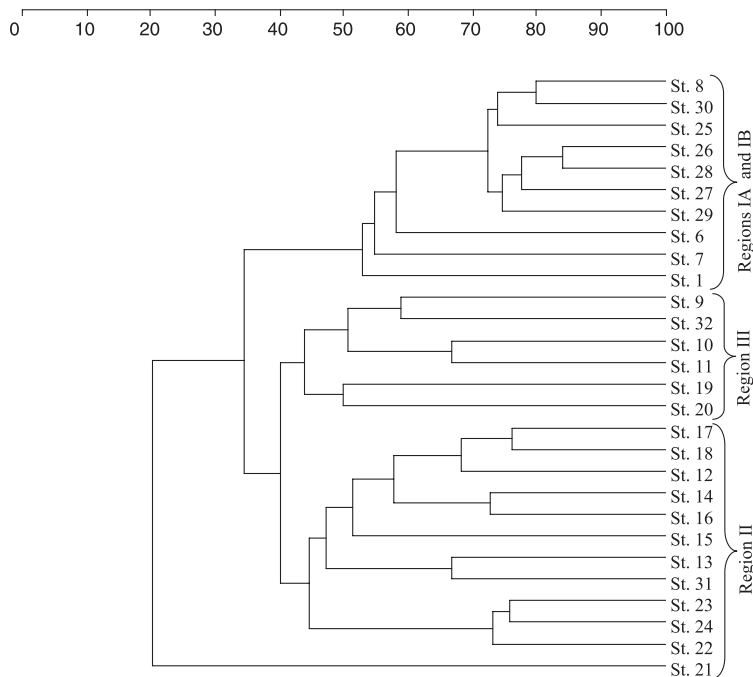


Fig. 4. Floristic similarity between stations in the south-western Kara Sea.

out using the weighted pair-group average technique (Sneath & Sokal 1973).

Detailed information on the oceanographic and chemical data obtained during the cruise has been published elsewhere (Shirokolobov 1982).

## Results

### *The taxonomic composition of microphytoplankton*

The species numbers of diatoms (49) and dinoflagellates (55) were almost the same. Only one representative was found from each of four other classes (Chrysophyceae, Dictyochophyceae, Ebrionophyceae and Prasinophyceae), but the real taxonomic compositions of flagellated phytoplankton is badly biased due to inadequate preservation as formaldehyde is far from the best fixative for unamoured flagellates (including all gymnodinoid dinoflagellates).

As in any shelf marine basin, the phytoplankton of the Kara Sea is characterized by a clear predominance of the neritic flora—68 % and 62 % of the species numbers for diatoms and dinoflagellates, respectively. In the composition of the

diatom assemblage the share of oceanic forms was nearly negligible, while it was rather significant for dinoflagellates (about 27 %). The presence of typical benthic species (13 %) also contributed to the neritic character of the diatom assemblage.

### *The horizontal distribution of the cell numbers and biomass*

There were three zones of elevated densities of microalgal cells in the study area (Fig. 2a). The first one was located off the south-eastern coast of Severny, the northern island of the Novaya Zemlya Archipelago. The second was found at the north-western side of the Yamal Peninsula, and the third at the western margin of the Ob-Enisei Shallows. The horizontal distribution of the microalgal biomass exhibited only one maximum off Novaya Zemlya corresponding with the location of the first zone above (Fig. 2b). The biomass distributions drawn separately for dinoflagellates (Fig. 3a) and diatoms (Fig. 3b) repeated in general that of the total community biomass, and, therefore, the population maxima of both groups overlapped in the study area. However, the dinoflagellate population accounted here for less than 20 % of the total biomass.

### Ecological regions of the study area

Clustering of the stations on the basis of their floristic similarity revealed (on the level of the similarity coefficients exceeding 40 %) three large groupings of stations (Fig. 4). Superimposed on the map, these results subdivided the study area into four large floristic regions IA, IB, II and III (Fig. 5), which differed with the composition of the microalgal assemblages. The distribution of the regions exhibited a characteristic “layered” structure, typical for distributions of most physical and chemical variables in the south-western Kara Sea (Kuznetsov 1997).

### The composition and distribution of the microalgal assemblages

At the level of the similarity coefficients  $\geq 50\%$ , three algal assemblages are delimited (Fig. 6):

(1) *Attheya septentrionalis*, *Chaetoceros diadema*, *Eucampia groenlandica*, *Skeletonema costatum*, *Thalassiosira* cf. *gravidata*, *Cylindrotheca closterium*, *Pseudo-nitzschia delicatissima*, *P. seriata*, *Dinophysis acuminata*, *D. pulchella*, *Gymnodinium arcticum*, *G. fusus*, *G. wulffii*, *Gyrodinium prunus*, *Protoperidinium bipes*, *Zygabikodinium lenticulatum* and *Dinobryon balticum*;

(2) *Chaetoceros decipiens*, *Ceratium arcticum*, *Gyrodinium lachryma*, *Dinophysis arctica*, *P. brevipes*, *P. granii*, *P. pellucidum* and *Scrippsiella trochoidea*;

(3) *Dinophysis norvegica*, *D. rotundata*, *Protoperidinium breve*, *P. ovatum* and *P. monacanthus*.

The first assemblage was dominated by the late spring neritic diatoms and chloroplast-containing dinoflagellates, with heterotrophic dinoflagellates being of secondary significance. In contrast, the heterotrophic dinoflagellates comprised the majority of the second assemblage, while autotrophic forms were represented by only three species: *C. decipiens*, *C. arcticum* and *S. trochoidea*. The third species complex consisted exclusively of armoured heterotrophic dinoflagellates from the genera *Protoperidinium* and *Dinophysis*.

The representatives of assemblages 1 and 2 were most widely distributed over region IA (14 - 17 taxa per station) as well as at station 8 of region IB (7 - 8 taxa per station). In addition, the biomass maxima of nearly all populations belonging to both species complexes (except for *Chaetoceros decipiens*) were located in region I

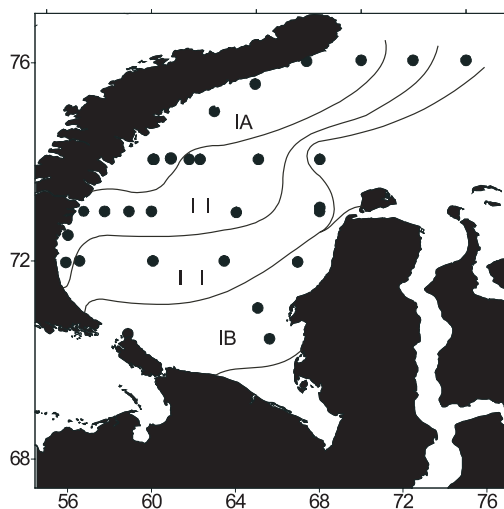


Fig. 5. Floristic regions of the south-western Kara Sea (see text).

(Fig. 7a, b). Since all autotrophic components of the algal community were from the two assemblages, the horizontal distribution of their depth-integrated biomass determined that of the total autotrophs in the study area (Fig. 8a).

At stations 1, 6 and 7 in region IB, there was a partial disappearance of autotrophic taxa, largely diatoms, and only 7 - 8 and 4 - 5 representatives of assemblages 1 and 2 were recorded here at each station. This impoverishment was accompanied by a drastic decline in the algal biomass and by a shift to a dominance of mixotrophic (chloroplast-containing dinoflagellates) and heterotrophic forms. In regions II and III, apart from rare records of algae from assemblage 1 only in region II, the core of the community was formed by representatives of assemblage 2 (4 - 7 species per station).

The entirely heterotrophic small complex of armoured dinoflagellates (assemblage 3) was distributed almost exclusively in region II, exhibiting a biomass maximum at the deepest stations situated above the East Novaya Zemlya Trough (Fig. 7c). This species group consisted of oceanic forms (with the exception of *Dinophysis norvegica*, which is usually called neritic or sometimes panthalassic), and its representatives were encountered only sporadically in the other, shallower areas. Therefore, assemblage 3 seemed to represent an end member of the algal seasonal succession largely characteristic of the deep areas of the Kara Sea.



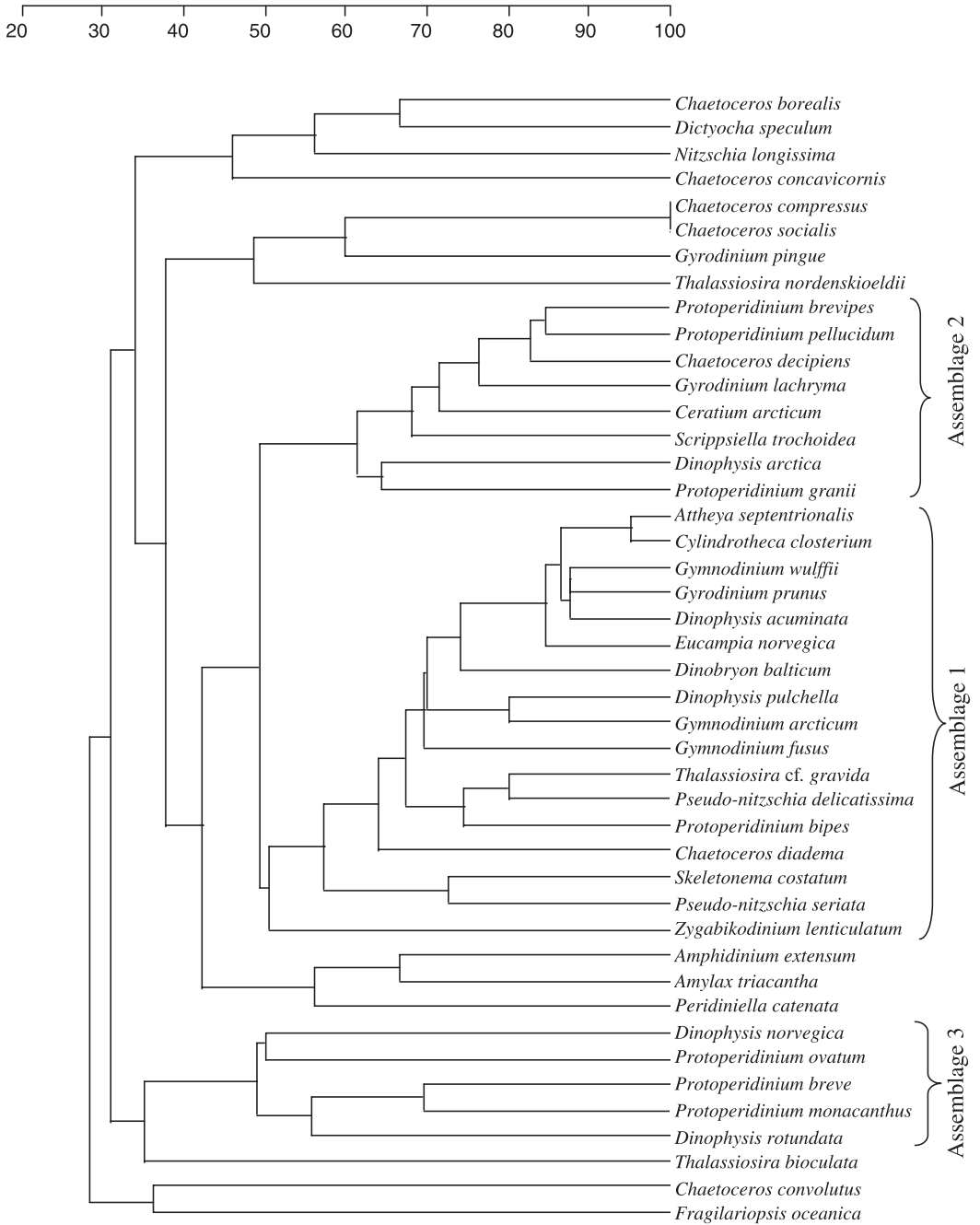


Fig. 6. Algal assemblages in the south-western Kara Sea in August–September 1981.

### Vertical distribution of phytoplankton

The surface values of salinity and temperature ranged widely over the study area—from 14 - 17 ‰

at the easternmost stations up to 31 ‰ in the north-west, and from -0.3 °C at the northern and eastern stations to 8 °C at the southernmost ones (see Shirokolobov 1982). Nonetheless, the main



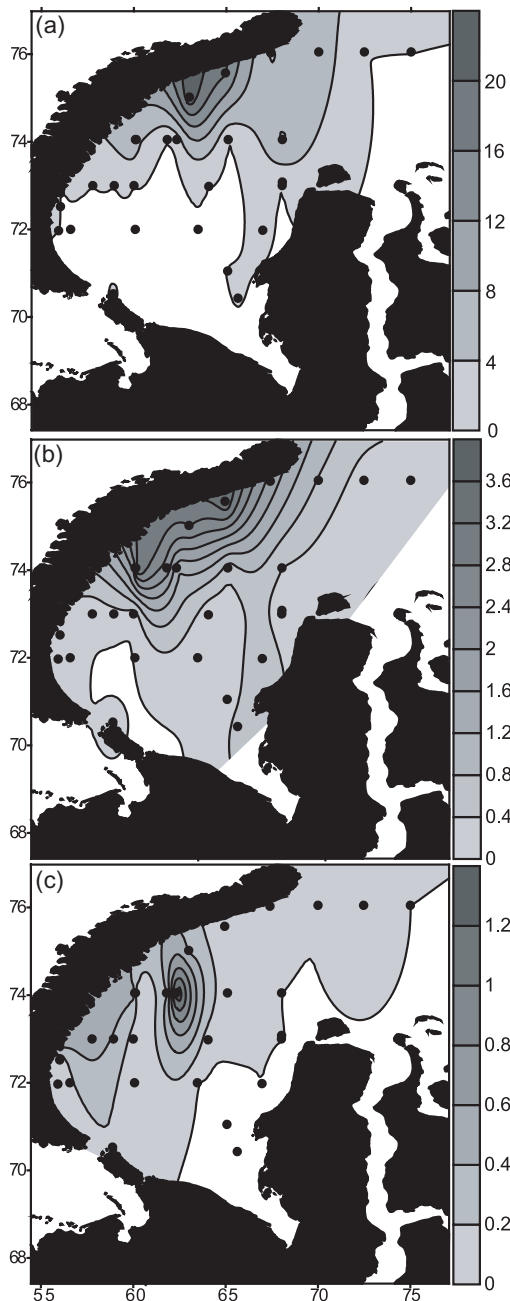


Fig. 7. Horizontal distribution of biomass (g wet weight  $m^{-2}$ ) of the floristic assemblages (a) I, (b) II, and (c) III.

features of the structure of the water column were rather uniform at most stations (except for the shallowest ones). The upper mixed layer did not form, and there was a typical near-surface pycno-

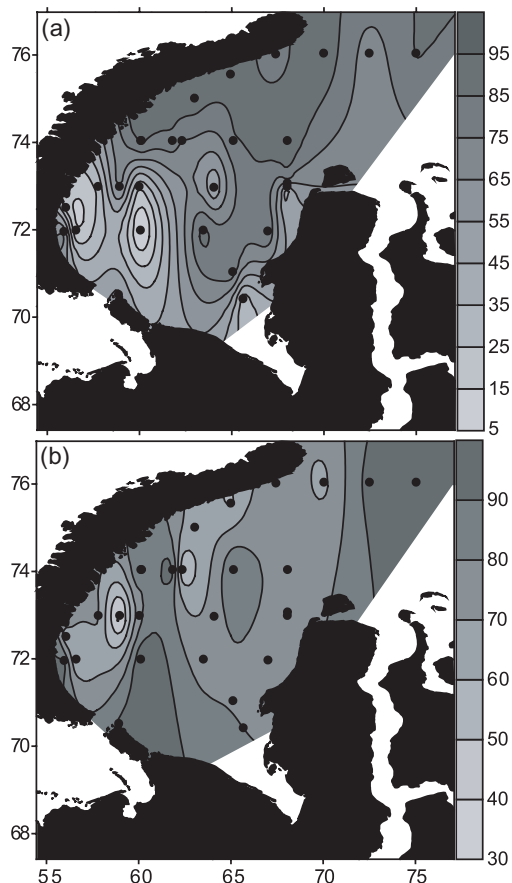


Fig. 8. (a) Relative biomass (%) of autotrophic (including mixotrophic) forms in the top 100 m layer; (b) percentage of algal biomass concentrated in the upper 50 m of the water column.

cline (Fedorov & Ginsburg 1992) with strong vertical gradients of temperature and salinity (Figs. 9-12). At depths of 30 to 50 m, the thermohaline characteristics stabilized with temperatures close to the freezing point ( $-1.7$  to  $-1.9$  °C) and salinity higher than 34 - 34.5 ‰. Such a structure of the water column appeared to play a decisive role in the formation of a pelagic habitat suitable for the development of planktonic algae. With the exception of one station, more than 50 % of the total biomass of the phytoplankton was concentrated within the upper 50 m layer (Fig. 8b). Moreover, for 20 of 28 stations this value exceeded 70 %.

In region IA and station 8 (region IB), where the spring bloom was underway and the phytoplankton biomass was high (up to  $28 g m^{-2}$ ), there were two types of vertical distribution of biomass, with one (surface) or two (surface and subsur-

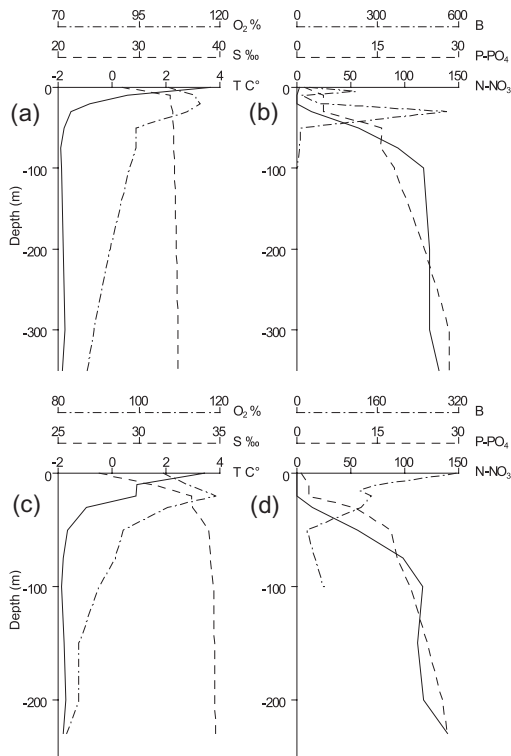


Fig. 9. For station 25, region IA: (a) vertical distribution of temperature ( $T$  °C), salinity ( $S$  ‰) and oxygen ( $O_2$  % of saturation); and (b) vertical distribution nitrate ( $N-NO_3$   $\mu\text{g litre}^{-1}$ ), phosphate ( $P-PO_4$   $\mu\text{g litre}^{-1}$ ), and phytoplankton biomass ( $B$ ,  $\mu\text{g wet weight litre}^{-1}$ ). For station 26, region IA: (c) vertical distribution of temperature, salinity and oxygen; and (d) nitrate, phosphate, and phytoplankton biomass.

face) maxima (Fig. 9). The surface biomass maximum was formed largely by representatives of assemblage 1, consisting of the late spring forms, whereas the subsurface maximum (at the base of the pycnocline at depths of 30 - 50 m) was due to the sinking biomass of the early spring forms, such as *Thalassiosira cf. gravida*, *T. bioculata* and, more rarely, *Fragilariopsis oceanica* and *Navicula vanhoeffenii*, originating from a previous ice edge bloom (Usachev 1968; Druzhkov & Makarevich 1999). Figure 9a illustrates the most pronounced example of the subsurface maximum, which at most stations had lower biomass than the surface maximum or was not present (Fig. 9b). The low surface concentrations of nutrients evidenced high previous activity of algal populations and possibly a conclusive phase of the phytoplankton bloom. The location of the lower boundary of the nutriclines was much deeper than that

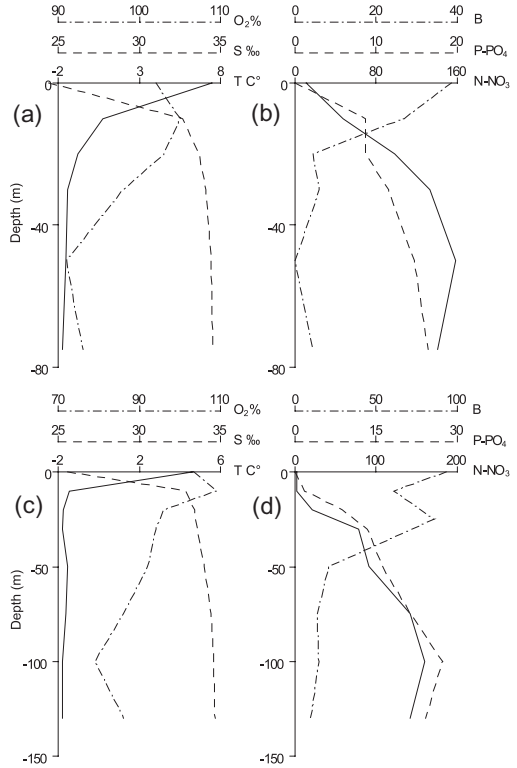


Fig. 10. For station 1, region IB: (a) vertical distribution of temperature ( $T$  °C), salinity ( $S$  ‰) and oxygen ( $O_2$  % of saturation); and (b) vertical distribution nitrate ( $N-NO_3$   $\mu\text{g litre}^{-1}$ ), phosphate ( $P-PO_4$   $\mu\text{g litre}^{-1}$ ), and phytoplankton biomass ( $B$ ,  $\mu\text{g wet weight litre}^{-1}$ ). For station 8, region IB: (c) vertical distribution of temperature, salinity and oxygen; and (d) nitrate, phosphate, and phytoplankton biomass.

of the pycnocline, possibly due to consumption by the sinking biomass of the ice edge bloom. Stabilization of nutrient concentrations occurred at a depth of about 100 m, suggesting the development of active photosynthetic (and possibly bacterial) processes at the base of the pycnocline and even in deeper layers. The layer with the highest oxygen saturation values, indicating most active algal photosynthesis, was situated from the middle to lower portions of the pycnocline, and very rarely at the surface. With the exception of the shallowest stations, the same tendencies in the vertical distributions of nutrients and oxygen were characteristic for the rest of the study area.

In region IB, the phytoplankton biomass was lower than in region IA by one order of magnitude (Fig. 10), indicating that the bloom was declining here. The exception was at station 8, where the taxonomic composition was most simi-

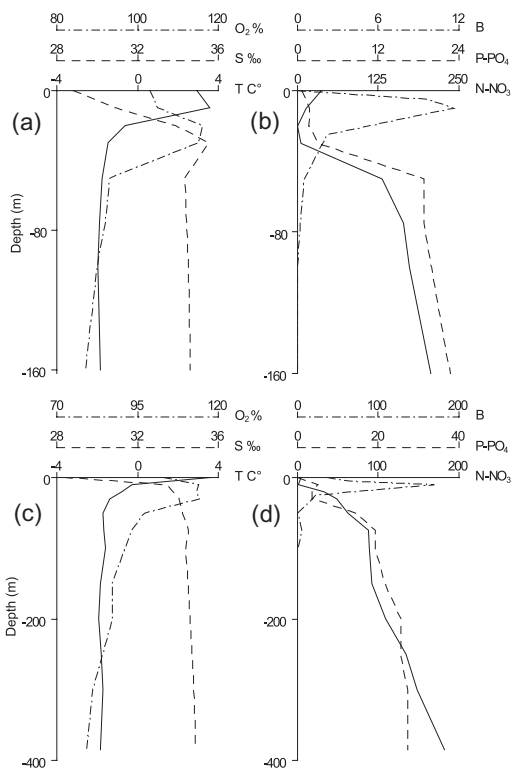


Fig. 11. For station 12, region II: (a) vertical distribution of temperature ( $T$  °C), salinity (S ‰) and oxygen ( $O_2$  % of saturation); and (b) vertical distribution nitrate ( $N-NO_3$   $\mu\text{g litre}^{-1}$ ), phosphate ( $P-PO_4$   $\mu\text{g litre}^{-1}$ ), and phytoplankton biomass (B,  $\mu\text{g wet weight litre}^{-1}$ ). For station 24, region II: (c) vertical distribution of temperature, salinity and oxygen; and (d) nitrate, phosphate, and phytoplankton biomass.

lar to region IA and the phytoplankton biomass was higher than in the rest of the area. The subsurface biomass maximum was found only at this station and, similar to the north-western areas, it formed due to the sinking biomass of *Thalassiosira* spp. (mainly *T. bioculata* and *T. nordenskiöldii*).

The stations of region II were characterized by a typical subsurface biomass maximum and, in most cases, rather low algal biomass (less than  $50 \mu\text{g litre}^{-1}$ ; Fig. 11a). At stations with higher biomass maximum (up to  $170 \mu\text{g litre}^{-1}$ ; Fig. 11b), it was generated largely by one species, *Chaetoceros decipiens*. Still lower biomass was observed in region III, characterized by a predominance of heterotrophic dinoflagellates (Fig. 12). Their biomass maxima were located either at the surface or in deeper (down to 50 m) layers, but they seemed to be of a stochastic nature and orig-

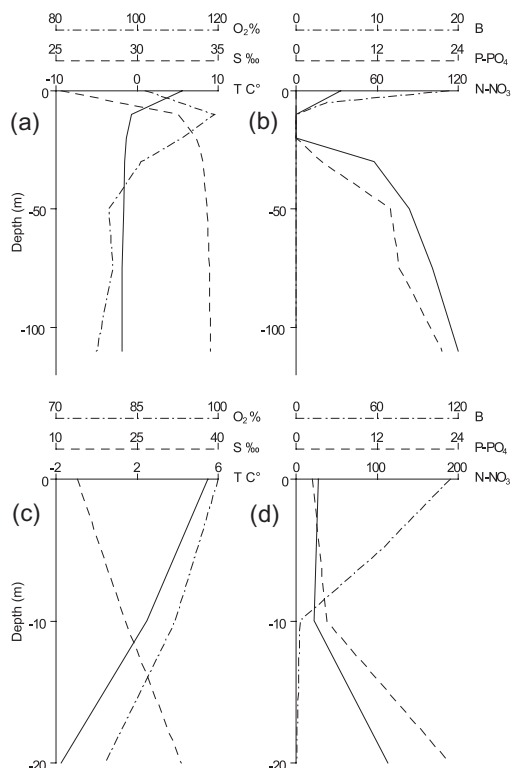


Fig. 12. For station 10, region III: (a) vertical distribution of temperature ( $T$  °C), salinity (S ‰) and oxygen ( $O_2$  % of saturation); and (b) vertical distribution nitrate ( $N-NO_3$   $\mu\text{g litre}^{-1}$ ), phosphate ( $P-PO_4$   $\mu\text{g litre}^{-1}$ ), and phytoplankton biomass (B,  $\mu\text{g wet weight litre}^{-1}$ ). For station 20, region III: (c) vertical distribution of temperature, salinity and oxygen; and (d) nitrate, phosphate, and phytoplankton biomass.

inated from random variations in the extremely low biomass.

## Discussion

Recently, Druzhkov & Makarevich (1999) demonstrated that the south-western Kara Sea (together with the Pechora Sea) is a floristic entity: the Novaya Zemlya Phytogeographic Province. The floristic regions established in the present work are to be interpreted as the areas occupied by the microphytoplankton community during different stages of the seasonal succession and, correspondingly, the microalgal groupings as seasonal assemblages changing in the course of the phytoplankton growth season.

The growth season in the Arctic pelagic zone starts with the late winter—early spring bloom by

the cryoflora (Horner 1989; Cota & Smith 1991; Cota et al. 1991; Horner et al. 1992; Gradinger 1998), followed by the ice edge phytoplankton bloom (Alexander 1980; Rey & Loeng 1985; Rey et al. 1987; Skjoldal et al. 1987; Smith 1987; Harrison & Cota 1991; Druzhkov, Druzhkova et al. 2001). The ice was entirely absent in the south-western Kara Sea during our study; therefore, we missed the early stages of the seasonal succession in the surface layer. Indeed, in August–September of 1981 rare isolated ice floes were observed only at the northernmost point of Novaya Zemlya, and the rest of the study area was entirely ice-free (D. V. Shirokolobov, pers. comm.). The sinking ice edge bloom, mostly populations of *Thalassiosira* cf. *gravidata* and *T. bioculata*, was found only at stations off the north-eastern coast of Novaya Zemlya in the 20 - 75 m layer (region IA). This biomass sometimes formed a clear subsurface maximum of chlorophyll *a* (Bobrov et al. 1989). In the surface layer, the major portion of the pelagic autotrophs consisted of arcto-boreal late spring neritic diatoms and autotrophic dinoflagellates. The biomass maxima of most armoured heterotrophic dinoflagellates, e.g. *Dinophysis* spp. and *Protoberidinium* spp., were also located in this area.

Region IB, located in the southernmost portion of the study area, was populated by a seasonally “older” phytoplankton assemblage. Although the taxonomic composition here was similar to that in region IA, the cell numbers and phytoplankton biomass were much lower. Obviously, region IA was cleared of ice cover only recently when it was sampled, and here we found the earliest stage of the seasonal succession in the study area (assemblage 1). It undoubtedly corresponds to the late spring bloom in the sense of Usachev (1968), which forms after the ice cover is gone, the marginal ice zone retreats and the ice edge bloom sinks. This is confirmed by the significant role played by the cosmopolitan and oceanic forms in the composition of the diatom and dinoflagellate assemblages characteristic of the late spring period. In contrast, the early spring (ice edge) blooms in the Kara and other Siberian seas are formed almost exclusively by the arcto-boreal neritic flora (Usachev 1968; Druzhkov & Makarevich 1999). The late spring phytoplankton bloom is fuelled by continental run-off (Druzhkov, Grönlund et al. 1997; Kuznetsov, Grönlund et al. 1997), well evidenced by the near-shore local maxima in regions IA and IB. In the latter case, it might also

be initiated by the coastal upwelling which has been reported for the western coast of the Yamal Peninsula (Kuznetsov 1997).

The composition of pelagic microalgae in region II was of an intermediate character, with rather low biomass and co-dominance of diatoms and dinoflagellates. The phytoplankton community was obviously declining in region III. The cell numbers and biomass of pelagic algae here were very low, and their composition was dominated by heterotrophic dinoflagellate species from the genera *Dinophysis* and *Protoberidinium*. In summer the central portion of the study area (the core of the large cyclonic gyre of the south-western Kara Sea) is strongly depleted in nutrients (Kuznetsov, Bardan et al. 1998) and, therefore, depopulated with phytoplankton. The dominance of heterotrophic dinoflagellates evidenced intense heterotrophic processing of organic matter by microplankton populations developing in the pelagic zone toward the end of the phytoplankton growth season (Druzhkov & Druzhkova 1999). During the study period, just in this area the surface chlorophyll *a* concentrations and surface primary production were minimal, less than 0.25 mg m<sup>-3</sup> and 0.1 mg C m<sup>-3</sup> h<sup>-1</sup>, respectively (Bobrov et al. 1989). This stage of the seasonal succession may be designated, after Usachev (1968), as the summer minimum. The autumn phytoplankton bloom in the Siberian shelf seas does not form because of unfavourable light conditions in the period of degradation of the seasonal stratification. We conclude that the annual cycle of the phytoplankton in the south-western Kara Sea consists of three seasonal stages: (1) ice edge (early spring) bloom; (2) late spring bloom; and (3) summer minimum, followed by autumnal decline of the community.

It is possible that in the study area the late spring bloom stage develops only in coastal waters and does not really occur in the central deep-water region, located above the eastern Novaya Zemlya Trough and not influenced directly by continental run-off.

As in the case of chemical parameters (see, e.g. Kuznetsov 1997), the biological structure of the pelagic zone in south-western Kara Sea exhibits a characteristic “layered” structure, evidently following the routes of receding marginal ice zones. The main directions of the spring ice migration in the area of interest are to the north and north-east (Usachev 1968). As can easily be seen in Figs. 2, 3 and 5, the earlier stages of the seasonal suc-

cession were located in just these directions (presumably migrated before sampling). This all is in accord with the concept of structuring of the pelagic zone by the freezing–melting cycles of the ice cover in polar seas (Eicken 1992). Even after its disappearance, the ice cover retains a key role in influencing the phytoplankton seasonal succession.

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