Findings of new phytoplankton species in the Barents Sea as a consequence of global climate changes

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Over the past few decades, the Earth's climate has been characterized by a stable increase in temperature, which in many regions leads to a change in the composition of flora and fauna. A striking manifestation of this process is the appearance in ecological communities of new, uncharacteristic for them, species of animals and plants. One of the most productive and at the same time the most vulnerable in this respect are the marine ecosystems of the Arctic. This article is devoted to the analysis of findings of vagrant phytoplankton species in the Barents Sea, a body of water experiencing especially rapid warming due to an increase in the volume and temperature of incoming Atlantic water. For the first time, fundamental questions are considered: how widely these species are distributed over the Barents Sea area, and in what seasons do they reach high levels of abundance.

The material for the present work was planktonic collections made during expedition surveys of 2007-2019 in different seasons throughout the Barents Sea. The water samples were taken using a rosette Niskin bottle sampler. The plankton net with a 29 μm mesh size was applied for filtering. The obtained material was processed according to standard hydrobiological methods and followed by subsequent microscopy for taxonomic identification of organisms and cell counting.

The results of our observations show that vagrant microplankton species do not create a stable population that persists throughout the annual development cycle. Their major presence is noted in the autumn-winter period, the smallest – in the summer. The distribution of invaders is strictly tied to warm jets of currents, while the weakening of the inflow of Atlantic water masses deep into the Barents Sea from the west is a limiting factor for their penetration into its eastern part. The southwestern and western parts of the basin are characterized by the most significant number of floristic finds; from here, towards the north and east, their number decreases. It can be concluded that at present the proportion of vagrant species in the Barents Sea, both in species diversity and in the total biomass of the algocenosis, is insignificant. They do not change the structure of the community as a whole, and their presence does not have any negative impact on the ecosystem of the Barents Sea pelagic. However, at this stage of research, it is too early to predict the environmental consequences of the phenomenon under study. Given the growing number of recorded cases of finds of species uncharacteristic for the Arctic, there is a possibility that this process may disrupt the biological stability of the ecosystem and even lead to its destabilization.

1 # Findings of new phytoplankton species in the Barents
2 # Sea as a consequence of global climate changes

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16 ## Abstract

17 **Background**: Over the past few decades, the Earth's climate has been characterized by a stable
18 increase in temperature, which in many regions leads to a change in the composition of flora and
19 fauna. A striking manifestation of this process is the appearance in ecological communities of
20 new, uncharacteristic for them, species of animals and plants. One of the most productive and at
21 the same time the most vulnerable in this respect are the marine ecosystems of the Arctic. This
22 article is devoted to the analysis of findings of vagrant phytoplankton species in the Barents Sea,
23 a body of water experiencing especially rapid warming due to an increase in the volume and
24 temperature of incoming Atlantic water. For the first time, fundamental questions are considered:
25 how widely these species are distributed over the Barents Sea area, and in what seasons do they
26 reach high levels of abundance.
27 **Methods**: The material for the present work was planktonic collections made during expedition
28 surveys of 2007-2019 in different seasons throughout the Barents Sea. The water samples were
29 taken using a rosette Niskin bottle sampler. The plankton net with a 29 μm mesh size was
30 applied for filtering. The obtained material was processed according to standard hydrobiological
31 methods and followed by subsequent microscopy for taxonomic identification of organisms and
32 cell counting.
33 **Results**: The results of our observations show that vagrant microplankton species do not create a
34 stable population that persists throughout the annual development cycle. Their major presence is
35 noted in the autumn-winter period, the smallest – in the summer. The distribution of invaders is
36 strictly tied to warm jets of currents, while the weakening of the inflow of Atlantic water masses
37 deep into the Barents Sea from the west is a limiting factor for their penetration into its eastern
38 part. The southwestern and western parts of the basin are characterized by the most significant
39 number of floristic finds; from here, towards the north and east, their number decreases. It can be

40 concluded that at present the proportion of vagrant species in the Barents Sea, both in species
41 diversity and in the total biomass of the algocenosis, is insignificant. They do not change the
42 structure of the community as a whole, and their presence does not have any negative impact on
43 the ecosystem of the Barents Sea pelagic. However, at this stage of research, it is too early to
44 predict the environmental consequences of the phenomenon under study. Given the growing
45 number of recorded cases of finds of species uncharacteristic for the Arctic, there is a possibility
46 that this process may disrupt the biological stability of the ecosystem and even lead to its
47 destabilization.

48 **Introduction**

49   One of the most important fields of bio-oceanology in recent decades has been the study
50 of modern climatic changes and their consequences for marine ecosystems (*Comiso & Hall,*
51 *2014; Dong et al., 2020*). The manifestation of this process is that the increased temperature
52 might make it possible for new species to colonize new areas after being transported with the
53 currents (*Reid et al., 2007*).

54   This phenomenon is especially important in Arctic pelagic ecosystems, which are the
55 most productive and, at the same time, the most vulnerable from an ecological point of view
56 (*Fermandez, Kaiser & Vestergaard, 2014*). It is at high latitudes that natural variations in
57 climatic parameters reach their maximum extent, in particular, water temperatures in the Arctic
58 Ocean are rising faster than in other parts of the globe, and this trend is expected to intensify in
59 the coming century (*IPCC, 2013*). At the same time, even relatively small changes in the natural
60 environment can go beyond the adaptive capacity of some species of flora and fauna, which will
61 inevitably lead to serious disturbances, both in individual communities and in the ecosystem as a
62 whole (*Fermandez, Kaiser & Vestergaard, 2014*).

63   In the Barents Sea, the described process is named by specialists as "Atlantification"
64 (*Årthun et al., 2012; Bagøien et al., 2018*). Since the 1980s, under the influence of global climate
65 change, this water body has been undergoing a rapid warming trend (*Ingvaldsen & Loeng, 2009*).
66 This is due to changes in the hydrological parameters of the Barents Sea as a result of the
67 increased volume and temperature of incoming Atlantic water (*Neukermans, Oziel & Babin,*
68 *2018*). Oceanic currents and increased water temperature directly contribute to the establishment
69 of vagrant species in new water areas for them (*Occhipinti-Ambrogi, 2007; Sorte, Williams &*
70 *Zerebecki, 2010*). But only a fraction of them can adapt to their new environments (*Crooks &*
71 *Soulé, 1999; Mack, Simberloff & Lonsdale, 2000*). Examples include northward and the eastward
72 expansion of the ranges of Barents Sea crab populations: snow crab *Chionoecetes opilio* and king
73 crab *Paralithodes camtschaticus* (*Starikov et al., 2015; Spiridonov & Zalota, 2017; Zalota,*
74 *Spiridonov & Vedenin, 2018*). The same climatic changes are thought to result in a shift to the
75 north and east of the sea of the boundaries separating warm-water and cold-water Decapoda
76 complexes (*Zimina et al., 2015*) and boreal and arctic fish species communities (*Fossheim et al.,*
77 *2015; Bagøien et al., 2018*).

78   But most of all, the increased inflow of Atlantic waters and warming affect the structure
79 of pelagic algocenoses, causing changes in their taxonomic composition due to the penetration of

80   new species of tropical and tropical-boreal origin (*Oleinik, 2014; Ardyna & Arrigo, 2020;*
81   *Ardyna et al., 2020; Wang et al., 2018*). A number of our papers have detailed findings of
82   vagrant microplankton species in the Barents Sea (*Oleinik, 2014; Makarevich & Oleinik, 2017;*
83   *Makarevich & Oleinik, 2020*). However, these publications lack information on how widely
84   these species spread over the water body, how long they remain in the Barents Sea pelagic zone
85   throughout the year, and in which seasons they reach high abundance levels. The purpose of this
86   article was to analyze the materials obtained to answer these questions to estimate the scale of
87   possible changes in the structure of phytoplankton communities. Its results are of paramount
88   importance for predicting negative consequences for the Arctic marine ecosystems as a whole.

Materials & Methods

90   The material for the present work was planktonic collections made during expedition
91   surveys of 2007-2019 in different seasons throughout the Barents Sea (*Makarevich & Oleinik,*
92   *2020*). The scheme of sampling stations is shown in the figure (Fig. 1). Dates, time, sampling
93   coordinates, depths at the points of hydrobiological work are given in the appendix (Appendix
94   A1).

95   The water for phytoplankton samples were taken using a rosette Niskin bottle sampler
96   (Multi Water Sampler ROSETTE HydroBios MWS-12, Germany). Water samples were taken
97   from standard hydrobiological sampling horizons – 0, 5, 10, 25, 50, 100 meters and the bottom
98   layer, according to Recommendations on methods for marine biological studies
99   (*Recommendations..., 1979*). Additionally, a net with a filter cone made of gas with a mesh size
100 of 29 μm was used to catch the entire water layer. CTD profiles were performed at all sampling
101 points. The obtained material was processed according to standard hydrobiological methods:
102 samples of 1-2 L were concentrated using the reverse filtration method to a final volume of 4-5
103 ml; after that, they were fixed with a 40% formaldehyde solution, with final concentration 2-4%
104 (*Dodson & Thomas, 1964*). Fixed net samples of phytoplankton were concentrated by
105 sedimentation method (*Recommendations..., 1979*). After settling the sample in the dark, the
106 water over the settled precipitate was concentrated by dropping it with a thin glass siphon with
107 an upturned end to a volume of 2 ml.

108   For taxonomic identification of organisms and cell counting, a Palmer-Maloney counting
109 chamber was used (*Karlsen, Cusack & Beensen, 2010*). Microscopy study was performed under
110 an AxioImager D1 light microscope (Carl Zeiss, Germany) at 400x magnification. The names of
111 species and systematic groups, as well as phytogeographic characteristics of microalgae, are
112 given according to the nomenclature from electronic sources (*AlgaeBase, 2022; WoRMS, 2022*).

113   The dynamics of temperature anomalies in the waters of the Barents Sea is given on the
114 basis of year-round observations on the standard oceanographic section "Kola Meridian"
115 (*PINRO, 2023*). The standard oceanographic section "Kola Meridian" is located in the Barents
116 Sea to the north of the Kola Bay along 33°30′E from 69°30' to 77°00′N and it consists of 16
117 stations (Fig. 1). Its length is 450 miles. Depth at stations varies from 150 m to 310 m and
118 averages 245 m (Appendix A1). The stations of the section are located in the area of following
119 waters distribution: The Coastal and Main branches of the Murmansk and Central branches of

120   the North Cape currents (*Ozhigin et al., 2011*), i.e. the section crosses all the main water masses
121   of the Barents Sea in terms of its genesis – coastal, Atlantic and Arctic.

122   **Results**

123   In the period from 2007 to 2019, microalgae that had not previously been found in this
124   water body, or their findings were considered questionable, were found in the Barents Sea. The
125   list of species is given in Table 1. It includes 17 representatives of phytoplankton, of which 16
126   are dinoflagellates (Class Dinophyceae), and 1 is a diatom alga *Proboscia indica* (Class
127   Bacillariophyceae). See Appendix A2.

128   Figure 2 shows the scheme demonstrating the distribution of vagrant species detection
129   sites in the studied water area. The dense location of sampling stations, repeatability of surveys
130   at the same points in different years, and coverage of almost the entire area of the Barents Sea
131   allow to reliably draw borders of areas with different degrees of their occurrence.

132   Most of these invaders are common components of pelagic algocenoses of the seas of the
133   North Atlantic Basin. The diatom *Proboscia indica* is known from the Norwegian and North
134   Seas (*Nehring, 1998*), characterized as a thermophilic species, subtropical and boreal (*Hendey,*
135   *1964*). The boreal species *Amphidoma caudata*, the tropical-boreal *Corythodinium diploconus*,
136   *Dinophysis hastata*, *Mesoporos perforatus*, *Pseudophalacroma nasutum*, *Oxytoxum caudatum*,
137   *Podolampas palmipes,* and the tropical *Heterodinium milneri* are widely distributed in coastal
138   waters of Britain and Norway (*Okolodkov, 2000*). The boreal species *Protoperidinium laticeps*
139   was described from the waters of West Greenland (*Grøntved & Seidenfaden, 1938*) and
140   subsequently found in the Norwegian and Baffin Seas, temperate and subtropical regions of the
141   Northeast Atlantic (*Okolodkov, 2000*). The tropical-boreal *Pyrophacus horologicum* has been
142   noted in the Norwegian, White, and Baltic Seas (*Okolodkov, 2000; Hällfos, 2004*). The
143   dinoflagellate *Spatulodinium pseudonoctiluca*, also of tropical-boreal origin, has a wide range: it
144   is registered in the Northern and Baltic Seas, as well as in the Kara Sea and the Arctic Ocean
145   (*Kiselev, 1950; Dodge, 1982; Druzhkov & Makarevich, 1999; Wasmund et al., 2015*). The
146   species *Protoperidinium thulesense* is characterized as Pan-Arctic (*Okolodkov, 1996*): it was
147   observed in the White and Kara Seas, as well as in the Japan and boreal zone of the Pacific
148   Ocean (*Abé, 1981; Konovalova, 1998; Matsuoka et al., 2006*). Another group of microalgae:
149   boreal *Ceratium strictum*, tropical-boreal *Dinophysis ovata* and *Protoperidinium brochii*, and
150   *Gotoius mutsuensis* of unidentified origin are now reliably known only from materials from the
151   Black Sea and the Mediterranean (*Kiselev, 1950; Gómez, 2003; Krakhmal'niy, 2011*).

152   A comparison of the selected sites in terms of the number of finds of vagrant species
153   demonstrates the unconditional leadership of area A_1, in which all the vagrant species were
154   found and the maximum number of their registrations was observed (Fig. 2). Here also the
155   greatest values of the numbers reached by several organisms are marked. The second place is
156   occupied by area B_2 vagrant phytoplankters. Only one microalga, *Oxytoxum caudatum*, was
157   found in the water area of the other sites.

158   This species deserves special attention. It is present in the pelagic zone for almost the
159   entire period of studies, in all seasons, and throughout the water areas of regular and attenuated

160   occupation. Its populations reach concentrations an order of magnitude higher than those of other
161   vagrant organisms. It can be assumed that *Oxytoxum caudatum* is the only representative of
162   algoflora not typical of the Barents Sea, which has been adapting to new environmental
163   conditions in the initial stage.
164   The distribution of the number of finds by year is as follows. The maximum number of
165   encounters – 11 – is characterized by 2013, followed by 2014 – 5 cases, 2012, 2015, 2016, and
166   2019 – 4 registrations each, 2017 – 2 findings, 2007, 2010, and 2018 – 1 encounter each. A
167   similar comparison of the number of omnivore sightings by month shows this pattern. The
168   highest number of them (21) is in November, the other seasons are much less rich: June – 6
169   cases, April – 4, July, September and December – 2, January, August, and October – 1 (see Tab.
170   1). During the other periods of the year, no vagrant species of microalgae were detected in the
171   Barents Sea pelagic zone. However, it should be taken into account, that in February-March,
172   under-ice vegetation occurs in all Arctic seas (*Ardyna et al., 2020*), and in May, a peak of spring
173   phytoplankton bloom forms near the ice edge during the period of ice melting (*Perrette et al.*
174   *2011*); during these phases of the annual successional cycle, diatoms absolutely dominate in the
175   composition of alcogeoses, and the proportion of dinoflagellates is extremely low (*Makarevich,*
176   *Druzhkova & Larionov, 2012*).
177   It is also important to note that, based on the results of many years of research, it was found
178   that in the Barents Sea pelagic, according to the phytogeographic characteristics, approximately
179   40% of microalgae taxa are arcto-boreal species, 30% are cosmopolitan and 20 are boreal
180   (*Makarevich & Druzhkova, 2010*). As part of the new finds, most organisms are representatives of
181   the tropical-boreal and boreal algoflora, and a small number – are tropical and bipolar. Previously,
182   no species of tropical-boreal and tropical origin were recorded in the Barents Sea (*Matishov et el.,*
183   *2000; Makarevich & Druzhkova, 2010*).

Discussion

185   As already noted, the main indicator of the dynamics of climatic factors is seawater
186   temperature. We have at our disposal a multiyear series of year-round observations of
187   hydrological parameters, in particular temperature, on the standard oceanographic transect "Kola
188   Meridian" (Fig. 3). The series of observations are given from the site of Polar branch of the
189   FSBSI "VNIRO" PINRO named after N.M. Knipovich. Their analysis indicates a clear increase
190   in the advection of warm waters from the Atlantic to the Barents Sea in recent decades, which is
191   the main reason for the appearance of vagrant species in the Barents Sea waters. The second way
192   of transfer of vagrant organisms is anthropogenic activity, but for phytoplankton representatives
193   in the seas of the Arctic basin, reliable cases of such introduction are currently unknown
194   (*Stachowicz et al., 2002; Padilla & Williams, 2004*).
195

196   The inflow of Atlantic water masses into the Barents Sea occurs due to constant (non-periodic)
197   currents, which together form a relatively stable circulation system within the reservoir (Fig. 2).
198   These currents determine the general distribution of water masses in the Barents Sea water area
199   and its water exchange with the adjacent areas (*Potanin, Denisov & Ershtadt, 1985*). On the

200   western border, this water exchange is carried out with the Norwegian and Greenland Seas.
201   Through the largest strait, between the island of Medvezhiy and the mainland. The largest strait
202   between Medvezhiy and the mainland (Nordkapp), water flows from the Norwegian Sea to the
203   Barents Sea through two currents – the Norwegian Atlantic Current and the Norwegian Coastal
204   Current. Through another strait on the western border, between South Cape Island (Sørkapp –
205   Norwegian name; Svalbard archipelago) and Bear Island, the South Svalbard Current enters the
206   Barents Sea from the Norwegian Sea. The Norwegian Atlantic Current in the Barents Sea area is
207   divided into several streams, passing further in the northern and eastern directions (*Matishov,*
208   *Matishov & Moiseev, 2009*). The Northern Branch, following the Nadezhda Trough, divides into
209   smaller streams that move northward to the west of the Perseus Plateau and eastward between
210   the Perseus Plateau and the Central Bank (*Loeng, 1991*). Another part of the Northern Branch,
211   deviating westward, forms a flow along the western edge of the Medvezhiyski Trough, directed
212   into the Norwegian Sea (*Gawarkiewicz & Plueddemann, 1995*). Norwegian Coastal Current
213   extends eastward and appears in the Demidovsky Trough and above the Central Upland
214   (*Boytsov, 2006*). The Nordkapp South Current runs deep into the Barents Sea and divides into
215   the Murmansk Current and the Murmansk Coastal Current, which flows along the northern and
216   southern slopes of the Murman Rise in an easterly direction (*Hydrometeorology..., 1992*). On the
217   northern boundary of the reservoir, a complex system of surface currents is used to exchange
218   water with the adjacent Arctic Ocean water area.
219   The analysis of Figure 2 reveals a complete coincidence of the current directions (three
220   streams of Atlantic water entering the Barents Sea) and the areas of regular settlement. Area A_1
221   is directly influenced by Barents Sea Branch of the Norwegian Atlantic Current. In areas B_1 and
222   B_2, located near its borders, the speed of these currents is significantly reduced.
223   Area A_2 is the area affected by deep Atlantic water masses from the north, decreasing by
224   the South Spitsbergen Current, which decreases in the nearby areas B_3 and B_4 (as well as in area
225   B_2). In the eastern part of the Barents Sea, although there is an inflow of warm waters with jets
226   of the Novaya Zemlya current, it is already too weak, and therefore invaders are not found in this
227   area. Thus, there is a clear connection: the weakening of the currents leads to a decrease in the
228   number of finds of vagrant species up to their complete disappearance. As a result, a completely
229   natural situation is observed, when the richest in the number of vagrant species and registered
230   encounters in area A_1, in which all 17 species are found. Area B_2, containing 5 representatives of
231   vagrant algoflora, is under the influence of two less strong flows, and only one species of
232   *Oxytoxum caudatum* is found in the other selected areas. Characteristically, this microalga
233   reaches maximum concentrations (300-400 cells/l) in area A_1, being present throughout the
234   studied water area during the entire period of research.
235   It should also be noted that the indicated abundance values of *Oxytoxum caudatum* were
236   observed only in November, and lower, but comparable to the data (50-200 cells/l) – in April-
237   May (Table 1), and only on one depth level 200 m. At the same time, in the winter season
238   (November-December), this species was often included in the composition of the dominant
239   forms of the phytoplankton community (against the background of low general taxonomic

240 diversity and low concentrations of organisms), and in some cases it was the only dominant
241 (Appendix A2). Among the other algae reaching relatively high abundance levels (more than 20
242 cells/l), these were recorded in one month of the year, also predominantly in November (Table
243 1). At the same time, the rarest (single) findings were recorded in June (*Gotoius mutsuensis*),
244 July (*Spatulodinium pseudonoctiluca*), and also in November (*Heterodinium milneri,*
245 *Pseudophalacroma nasutum*).
246   It should be emphasized that during the entire period of our research, the phytoplankton
247 community in each hydrological season was represented by a microalgae complex, a set of
248 dominants, and quantitative characteristics standard for a particular vegetation phase
249 (*Makarevich, Druzhkova & Larionov, 2012*). The indicators of introduced species development
250 were relatively stable from year to year, and the observed intra-annual fluctuations in the number
251 of individual species corresponded to seasonal levels of abundance of algocenoses (*Hopes &*
252 *Mock, 2015*). Thus, in no area do vagrant species create a stable population that would persist for
253 a long period (at least one stage of the annual successional cycle). There is only their temporary
254 presence in the Barents Sea, with the highest concentrations being recorded in the autumn-winter
255 season when active growth has already stopped, and the lowest in summer. This fact can most
256 likely be explained by the fact that it is November when the maximum volume of Atlantic water
257 enters the water body (*Ingvaldsen, Asplin & Loeng, 2004a; Ingvaldsen, Asplin & Loeng, 2004b*).
258   The comparison of the number of the omnivore finds in different years shows that their
259 maximum number is in 2013, the years 2012 and 2014-2016, as well as 2019, are less rich in the
260 number of encounters, the periods from 2007 to 2011, 2017 and 2018 are represented only by
261 isolated cases. The graph of temperature anomalies in the "Kola Meridian" oceanographic
262 transect (Fig. 3) shows that the interval from 2012 to 2016 is characterized by high positive
263 values of this indicator (with a peak in 2013), while the previous and subsequent periods are
264 negative. This relationship strongly indicates that increased water temperature is a necessary
265 condition for the adaptation of warm-water species in the Arctic basin, in particular, in the
266 Barents Sea.
267   The process of organism's introduction includes a donor region, a vector, a corridor, a
268 recipient region, a candidate species, and many factors that impede this process. All of these
269 parameters are important in understanding the success or failure of a non-native species.
270 However, characteristics of the recipient area, such as low species diversity, climate change,
271 which are often considered to facilitate the process of introduction into terrestrial ecosystems,
272 may be of much less importance in the marine environment; on the contrary, the role of the
273 vector and the corridor can be underestimated (*Boudouresque & Verlaque, 2012*).

Conclusions

275   Overall, the data presented suggest that the distribution of vagrant microphytoplankton
276 species in the Barents Sea is tied to the warm currents coming from the Atlantic Ocean. The
277 weakening force of these water masses penetrating deep into the Barents Sea from the west turns
278 out to be the main factor limiting the presence of vagrant species in the eastern part of the
279 reservoir. As a result, the southwestern and western parts of the water area are characterized by

280 the greatest number of floristic findings, and further to the north and east the number of such
281 species decreases. The maximum diversity of this group of organisms is confined to the warmest
282 years when the inflow of Atlantic water masses increases.
283   At present, the share of pelagic microalgae new to the Barents Sea in the total taxonomic
284 diversity is insignificant. There is no mass development of them in any season of the year, they
285 do not form high biomasses and do not change the community structure as a whole. As a result,
286 their appearance does not lead to the destabilization of planktonic algocenoses themselves and
287 does not have any negative impact on other components of the Barents Sea pelagic ecosystems.
288   Nevertheless, at this stage of research, it is too early to predict the ecological
289 consequences of the occurrence of vagrant microalgae species in Arctic waters. Moreover, taking
290 into account the increasing number of recorded finds of phytoplankton representatives
291 uncharacteristic for the Arctic, we can assume that if the positive temperature trend persists, the
292 process of occupation will increase its intensity. In this case, negative consequences are possible:
293 changes in the community structure, oppression of native species, and decrease in biological
294 stability of pelagic ecosystems.

References

295 **References**
296   1. Abé TH. 1981. Studies of the family Peridinidae an unfinished monograph of the armoured
297   dinoflagellata. *Publications of the Seto Marine Biological Laboratory. Special Publication*
298   *Series* 6:1-409.

299   2. AlgaeBase. 2022. World-wide electronic publication, National University of Ireland,
300   Galway. *Available at http://www.algaebase.org* (accessed on 05.12.2022).

301   3. Ardyna M, Arrigo K. 2020. Phytoplankton dynamics in a changing Arctic Ocean. *Nature*
302   *Climate Change* 10:892-903.

303   4. Ardyna M, Mundy CJ, Mayot N, Matthes LC, Oziel L, Horvat C, Leu E Assmy P, Hill V,
304   Matrai PA, Gale M, Melnikov IA, Arrigo KR. 2020. Under-ice phytoplankton blooms:
305   Shedding light on the "invisible" part of arctic primary production. *Front. Mar. Sci.*
306   7:608032. DOI: 10.3389/fmars.2020.608032.

307   5. Årthun MA, Eldevik T, Smedsrud LH, Skagseth O, Ingvaldsen RB. 2012. Quantifying the
308   influence of Atlantic heat on the Barents Sea ice variability and retreat *Journ. Clim.*
309   25:4736-4743.

310   6. Bagøien E., Benzik A., Bogstad B, Chetyrkin AA, Dalpadado P, Dolgov AV, Eriksen E,
311   Filin AA, Gjøsæter H, Hallfredsson EH, Heldal HE, Johannesen E, Jørgensen LL, Lien V,
312   Klepikovsky RN, Nedreaas K, Prokhorova TA, Prokopchuk IP, Prozorkevich DV, Rey F,

313 Skaret G, Skjoldal HR, Strelkova NA, Russkikh AA, Trofimov AG, Zhilin AYu. 2018.
314 The state and trends of the Barents Sea in 2017. *Interim Report of the Working Group on*
315 *the Integrated Assessments of the Barents Sea (WGIBAR)* 5:69-210.

316 7. Boytsov VD. 2006. *Variability of water temperature in the Barents Sea and its forecasting.*
317 Murmansk: PINRO Publ.

318 8. Boudouresque C, Verlaque M. 2012. An overview of species introduction and invasion
319 process in marine and coastal lagoon habitats. *Cah. Biol. Mar.* 53:309-317.

320 9. Comiso JC, Hall DK. 2014. Climate trends in the Arctic as observed from space. *Wiley*
321 *Interdiscip. Rev. Clim. Change* 5(3):389-409. DOI: 10.1002/wcc.277.

322 10. Crooks KR, Soulé ME. 1999. Mesopredator release and avifaunal extinctions in a
323 fragmental system. *Nature* 400:563-566.

324 11. Dodge JD. 1982. *Marine dinoflagellates of the British Isles.* London: Her Majesty's
325 Stationary Office.

326 12. Dodson AN, Thomas WH. 1964. Concentrating plankton in a gentle fashion. *Limnol. &*
327 *Oceanogr.* 9:455-456.

328 13. Dong K., Kvile ØK, Stenseth NC, Stige LC. 2020. Associations among temperature, sea
329 ice and phytoplankton bloom dynamics in the Barents Sea. *Mar. Ecol.-Progr. Ser.* 635:25-
330 36.

331 14. Druzhkov NV, Makarevich PR. 1999. Comparison of the phytoplankton assemblages of
332 the south-eastern Barents Sea and south-western Kara Sea: phytogeographical status. *Bot.*
333 *Mar.* 42:103-115.

334 15. Fermandez L, Kaiser BA, Vestergaard N. 2014. Marine invasive species in the Arctic.
335 *Nordic Council of Ministers* DOI: 10.6027/TN2014-547.

336 16. Fossheim M, Primicerio R, Johannesen E, Ingvaldsen RB, Aschan MM, Dolgov AV. 2015.
337 Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nature*
338 *Climate Change* 5:673-677.

17. Gawarkiewicz GG, Plueddemann AJ. 1995. Topographic control of thermohaline frontal structure in the Barents Sea Polar Front on the south flank of Spitsbergen Bank. *Journ. Geophys. Res.* 100(C3):4509-4524.

18. Gómez F. 2003. Checklist of Mediterranean Free-living Dinoflagellates. *Bot. Mar.* 46:215-242.

19. Grøntved J, Seidenfaden G. 1938. The phytoplankton of the waters west of Greenland. The Godthab Exp., 1928. *Meddelelser om Grønland (Monographs on Greenland). København: Kommissionen for Videnskabelige undersøgelser i Grønland (Commission for Scientific Investigations in Greenland)* 82(5):1-380.

20. Hällfos G. 2004. Checklist of Baltic Sea Phytoplankton Species. *Baltic Sea Environment Proceedings* 95:1-208.

21. Hendey NI. 1964. *An introductory account of the smaller algae of the British coastal waters. Part V: Bacillariophyceae (Diatoms).* London: Her Majesty's Stationery Office.

22. Hopes A, Mock T. 2015. Evolution of microalgae and their adaptation in different marine ecosystems. In: eLS. John Wiley & Sons, Ltd: Chichester, 1-9. DOI: 10.1002/9780470015902.a0023744

23. *Hydrometeorology and hydrochemistry of the seas of the USSR. Vol. 1. Barents Sea. Iss. 2. Hydrochemical conditions and oceanological foundations of the formation of biological productivity.* 1992. (Terziev FS, ed.). St.Petersburg: Gidrometeoizdat.

24. Ingvaldsen R, Loeng H. 2009. Physical oceanography. In: Sakshaug E, Johnsen G, Kovacs KM, eds. *Ecosystem Barents Sea.* Trondheim: Tapir Academic Press, 33-64.

25. Ingvaldsen RB, Asplin L, Loeng H. 2004a. The seasonal cycle in the Atlantic transport to the Barents Sea during 1997-2001. *Continental Shelf Res.* 24:1015-1032.

26. Ingvaldsen RB, Asplin L, Loeng H. 2004b. Velocity field of the western entrance to the Barents Sea. *Journ. Geophys. Res.* 109:1-12.

27. IPCC. 2013. Summary for Policymakers. In: Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM, eds. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment*

Report of the Intergovernmental Panel on Climate Change. Cambridge: Cambridge University Press.

28. Karlsen B, Cusack C, Beensen E. 2010. Microscopic and molecular methods for quantitative phytoplankton analysis. In: *IOC Manuals and Guides, No. 55.* Paris: UNESCO Press, 1-110.

29. Kiselev IA. 1950. *Armored flagellates.* M.-L.: AS USSR Publ.

30. Konovalova GV. 1998. *Dinoflagellates (Dinophyta) of the Far Eastern Seas of Russia and adjacent water areas of the Pacific Ocean.* Vladivostok: Dalnauka.

31. Krakhmal'niy AF. 2011. *Dinophyte algae of Ukraine (Illustrated key).* Kyiv: Alterpres.

32. Loeng H. 1991. Features of the physical oceanographic conditions of the Barents Sea. In: *Proceedings of the PRO MARE Symposium on Polar Marine Ecology, Trondheim, 12–16 May 1990. Polar Res.* 10(1):5-18.

33. Mack RN, Simberloff D, Lonsdale WM. 2000. Biotic invasions: cause, epidemiology, global consequences, and control. *Ecol. Appl.* 10:689-710.

34. Makarevich PR, Druzhkova EI, Larionov VV. 2012. Primary producers of the Barents Sea. In: *Diversity of Ecosystems.* Rijeka: InTech, 367-393. *Available at http://www.intechopen.com/books/diversity-of-ecosystems/primaryproducers-of-the-barents-sea.*

35. Makarevich PR, Druzhkova EI. 2010. *Seasonal cyclic processes in coastal planktonic algocenoses of the northern seas.* Rostov-na-Donu: SSC RAS Publ.

36. Makarevich PR, Oleinik AA. 2017. Microplankton of the Barents Sea: modern composition and structure in the pre-winter period. *Bulletin of MSTU* 20:316-325.

37. Makarevich PR, Oleinik AA. 2020. Floristic findings in the Barents Sea: climate trend as a factor of florogenesis. *Russian Journ. of Biol. Invasions* 3:40-50.

38. Matishov G, Makarevich P, Timofeev S, Kuznetsov L, Druzhkov N, Larionov V, Golubev V, Zuev A, Adrov N, Denisov V, Iliyn G, Kuznetsov A, Denisenko S, Savinov V, Shavykin A, Smolyar I, Levitus S, O'Brien T, Baranova O. 2000. *Biological Atlas of the Arctic Seas 2000: Plankton of the Barents and Kara Seas. National Oceanographic Data*

395   *Center/NOAA, Silver Spring MD USA, NOAA Atlas NESDIS 39.* Wash., DC: U.S. Gov.
396   Printing Office.

397   39. Matishov GG, Matishov DG, Moiseev DV. 2009. Inflow of Atlantic-origin waters to the
398   Barents Sea along glacial troughs. Oceanologia 51(3):321-340.

399   40. Matsuoka K, Kawami H, Fujii RH, Iwataki M. 2006. Further examination of the cyst-theca
400   relationship of Protoperidinium thulesense (Peridiniales, Dinophyceae) and the
401   phylogenetic significance of round brown cysts. *Phycologia* 45(6):632-641. DOI:
402   10.2216/05-42.1.

403   41. Nehring S. 1998. Establishment of thermophilic phytoplankton species in the North Sea:
404   biological indicators of climate changes? *ICES J. Mar. Sci.* 55: 818-823.

405   42. Neukermans G, Oziel L, Babin M. 2018. Increased intrusion of warming Atlantic water
406   leads to rapid expansion of temperate phytoplankton in the Arctic. *Global Change Biology*
407   24(6):2545-2553.

408   43. Occhipinti-Ambrogi A. 2007. Global change and marine communities: Alien species and
409   climate change. *Mar. Poll. Bull.* 55:342-352.

410   44. Okolodkov YB. 1996. Net phytoplankton from the Barents Sea and Svalbard waters
411   (collected on the cruise of the research vessel. *Geolog Fersman.*, in July-September 1992),
412   with emphasis on the *Ceratium* species as indicators of the Atlantic waters. *Botanical*
413   *Journal, Russian Academy of Sciences* 81:1-9.

414   45. Okolodkov YuB. 2000. Dinoflagellates (Dinophyceae) of the seas of the Eurasian Arctic.
415   D. Biol. Sci. Thesis, St.Petersburg University.

416   46. Oleinik AA. 2014. New dinoflagellates (Dinophyceae) of plankton of the Barents Sea.
417   *Botanical Journal, Russian Academy of Sciences* 99:756-765.

418   47. Ozhigin VK, Ingvaldsen RB, Loeng H, Boitsov VD, Karsakov AL. 2011. Introduction to
419   the Barents Sea. In: Gjøsæter H, Haug T, Jakobsen T et al., eds. *The Barents Sea:*
420   *ecosystem, resources, management. Half a century of Russian-Norwegian cooperation.*
421   Trondheim: Tapir Academic Press, 39-76.

422   48. Padilla DK, Williams SL. 2004. Beyond ballast water: aquarium and ornamental trades as
423   sources of invasive species in aquatic ecosystems. *Front. Ecol. Environ.* 2:131-138.

424   49. Perrette M, Yool A., Quartly GD, Popova EE. 2011. Near-ubiquity of ice-edge blooms in
425   the Arctic. *Biogeosciences.* 8:515-524.

426   50. PINRO. 2023. Kola Meridian Section. History of observation. *Available at*
427   *http://pinro.vniro.ru/ru/razrez-kolskij-meridian/istoriya-nablyudenij*   (accessed   on
428   01.03.2023).

429   51. Potanin VA, Denisov VV, Ershtadt MA. 1985. Water dynamics. In: Matishov GG, ed. *The*
430   *life and the conditions of its existence in the pelagic zone of the Barents Sea.* Apatity: CSC
431   RAS Publ., 18-30.

432   52. Recommendations for marine biological studies in the Baltic Sea. Phytoplankton and
433   chlorophyll. 1979. Baltic Mar. Biol. Publ. 3:1-38.

434   53. Reid PC, Johns DG, Edwards M, Star M, Pouli M, Snoeijs, P. 2007. A biological
435   consequence of reducing Arctic ice cover: arrival of the Pacific diatom
436   Neodenticulaseminae in the North Atlantic for the first time in 800,000 years. *Global*
437   *Change Biology* 13(9):1910-1921.

438   54. Sorte CJB, Williams SL, Zerebecki RA. 2010. Ocean warming increases threat of invasive
439   species in a marine fouling community. *Ecology* 91:2198-2204.

440   55. Spiridonov VA, Zalota AK. 2017. Understanding and forecasting dispersal of non-
441   indigenous marine decapods (Crustacea: Decapoda) in East European and North Asian
442   waters. *Journ. Mar. Biol. Assoc. UK* 97:591-611.

443   56. Stachowicz JJ, Terwin HH, Whitlatch RB, Osman, RW. 2002. Linking climate change and
444   biological invasions: ocean warming facilitates nonindigenous species invasions.
445   *Proceedings of the National Academy of Sciences* 99:15497-15500.

446   57. Starikov YuV, Spiridonov VA, Naumov AD, Zuev YuA. 2015. The first find and the
447   possibility of population formation of the red king crab *Paralithodes camtschaticus*
448   (Crustacea Decapoda Lithodidae) in the White Sea. *Russian Journ. of Biol. Invasions* 8:79-
449   95.

450   58. Wang Y, Xiang P, Kang J-H, Ye Y-Y, Lin G-M, Yang Q-L, Lin M. 2018.
451   Microphytoplankton community structure in the western Arctic Ocean: surface layer
452   variability of geographic and temporal considerations in summer. *Hydrobiologia* 811:295-
453   312. DOI: 10.1007/s10750-017-3500-0.

454   59. Wasmund N, Dutz J, Pollehne F, Siegel H, Zettler ML. 2015. Biologische
455   Zustandseinschätzung der Ostsee im Jahr 2014 (Biological assessment of the Baltic Sea
456   2014). *Meereswiss. Ber. (Mar. Sc. Rep.)* 98:3-90.

457   60. WoRMS.   2022.   World   Register   of   Marine   Species.   *Available   at*
458   *http://www.marinespecies.org/index.php* (accessed on 05.12.2022).

459   61. Zalota AK, Spiridonov VA, Vedenin AA. 2018. Development of snow crab *Chionoecetes*
460   *opilio* (Crustacea: Decapoda: Oregonidae) invasion in the Kara Sea. *Polar Biology*
461   41:1983-1994.

462   62. Zimina OL, Lyubin PA, Jørgensen LL, Zakharov DV, Lyubina OS. 2015. Decapod
463   crustaceans of the Barents Sea and adjacent waters: species composition and peculiarities
464   of distribution. *Arthropoda Selecta* 24:417-428.

Figure 1

Sampling stations location

Red dots – stations related to the Kola Meridian section

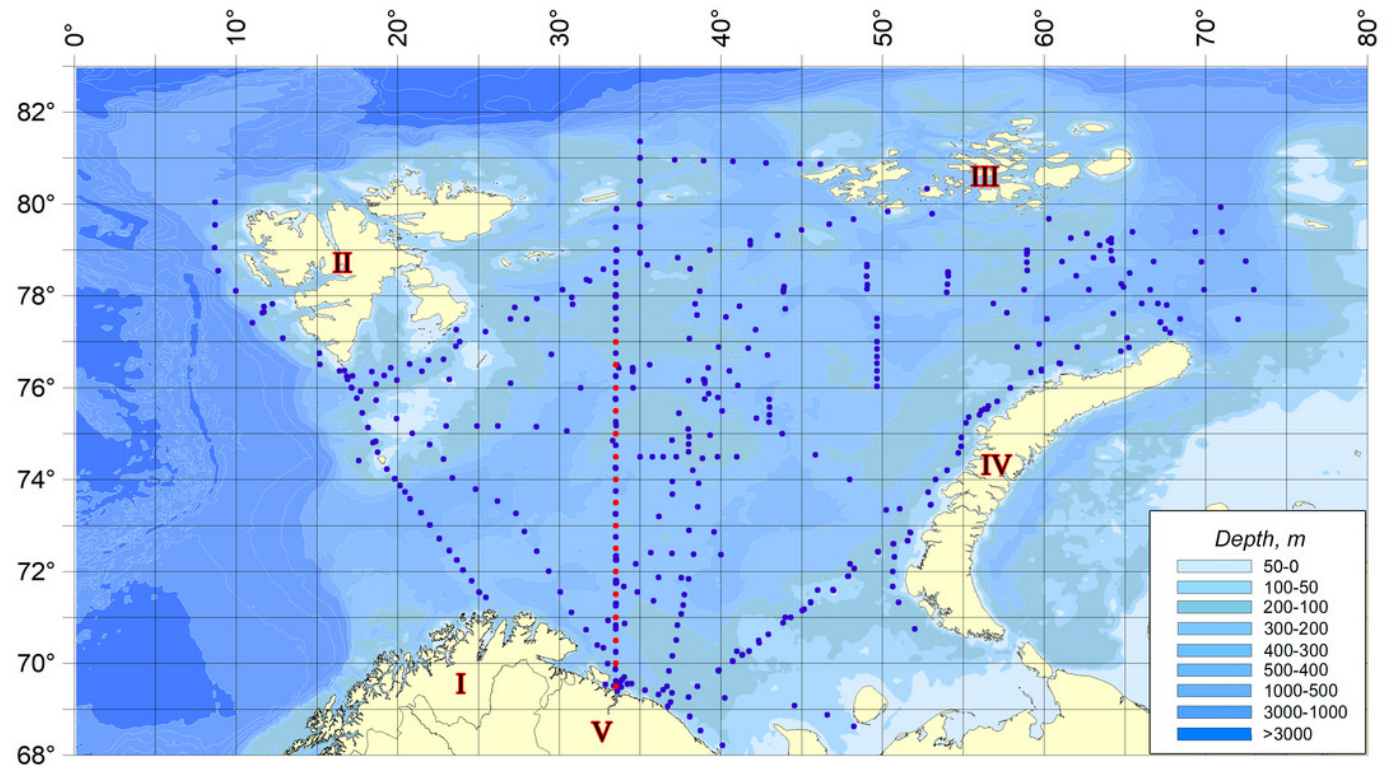



Figure 2

The distribution of vagrant species detection sites in the studied water area

(A) In areas marked on the map with letter A (A_1 and A_2) – a zone of regular infestation – the vagrant species were registered at every observation. In areas marked with B (B_1, B_2, B_3, and B_4) – the zone of weakened occupation – only in individual years. In the rest of the water body, species not typical of the Barents Sea pelagic algoflora were not found. I – Scandinavian Peninsula; II – Svalbard; III – Franz Jozef Land; IV – Novaya Zemlya; V – Kola Peninsula; 1 – Norwegian Atlantic Current; 2 – Fram Strait Branch; 3 – Barents Sea Branch; 4 – Norwegian Coastal Current; 5 – Murmansk Current; 6 – Murmansk costal Current. 7 – West Branch of Novaya Zemlya current; 8 – Coastal Branch of Novaya Zemlya current; 9 – South Svalbard Current; Dashed line – Atlantic water bottom current

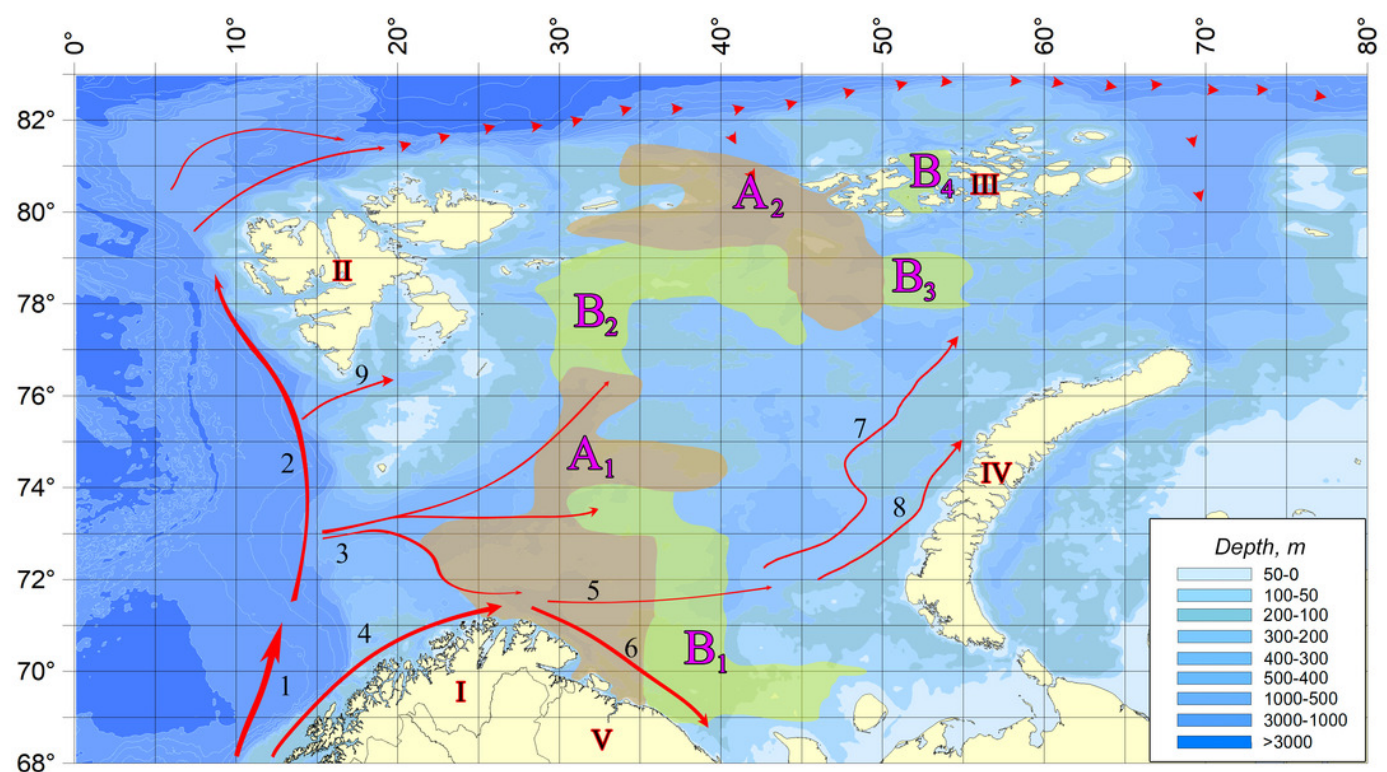
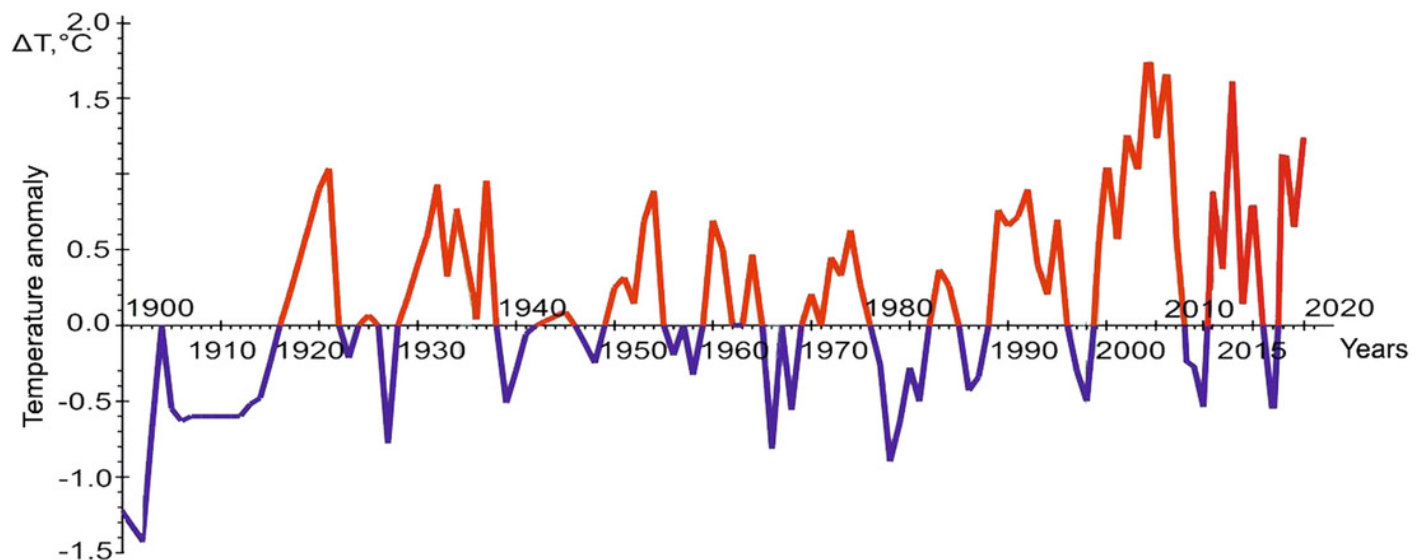



Figure 3

The graph of temperature anomalies in the oceanographic transect "Kola Meridian".
Figure based on Matishov, Matishov & Moiseev, 2009, with additional data from PINRO,
2023

List of pelagic microalgae species first observed in the Barents Sea (phytogeographic characteristics according to: http://www.algaebase.org)

1 **Table 1:**
2 List of pelagic microalgae species first observed in the Barents Sea (phytogeographic
3 characteristics according to: http://www.algaebase.org)

Species	Area	Year/Month	Max N, cells/l (Year/Month; Area)
Amphidoma caudata Halldal	A_1	2012/XI; 2013/XI	25 (2012/XI)
Ceratium strictum Kofoid	A_1, B_2	2014/VI; 2015/VII,XI; 2019/XI	20 (2015/VII; A_1)
Corythodinium diploconus Taylor	A_1	2012/XI; 2013/XI	less than 10 cells identified
Dinophysis hastata Stein	A_1	2013/XI	less than 10 cells identified
Dinophysis ovata Claparede et Lachmann	A_1, B_2	2013/XI; 2014/VI; 2015/XI; 2016/IV	less than 10 cells identified
Gotoius mutsuensis Matsuoka	A_1	2014/VI	less than 10 cells identified
Heterodinium milneri Kofoid	A_1	2013/XI	less than 10 cells identified
Mesoporos perforatus Lillick	A_1, B_2	2013/XI	53 (A_1)
Oxytoxum caudatum Schiller	A_1, A_2, B_1, B_2, B_3, B_4	2007/VIII,IX; 2010/IX,X; 2012/XI; 2013/XI; 2014/VI; 2015/XI; 2016/IV; 2017/XII; 2019/XI	400 (2013/XI; A_1) 300 (2012/XI; 2015/XI; A_1) 55 (2016/IV; B_4) 200 (2016/IV; B_2)
Podolampas palmipes Stein	A_1	2013/XI; 2016/IV; 2017/XII; 2018/I; 2019/XI	less than 10 cells identified
Proboscia indica Hernandez-Becerril	A_1	2016/IV	less than 10 cells identified
Protoperidinium brochii Balech	A_1	2013/XI	less than 10 cells identified
Protoperidinium laticeps Balech	A_1	2014/VI; 2019/XI	98 (2014/VI)
Protoperidinium thulesense (Balech) Balech	A_1	2012/VI	less than 10 cells identified
Pseudophalacroma nasutum Jörgensen	A_1	2013/XI	less than 10 cells identified
Pyrophacus horologicum Stein	A_1, B_2	2013/XI	less than 10 cells identified
Spatulodinium pseudonoctiluca Cachon et Cachon	A_1	2015/VII	less than 10 cells identified