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

Pavel Makarevich [1], **Viktor Larionov** [1], **Anatoly Oleynik** [1], **Pavel Vashchenko** [Corresp. 2]

[1] Department of plankton, Murmansk marine biological institute of Russian Academy of Science, Murmansk, Murmansk region, Russia

[2] Department of environmental engineering, Murmansk marine biological institute of Russian Academy of Science, Murmansk, Murmansk region, Russia

Corresponding Author: Pavel Vashchenko
Email address: pavelvashenko@gmail.com

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 biocenoses 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 alien 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: samples of 1-2L were concentrated using the reverse filtration method to a final volume of 4-5 ml; after that, they were fixed with a 40% formaldehyde solution, with final concentration 2-4%. Subsequent microscopy for taxonomic identification of organs and cell counting was performed in counting chambers of various volumes under an AxioImager D1 light microscope at 400x magnification.

The results of our observations show that alien 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 alien 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.

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

Pavel Robertovich Makarevich[1], Viktor Vitalievich Larionov[1], Anatoly Anatolievich Oleynik[1], Pavel Sergeyevich Vashchenko[2]

[1] Department of plankton, Murmansk marine biological institute of Russian Academy of Science, Murmansk, Russia
[2] Department of environmental engineering, Murmansk marine biological institute of Russian Academy of Science, Murmansk, Russia

Corresponding Author:
Pavel Vashchenko[2]
Vladimirskaya Street, Murmansk, Murmansk region, 184606, Russia
Email address: pavelvashenko@gmail.com

Abstract

Background: 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 biocenoses 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 alien 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.

Methods: 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 (Multi Water Sampler MWS 12, HYDRO-BIOS, Germany). The plankton net with a 29 µm mesh size was applied for filtering. The obtained material was processed according to standard hydrobiological methods: samples of 1-2 L were concentrated using the reverse filtration method to a final volume of 4-5 ml; after that, they were fixed with a 40% formaldehyde solution, with final concentration 2-4%. Subsequent microscopy for taxonomic identification of organs and cell counting was performed in counting chambers of various volumes under an AxioImager D1 light microscope (Carl Zeiss, Germany) at 400x magnification.

Results: The results of our observations show that alien 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 alien 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.

Introduction

One of the most important fields of bio-oceanology in recent decades has been the study of modern climatic changes and their consequences for marine ecosystems (*Comiso & Hall, 2014; Dong et al., 2020*). The most pronounced manifestation of this process is a steady increase in water temperature, leading to the interoceanic transport of non-native species that, under certain conditions, can actively live and reproduce in new areas of water areas for them (*Reid et al., 2007*).

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

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

But most of all, the increased inflow of Atlantic waters and warming affect the structure of pelagic algocenoses, causing changes in their taxonomic composition due to the penetration of new species of tropical and tropical-boreal origin (*Oleinik, 2014; Ardyna & Arrigo, 2020; Ardyna et al., 2020; Wang et al., 2018*). A number of our papers have detailed findings of alien microplankton species in the Barents Sea (*Oleinik, 2014; Makarevich & Oleinik, 2017; Makarevich & Oleinik, 2020*). However, these publications lack information on how widely these species spread over the water body, how long they remain in the Barents Sea pelagic zone throughout the year, and in which seasons they reach high abundance levels. The purpose of this article was to analyze the materials obtained to answer these questions to estimate the scale of possible changes in the structure of phytoplankton communities. Its results are of paramount importance for predicting negative consequences for the Arctic marine ecosystems as a whole.

Materials & Methods

The material for the present work was planktonic collections made during expedition surveys of 2007-2019 in different seasons throughout the Barents Sea (*Makarevich & Oleinik, 2020*). The water samples were taken using a rosette Niskin bottle sampler (Multi Water Sampler MWS 12, HYDRO-BIOS, Germany). The plankton net with a 29 µm mesh size was applied for filtering. The obtained material was processed according to standard hydrobiological methods: samples of 1-2 L were concentrated using the reverse filtration method to a final volume of 4-5 ml; after that, they were fixed with a 40% formaldehyde solution, with final concentration 2-4% (*Dodson & Thomas, 1964*). Subsequent microscopy for taxonomic identification of organisms and cell counting was performed in counting chambers of various volumes under an AxioImager D1 light microscope (Carl Zeiss, Germany) at 400x magnification. Hypochlorite solution followed by heating was used to enlighten objects. The names of species and systematic groups, as well as phytogeographic characteristics of microalgae, are given according to the nomenclature from electronic sources (*AlgaeBase, 2022; WoRMS, 2022*).

Results

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

Figure 1 shows the scheme demonstrating the distribution of alien species detection sites in the studied water area. The dense location of sampling stations, repeatability of surveys at the same points in different years, and coverage of almost the entire area of the Barents Sea allow to reliably draw borders of areas with different degrees of their occurrence.

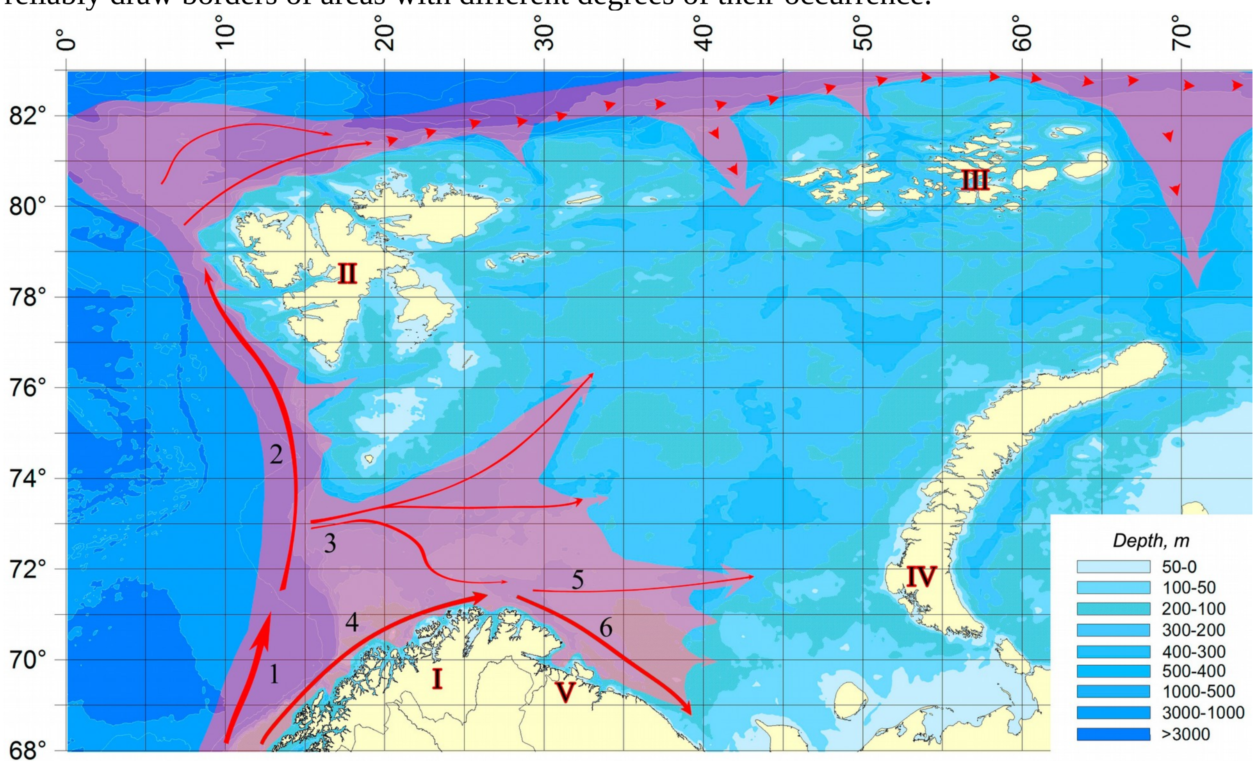

Figure 1: The main currents from the Atlantic within the research area of the Barents Sea. I – Scandinavian Peninsula; II – Svalbard; III – Franz Jozef Land; IV – Novaya zemlya; V – Kola Peninsula; 1 – Norwegian Atlantic Current; 2 – Fram Current; 3 – South Svalbard Current; 4 – Norwegian Coastal Current; 5 – Nordkapp Current; 6 – Nordkapp South Current.

Dashed line – Atlantic water bottom current. The red area is under influence of Atlantic water masses.

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

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

This species deserves special attention. It is present in the pelagic zone for almost the entire period of studies, in all seasons, and throughout the water areas of regular and attenuated invasion. Its populations reach concentrations an order of magnitude higher than those of other alien organisms. It can be assumed that *Oxytoxum caudatum* is the only representative of algoflora not typical of the Barents Sea, which has been adapting to new environmental conditions in the initial stage.

The distribution of the number of finds by year is as follows. The maximum number of encounters – 11 – is characterized by 2013, followed by 2014 – 5 cases, 2012, 2015, 2016, and 2019 – 4 registrations each, 2017 – 2 findings, 2007, 2010, and 2018 – 1 encounter each. A similar comparison of the number of omnivore sightings by month shows this pattern. The highest number of them (21) is in November, the other seasons are much less rich: June – 6 cases, April – 4, July, September and December – 2, January, August, and October – 1. During the other periods of the year, no alien species of microalgae were detected in the Barents Sea pelagic zone. However, it should be taken into account that subglacial vegetation takes place in February-March in all Arctic seas, and in May the peak of spring phytoplankton bloom is formed; during these phases of the annual successional cycle, diatoms dominate in the alcogeoses, and the proportion of dinoflagellates is extremely low (*Makarevich, Druzhkova & Larionov, 2012*).

It is also important to note that, based on the results of many years of research, it was found that in the Barents Sea pelagic, according to the phytogeographic characteristics, approximately 40% of microalgae taxa are arcto-boreal species, 30% are cosmopolitan and 20 are boreal (*Makarevich & Druzhkova, 2010*). As part of the new finds, most organisms are representatives of the tropical-boreal and boreal algoflora, and a small number – are tropical and bipolar. Previously, no species of tropical-boreal and tropical origin were recorded in the Barents Sea (*Matishov et el., 2000; Makarevich & Druzhkova, 2010*).

Discussion

As already noted, the main indicator of the dynamics of climatic factors is seawater temperature. We have at our disposal a multiyear series of year-round observations of hydrological parameters, in particular temperature, on the standard oceanographic transect "Kola Meridian" (Fig. 2). Their analysis indicates a clear increase in the advection of warm waters from the Atlantic to the Barents Sea in recent decades, which is the main reason for the appearance of alien species in the Barents Sea waters. The second way of transfer of alien organisms is anthropogenic activity, but for phytoplankton representatives in the seas of the Arctic basin, reliable cases of such introduction are currently unknown (*Stachowicz et al., 2002; Padilla & Williams, 2004*).

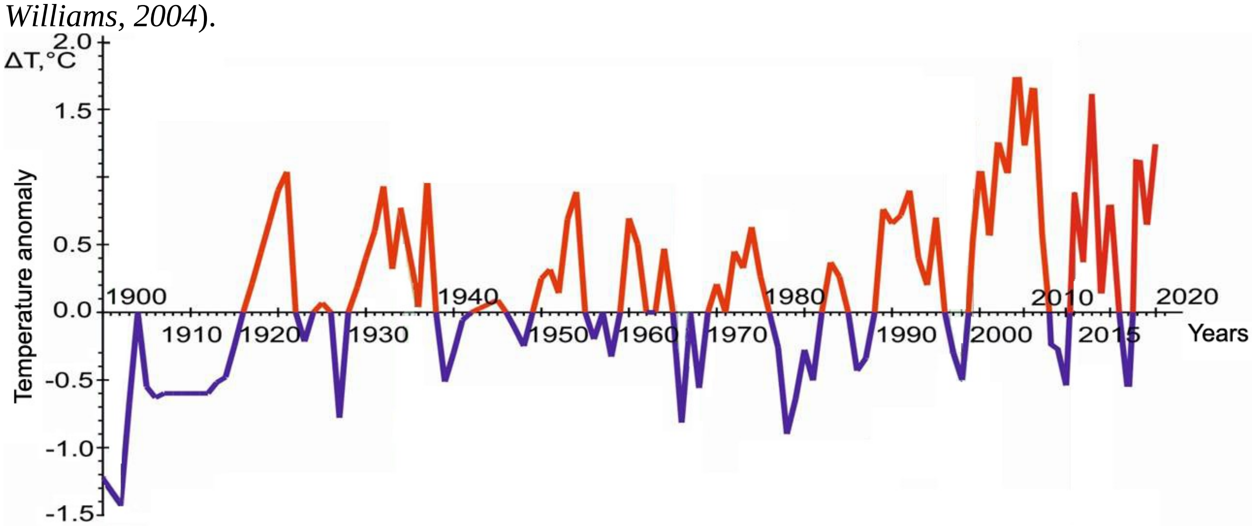

Figure 2: The graph of temperature anomalies in the oceanographic transect "Kola Meridian".

The inflow of Atlantic water masses into the Barents Sea occurs due to constant (non-periodic) currents, which together form a relatively stable circulation system within the reservoir (Fig. 3). These currents determine the general distribution of water masses in the Barents Sea water area and its water exchange with the adjacent areas (*Potanin, Denisov & Ershtadt, 1985*). On the western border, this water exchange is carried out with the Norwegian and Greenland Seas. Through the largest strait, between the island of Medvezhiy and the mainland. The largest strait between Medvezhiy and the mainland (Nordkapp), water flows from the Norwegian Sea to the Barents Sea through two currents – the Norwegian Atlantic Current and the Norwegian Coastal Current. When crossing the Nordkapp-Medvezhiy line, the continuation of these currents is referred to as the Nordkapp and Nordkapp South currents, respectively. In the opposite direction, this boundary is crossed by the Medvezhiynskaya (Nadezhda-Medvezhiynskaya) current. Through another strait on the western border, between South Cape Island (Sørkapp – Norwegian name; Svalbard archipelago) and Bear Island, the South Svalbard Current enters the Barents Sea from the Norwegian Sea, and the Zuidkap Current enters the Barents Sea in the opposite direction. The Nordkapp Current divides into two streams, the Northern and Central Branches, running further northward and eastward (*Matishov, Matishov & Moiseev, 2009*). The Northern Branch, following the Nadezhda Trough, divides into smaller streams that move northward to the west of the Perseus Plateau and eastward between the Perseus Plateau and the Central Bank (*Loeng, 1991*). Another part of the Northern Branch, deviating westward, forms a flow along the western edge of the Medvezhiyski Trough, directed into the Norwegian Sea (*Gawarkiewicz & Plueddemann, 1995*).

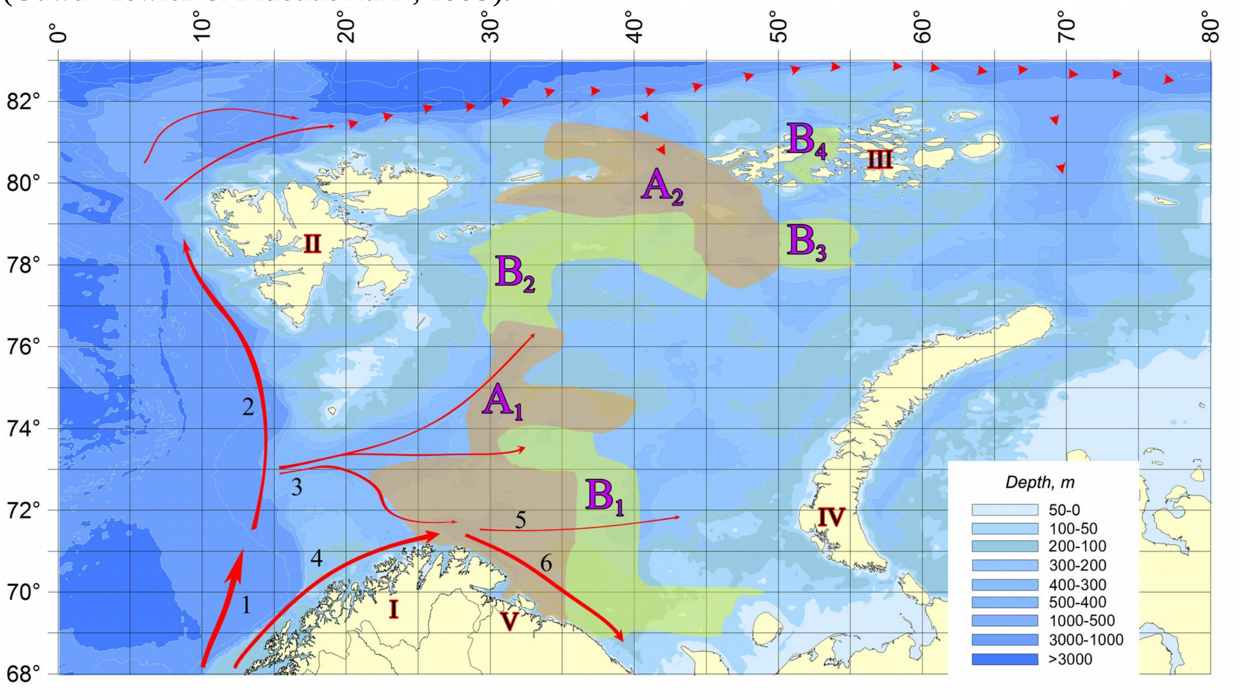

Figure 3: The distribution of alien species detection sites in the studied water area. (A) In areas marked on the map with letter A (A_1 and A_2) – a zone of regular infestation – the pests were registered at every observation. In areas marked with B (B_1, B_2, B_3, and B_4) – the zone of weakened invasion – only in individual years. In the rest of the water body, species not typical of the Barents Sea pelagic algoflora were not found. Currents (1-6) see Figure 1.

The central branch of the Nordkapp current extends eastward and appears in the Demidovsky Trough and above the Central Upland (*Boytsov, 2006*). The Nordkapp South Current runs deep into the Barents Sea and divides into the Murmansk Current and the Murmansk Coastal Current, which flows along the northern and southern slopes of the Murman Rise in an easterly direction (*Hydrometeorology..., 1992*). On the northern boundary of the reservoir, a complex system of surface currents is used to exchange water with the adjacent Arctic Ocean water area. Where there are significant depressions of the continental slope, the exchange of deep waters of the central part of the basin and bottom waters of the Barents Sea takes place (*Loeng, 1991*).

The analysis of Figures 1 and 3 reveals a complete coincidence of the current directions (three streams of Atlantic water entering the Barents Sea) and the areas of regular settlement. Area A_1 is directly influenced by the Nordkapp South Current and two branches of the Nordkapp Current. In areas B_1 and B_2, located near its borders, the speed of these currents is significantly reduced. Area A_2 is the area affected by the South Spitsbergen Current, which decreases in the nearby areas B_3 and B_4 (as well as in area B_2). Thus, there is a clear connection: the weakening of the currents leads to a decrease in the number of finds of alien species up to their complete disappearance. As a result, a completely natural situation is observed, when the richest in the number of alien species and registered encounters in area A_1, in which all 17 species are found. Area B_2, containing 5 representatives of alien algoflora, is under the influence of two less strong flows, and only one species of *Oxytoxum caudatum* is found in the other selected areas. Characteristically, this microalga reaches maximum concentrations (300-400 cells/l) in area A_1, being present throughout the studied water area during the entire period of research.

It should also be noted that the indicated abundance values of *Oxytoxum caudatum* were observed only in November, and lower, but comparable to the data (50-200 cells/l) – in April-May (Table 1), and only on one horizon – at a depth of 200 m. Among the other algae reaching relatively high abundance levels (more than 20 cells/l), these were recorded in one month of the year, also predominantly in November (Table 1). Thus, in no area do alien species create a stable population that would persist for a long period (at least one stage of the annual development cycle). There is only their temporary presence in the Barents Sea, with the highest concentrations being recorded in the autumn-winter season when active vegetation has already stopped, and the lowest in summer. This fact can most likely be explained by the fact that it is November when the maximum volume of Atlantic water enters the water body (*Ingvaldsen, Asplin & Loeng, 2004a; Ingvaldsen, Asplin & Loeng, 2004b*).

The comparison of the number of the omnivore finds in different years shows that their maximum number is in 2013, the years 2012 and 2014-2016, as well as 2019, are less rich in the number of encounters, the periods from 2007 to 2011, 2017 and 2018 are represented only by isolated cases. The graph of temperature anomalies in the "Kola Meridian" oceanographic transect (Fig. 2) shows that the interval from 2012 to 2016 is characterized by high positive values of this indicator (with a peak in 2013), while the previous and subsequent periods are negative. This relationship strongly indicates that increased water temperature is a necessary condition for the adaptation of warm-water species in the Arctic basin, in particular, in the Barents Sea.

Conclusions

Overall, the data presented suggest that the distribution of alien microphytoplankton species in the Barents Sea is tied to the warm currents coming from the Atlantic Ocean. The weakening force of these water masses penetrating deep into the Barents Sea from the west turns out to be the main factor limiting the presence of alien species in the eastern part of the reservoir. As a result, the southwestern and western parts of the water area are characterized by the greatest number of floristic findings, and further to the north and east the number of such species decreases. The maximum diversity of this group of organisms is confined to the warmest years when the inflow of Atlantic water masses increases.

At present, the share of pelagic microalgae new to the Barents Sea in the total taxonomic diversity is insignificant. There is no mass development of them in any season of the year, they do not form high biomasses and do not change the community structure as a whole. As a result, their appearance does not lead to the destabilization of planktonic algocenoses themselves and does not have any negative impact on other components of the Barents Sea pelagic ecosystems.

Nevertheless, at this stage of research, it is too early to predict the ecological consequences of the occurrence of alien microalgae species in Arctic waters. Moreover, taking into account the increasing number of recorded finds of phytoplankton representatives uncharacteristic for the Arctic, we can assume that if the positive temperature trend persists, the process of invasion will increase its intensity. In this case, negative consequences are possible: changes in the community structure, oppression of native species, and decrease in biological stability of pelagic ecosystems.

References

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

2. AlgaeBase. 2022. World-wide electronic publication, National University of Ireland, Galway. *Available at http://*[*www.algaebase.org*](http://www.algaebase.org) (accessed on 05.12.2022).
3. Ardyna M, Arrigo K. 2020. Phytoplankton dynamics in a changing Arctic Ocean. *Nature Climate Change* 10:892-903.
4. Ardyna M, Mundy CJ, Mayot N, Matthes LC, Oziel L, Horvat C, Leu E Assmy P, Hill V, Matrai PA, Gale M, Melnikov IA, Arrigo KR. 2020. Under-ice phytoplankton blooms: Shedding light on the "invisible" part of arctic primary production. *Front. Mar. Sci.* 7:608032. DOI: 10.3389/fmars.2020.608032.
5. Årthun MA, Eldevik T, Smedsrud LH, Skagseth O, Ingvaldsen RB. 2012. Quantifying the influence of Atlantic heat on the Barents Sea ice variability and retreat *Journ. Clim.* 25:4736-4743.
6. Bagøien E., Benzik A., Bogstad B, Chetyrkin AA, Dalpadado P, Dolgov AV, Eriksen E, Filin AA, Gjøsæter H, Hallfredsson EH, Heldal HE, Johannesen E, Jørgensen LL, Lien V, Klepikovsky RN, Nedreaas K, Prokhorova TA, Prokopchuk IP, Prozorkevich DV, Rey F, Skaret G, Skjoldal HR, Strelkova NA, Russkikh AA, Trofimov AG, Zhilin AYu. 2018. The state and trends of the Barents Sea in 2017. *Interim Report of the Working Group on the Integrated Assessments of the Barents Sea (WGIBAR)* 5:69-210.
7. Boytsov VD. 2006. *Variability of water temperature in the Barents Sea and its forecasting.* Murmansk: PINRO Publ.
8. Comiso JC, Hall DK. 2014. Climate trends in the Arctic as observed from space. *Wiley Interdiscip. Rev. Clim. Change* 5(3):389-409. DOI: 10.1002/wcc.277.
9. Crooks KR, Soulé ME. 1999. Mesopredator release and avifaunal extinctions in a fragmental system. *Nature* 400:563-566.
10. Dodge JD. 1982. *Marine dinoflagellates of the British Isles.* London: Her Majesty's Stationary Office.
11. Dodson AN, Thomas WH. 1964. Concentrating plankton in a gentle fashion. *Limnol. & Oceanogr*. 9:455-456.
12. Dong K., Kvile ØK, Stenseth NC, Stige LC. 2020. Associations among temperature, sea ice and phytoplankton bloom dynamics in the Barents Sea. *Mar. Ecol.-Progr. Ser.* 635:25-36.

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

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

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

16. 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.

17. 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.

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

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

20. 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.

21. *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.

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

23. 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.

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

25. 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.

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

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

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

29. 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.

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

31. 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.*

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

33. 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.

34. 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.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Table 1(on next page)

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

Table 1:
List of pelagic microalgae species first observed in the Barents Sea (phytogeographic 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	
Dinophysis hastata Stein	A_1	2013/XI	
Dinophysis ovata Claparede et Lachmann	A_1, B_2	2013/XI; 2014/VI; 2015/XI; 2016/IV	
Gotoius mutsuensis Matsuoka	A_1	2014/VI	
Heterodinium milneri Kofoid	A_1	2013/XI	
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	
Proboscia indica Hernandez-Becerril	A_1	2016/IV	
Protoperidinium brochii Balech	A_1	2013/XI	
Protoperidinium laticeps Balech	A_1	2014/VI; 2019/XI	98 (2014/VI)
Protoperidinium thulesense (Balech) Balech	A_1	2012/VI	
Pseudophalacroma nasutum Jörgensen	A_1	2013/XI	
Pyrophacus horologicum Stein	A_1, B_2	2013/XI	
Spatulodinium pseudonoctiluca Cachon et Cachon	A_1	2015/VII	

Figure 1

Figure 1: The main currents from the Atlantic within the research area of the Barents Sea.

I – Scandinavian Peninsula; II – Svalbard; III – Franz Jozef Land; IV – Novaya zemlya; V – Kola Peninsula; 1 – Norwegian Atlantic Current; 2 – Fram Current; 3 – South Svalbard Current; 4 – Norwegian Coastal Current; 5 – Nordkapp Current; 6 – Nordkapp South Current. Dashed line – Atlantic water bottom current. The red area is under influence of Atlantic water masses.

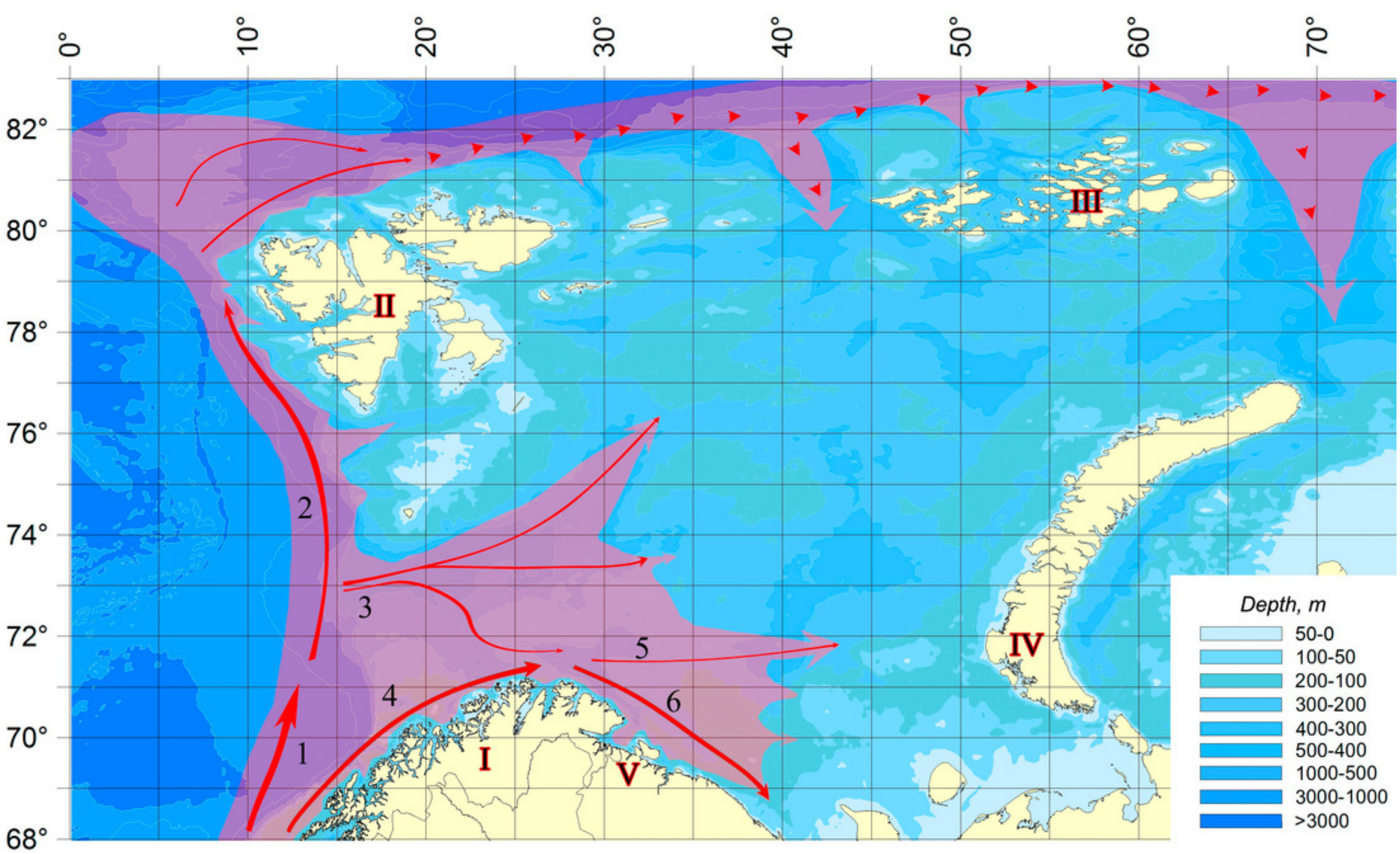

Figure 2

Figure 2: The graph of temperature anomalies in the oceanographic transect "Kola Meridian"

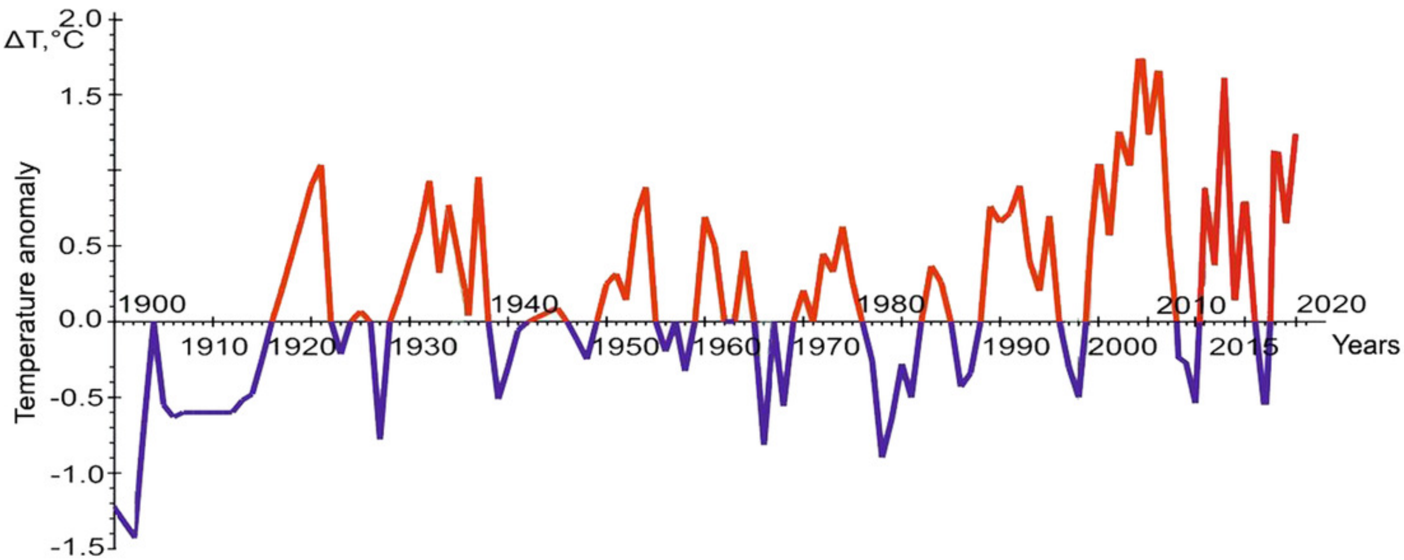

Figure 3

Figure 3: The distribution of alien 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 pests were registered at every observation. In areas marked with B (B_1, B_2, B_3, and B_4) – the zone of weakened invasion – only in individual years. In the rest of the water body, species not typical of the Barents Sea pelagic algoflora were not found. Currents (1-6) see Figure 1