Biodiversity and biogeography of planktonic dinoflagellates in the Arctic Ocean

Yuri B. Okolodkov\textsuperscript{a}, John D. Dodge\textsuperscript{b, *}

\textsuperscript{a}Department of Algology, Komarov Botanical Institute, Russian Academy of Sciences, 2 Prof. Popov St., St. Petersburg, 197376, Russia

\textsuperscript{b}Department of Biology, Royal Holloway, University of London, Egham, Surrey, TW20 0EX, UK

Abstract

Data on the species diversity and distribution of arctic planktonic dinoflagellates was obtained from a large number of samples collected during sixteen expeditions and from the relevant literature. Based on an analysis of the ranges of about 250 dinoflagellate species recorded, only four Arctic–boreal species, \textit{Alexandrium ostenfeldii}, \textit{Amylax triacantha}, \textit{Ceratium arcticum} and \textit{Dinophysis norvegica}, and four provisionally bipolar species, \textit{Dinophysis arctica}, \textit{Protoperidinium islundicum}, \textit{P. sultans} and \textit{P. thulesense}, were recognized. No purely Arctic species or genera endemic to the Arctic were discovered and this may be considered evidence for the unity of the Arctic–boreal biogeographical zone. An increased number of species were found in the areas influenced directly by the warm Atlantic or Pacific currents, such as the Norwegian, Barents and Chukchi Seas, mainly due to the invasion of tropical–boreal and Antarctic–tropical–boreal species. These forms tend to penetrate into the Arctic along the western coasts of the continents. Only two species, \textit{Peridiniella catenata} and \textit{Gymnodinium cf. punctatum}, are reliably associated with sea ice. Analysis by the multivariate techniques, Twinspan and Decorana, revealed two main clusters; one, influenced by the warmer waters of the Atlantic and Pacific currents, and the other consisting of the cold water regions.

Keywords: Arctic ocean; Biogeography; Dinoflagellate; Plankton

1. Introduction

Among phytoplanktonic organisms, the biodiversity of dinoflagellates is comparable only with that of diatom algae. About 1500 diatoms and 1400 to 1800 dinoflagellate species constitute marine phytoplankton in the world oceans (Sournia et al., 1991).
Arctic phytoplankton have been considered to be composed primarily of diatoms. However, in some Arctic seas, namely, the Norwegian Sea, in summer the number of dinoflagellate species may exceed the number of planktonic diatoms. The aim of the present study was to assess the biodiversity of dinoflagellates, here defined as species richness, in the whole Arctic Ocean (Fig. 1) and also, to compare different regions, and to try to understand the causes of the differences found.

2. Materials and methods

Most plankton samples were collected by net, mesh 70 μm, or in some cases, 20 μm. Other samples were obtained by use of water bottles with filtration through Nuclepore
filters (pore size of 1 μm), with the aid of a reverse-filtration device. In all, samples from about 600 stations occupied during sixteen marine and aircraft expeditions to all European Arctic and Siberian seas, in the period 1980–1993, have been analysed. Live and fixed algae were studied under the light microscope with a variety of techniques, including Nomarsky interference and anoptral contrast, and staining with Trypan Blue. More than 400 literary sources on dinoflagellate records in the Arctic and world-wide were used to map the species ranges and to establish the northern boundary of distribution of tropical–boreal and Antarctic–tropical–boreal, and the southern boundary for Arctic–boreal species.

A PC multivariate analysis package VESPAN II (Malloch, 1988) was used. The TWINSPAN (Two-Way INdicator SSpecies ANalysis) and DECORANA (DEtrended CORrespondence ANAlysis) programmes were run, to perform a divisive cluster analysis and diagrams of the ordinations for the arctic regions. This package, designed for plant ecological work, has been successfully used in earlier studies to analyse data on the dinoflagellate biogeography and ecology of the North Atlantic and Western Pacific (Dodge, 1993a,b; Dodge and Marshall, 1994).

3. Results and discussion

According to the classification of Fensome et al. (1993), the marine Arctic dinoflagellate planktonic flora is represented by about 250 species from 41 genera and 21 families (only 201 of these species were used for analysis in the present study because of the large number of dubious taxa). More than half (52.3%) of the total number of species recorded in the Arctic belong to the families Congruentidiaceae (also known as Peridiniaceae) and Gymnodiniaceae. Among others, the most important are Dinophysaceae (10.9%), Ceratiaceae (7.5%), Gonyaulacaceae (6.5%) and Prorocentraceae (5%). Most Congruentidiaceae species belong to the genus Protoperidinium (Fig. 2), being purely planktonic and almost entirely heterotrophic. Unlike the clearly marine family Congruentidiaceae, the family Gymnodiniaceae is mainly autotrophic and is distributed in fresh, brackish and saline waters, both in plankton and benthos. The real number of species of the family is considerably underestimated because of difficulties in the preservation and identification of these naked flagellates.

An increased number of species have been recorded in the regions influenced by the Atlantic (the Norwegian, Barents, Kara and White Seas) or Pacific currents (the Chukchi Sea) (Fig. 3). In the Norwegian Sea, a comparatively high number of species (eight) from the family Prorocentraceae is characteristic. On the whole, more species of the leading families and genera are found in southerly areas.

TWINSPAN analysis reveals two main clusters (Fig. 4). Cluster I includes the regions influenced by the warmer Atlantic and Pacific currents. Cluster II consists of relatively cold water regions that are not influenced by the warmer currents, possibly with the exception of the western Beaufort Sea. DECORANA analysis does not present a clear picture (Fig. 5). One may suppose, however, that different Arctic regions are distributed along axis 1 with a decrease in temperature. Also, the seas influenced by the Atlantic Current tend to be grouped in the left part of the diagram.
Out of about 250 dinoflagellate species recorded for the Arctic, only *Alexandrium ostenfeldii*, *Amylax triacantha*, *Ceratium arcticum* and *Dinophysis norvegica* are Arctic–boreal (Figs. 6 and 7), and four species, *Dinophysis arctica*, *Protoperidinium islandicum*, *P. thulesense* and *P. saltans*, are assumed to be bipolar. Only these species
are of value in solving the question about the unity of the Arctic–boreal zone. While the existence itself of bipolar species of dinoflagellates is questionable, Arctic–boreal species are recorded primarily to the north of the so-called Ortmann Line (Fig. 6), where the average sea surface temperature is 15°C in the Northern Hemisphere (Ortmann, 1896). The apparent discontinuity of their ranges may be explained by lack of data from some areas. It is clear that there are neither purely Arctic dinoflagellates, nor species or genera endemic to the Arctic–boreal zone. Thus, data on the distribution of dinoflagellates confirm the conclusion of Semina, 1974 about the unity of the Arctic–boreal phytoplankton, on which she based a scheme for the biogeographical division of the Pacific Ocean.

Tropical–boreal and Antarctic–tropical–boreal dinoflagellates are allochthonous to the Arctic. In some cases, it is difficult to refer any given species to one of the categories. Not less than 40 tropical–boreal and 17 provisionally Antarctic–tropical–boreal dinoflagellates have been recorded in the Arctic. About half of the tropical–boreal
Fig. 4. A cluster diagram, based on the TWINSPIAN analysis, to show the relationships of the Arctic regions.

Fig. 5. An ordination diagram, based on the DECORANA analysis, to show the relationships of Arctic regions (ABa, Arctic Basin; Bar, Barents Sea; Baf, Baffin Bay; Bea, Beaufort Sea; CAA, Canadian Arctic Archipelago; Chu, Chukchi Sea; ESi, East Siberian Sea; Gre, Greenland Sea; Hud, Hudson Bay; Kar, Kara Sea; Lap, Laptev Sea; Nor, Norwegian Sea; Whi, White Sea).
Fig. 6. Distribution of the Arctic–boreal dinoflagellates *Alexandrium ostenfeldii* (1) and *Ceratium arcticum* (2).

Fig. 7. Distribution of the Arctic–boreal dinoflagellates *Amylax triacanthia* (1) and *Dinophysis norvegica* (2).
and almost all Antarctic–tropical–boreal species were found in the zone where non-Arctic and Arctic waters mix, between the so-called Dunbar Line (Dunbar, 1951, 1979) and the northern boundary of the Subarctic. Antarctic–tropical–boreal species seem to be more tolerant to the lower temperature compared to the tropical–boreal ones. Records of allochthonous species from the White and Western Kara Seas are more frequent than from the Hudson Bay. The tendency of penetration of the allochthonous species to the Arctic with the warmer currents along the eastern parts of the oceans is clear for the Pacific as well. Twelve tropical–boreal and Antarctic–tropical–boreal species were recorded at Point Barrow in the eastern Chukchi Sea.

The most severe ice conditions and lowest temperature in the surface water are observed in the Laptev and East Siberian Seas, and the Arctic Basin. These areas, with the exception of the north-western Laptev Sea, are not influenced directly by Atlantic and Pacific warmer waters. The peculiarities mentioned distinguish the regions considered from other Arctic areas. In our opinion, some dinoflagellates known from the literature as cosmopolitan cannot be considered as such until they have been found in the area not influenced by the warmer currents.

Annual ice is a peculiar feature of most of the Arctic seas and bays. Sea-ice flora associated with ice consists of more than 200 diatom species. By way of contrast, only two dinoflagellates can be considered cryophilic, Peridiniella catenata, developing both in plankton and at the lower ice surface, in the Kara and Laptev Seas (Okolodkov, unpublished), and Gymnodinium cf. punctatum, found to produce “blooming” on the lower ice surface, in a lagoon near the Zhokhov Island, the East Siberian Sea (Okolodkov, 1989, 1992). The former reached a concentration of $1.6 \times 10^5$ cells $l^{-1}$ of melted ice, contributing up to 40% of the total number of cells; the latter composed 99% with concentration of $9.0 \times 10^5$ cells $l^{-1}$ of melted ice. Meunier (1910) observed P. catenata in yellow snow on sea ice, in the Kara Sea, as well as in the water column. The distribution pattern of P. catenata is close to the Arctic–boreal species mentioned above, although it was also recorded near the Brasilean coast, south of the Tropic of Capricorn as well (Sevrin-Reyssac, 1981). The records of small phyto- and zooflagellates in Antarctic sea ice (Garrison and Buck, 1989; Garrison, 1991) allow us to suppose that the full biodiversity of naked dinoflagellates in Arctic sea ice is still unrevealed.

A recent study of the genus Ceratium in the North Atlantic (Dodge and Marshall, 1994) revealed that only two species, C. arcticum (Fig. 6) and C. longipes, of this large genus are found in the cold arctic waters and up to fourteen species are found in the warmer waters within the Arctic Circle. This genus is clearly tropical in its distribution, but a small number of species have adapted to very cold conditions and a larger number of the cosmopolitan species are able to tolerate water temperatures down to about 5°C. Perhaps much the same applies to the other main genera of planktonic dinoflagellates. Future work will be directed to an investigation of this problem.

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References


