

General Ecology of the Canadian Arctic Benthic Marine Algae¹

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ABSTRACT. The Canadian Arctic marine flora is basically a regional extension of Atlantic species. As the extreme environmental conditions of low temperature, low salinity and long periods of darkness intensify towards the western and northern parts of the Canadian Arctic, there is a marked reduction in the number of species. The protective cover of sea ice, together with the seasonal development of a low salinity layer from ice melt, hinders mixing between water layers, and nutrient replenishment is apparently a critical problem. Communities are generally small and isolated largely because of substrate limitations. A population may be extensive and dense, but this is attributed to the small number of species and the relative ineffectiveness of most of these in competing for the available space. Following seasonal ice melt, the intertidal habitat in colder regions remains unsuitable for algal growth, because of its exposure to a combination of adverse climatic and oceanographic conditions. The decreasing diversity of species, as the physical conditions become more adverse, together with the nearly complete absence of endemics, indicate a low level of adaptation, and the arctic communities are judged to be ecologically immature.

RÉSUMÉ: *Écologie générale des algues marines benthiques de l'Arctique canadien.* Fondamentalement, la flore marine du Canada arctique est une extension régionale d'espèces atlantiques. A mesure que les conditions de basse température, de faible salinité et de longues périodes d'obscurité s'intensifient vers l'ouest et le nord de l'Arctique canadien, il se produit une réduction marquée dans le nombre des espèces. La couche protectrice de glace de mer et le développement saisonnier d'une couche de faible salinité par suite de la fonte de la glace, nuit au mélange des couches d'eau, et le renouvellement des éléments nutritifs est apparemment un problème critique. Les communautés sont généralement petites et isolées, surtout à cause des limitations du substrat. Une population peut être étendue et dense, mais ceci est attribuable au petit nombre d'espèces et à l'inefficacité relative de la plupart d'entre elles à lutter pour l'espace disponible. Après la fonte saisonnière des glaces, le milieu intertidal des régions plus froides demeure impropre à la croissance des algues par son exposition à un complexe de conditions climatiques et océanographiques adverses. La diversité décroissante des espèces à mesure que les conditions physiques deviennent plus adverses, et l'absence presque complète d'endémiques, indiquent un faible niveau d'adaptation et ces communautés algaires doivent être jugées écologiquement immatures.

РЕЗЮМЕ. *Общая экология бентосных морских водорослей Канадской Арктики.* Основу морской флоры Канадской Арктики составляют атлантические виды. Число этих видов заметно убывает к западу и северу рассматриваемого региона, сокращаясь по мере обострения таких неблагоприятных условий среды, как низкая температура, низкая соленость и длительное отсутствие света. Защитный покров морских льдов и сезонный слой талой воды с пониженной соленостью препятствуют перемешиванию водной толщи, поэтому представляется вероятным, что проблема пополнения запаса питательных веществ является здесь критической. Сообщества обычно малы и разобщены, что связано, главным образом, с ограниченностью пригодного для заселения субстрата. Количество особей, однако, может быть большим и их густота —

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высокой, что объясняется малым числом видов и их пониженной способностью вести активную борьбу за имеющееся пространство. В связи с воздействием комплекса неблагоприятных климатических и океанографических факторов, приливо-отливная зона холодных районов постоянно непригодна для заселения водорослями — как зимой, так и после сезонного таяния льдов. Снижение разнообразия видов по мере роста неблагоприятных условий среды, вместе с почти полным отсутствием эндемиков, свидетельствует о низком уровне приспособления. В целом, арктические сообщества должны быть отнесены к экологически незрелым.

INTRODUCTION

For this report the Canadian Arctic (Fig. 1) is considered to include all the mainland shoreline lying between Cape Chidley ($60^{\circ}25'N.$, $64^{\circ}25'W.$) and the Yukon-Alaska border ($69^{\circ}40'N.$, $141^{\circ}00'W.$). Northward from these two points in a rough triangle is the Canadian Arctic Archipelago of over 70 islands.

Much more is known about the marine life in the southeastern side (Lancaster Sound to Hudson Strait and Hudson Bay) than elsewhere in the Canadian Arctic. That the northern and western sections are much more sequestered and have a less hospitable climate could account for the regional difference in knowledge. As a review of the literature shows, nearly all published accounts of Canadian Arctic algae are based on collections that were made during the nineteenth century ship voyages that attempted to penetrate the eastern channels in search.



FIG. 1. Location map.

directly or indirectly, of the Northwest Passage. Of historic interest, the first collection of marine algae in the Canadian Arctic was made in 1850-1851 by P. C. Sutherland, who was the medical officer on a "Search for Franklin" voyage of the *Lady Franklin* and *Sophia*. The specimens, which were from Baffin Bay and Barrow Strait (Fig. 1), were identified by Dickie (1852). Subsequent marine algae collected by ship officers on 5 other historic expeditions made during 1853 to 1878 were also examined by Dickie. The 6 lists of species reported by Dickie and one other by Ashmead (1864) were all that was known about Canadian Arctic algae, when Kjellman produced his 1883 classic, "The Algae of the Arctic Sea".

To date, there are some 22 published accounts, largely lists of species, on benthic marine algae from the eastern portion of arctic Canada. For the western area, there is a single paper (Collins 1927), which resulted from the Canadian Arctic Expedition of 1913-1918. Studies by Wilce (1959) and Ellis and Wilce (1961) provide an ecological description of intertidal communities in the south-eastern Canadian Arctic. The last-mentioned two papers are significant in that they stem from an endeavour of personal field work; the reports preceding that of Wilce (1959), with the exception of one or two, are based mainly on specimens and data received from members of geographic explorations.

From 1967 I made 4 collecting trips to the Canadian Arctic, of which one was in the eastern section and three were in the western. The areas sampled were in Hudson Strait, Baffin Bay, Lancaster Sound, Amundsen Gulf and from M'Clure Strait to Brock Island. As these surveys represent only indentations into a vast area that constitutes one third of Canada, this report merely attempts broadly to interpret the general relationship between the benthic marine flora and its environment.

OBSERVATIONS AND DISCUSSION

As discussed by Ekman (1953), although the arctic marine habitat supports relatively few animal species, each kind is represented by a greater abundance of individuals than in lower latitudes. With the marine plants, it is equally true that the number of species is small; for example, it amounts to about 35 per cent of the number Dawson (1961) has recorded from Alaska to Washington and 45 per cent of what Taylor (1957) has described from Labrador to the New England states. But the apparently high concentration of individuals of a given species should not be interpreted to be a particularly arctic adaptation. While studying attached community development in British Columbia (Lee 1966), there was clear evidence that the frequency of occurrence of a species could be modified by the degree of establishment of other species. With fewer species competing for the available growth space, the arctic populations can be expected to be large. Moreover, the overall pattern of distribution of the Canadian Arctic species, which is discussed below, indicates that as polar conditions intensify there is a pronounced decrease in species diversity (number). There is, then, the possibility that of the existing small number of arctic species, most are ineffectual com-

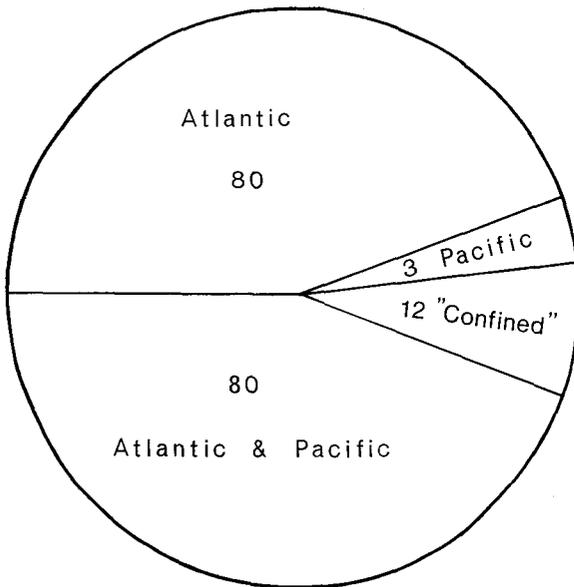


FIG. 2. Composition of the Canadian Arctic algal species relative to their occurrence in the Atlantic and Pacific.

petitors against those that find the conditions more favourable. Unless the high density of an arctic population is determined by a factor that somehow predominates over the effect of space competition, it cannot be attributed to be an arctic adaptation.

A notable feature of the Canadian Arctic marine flora is that despite the unique habitat its species composition is distinctly temperate Atlantic (Fig. 2). One apparent reason for such an affiliation is the relatively wide-open communication between the Atlantic and arctic waters. On the other hand, the continuous northward flow of Pacific water through the narrow Bering Strait should not be overlooked, for this intrusion occurs in a volume great enough to alter the character of the Arctic Ocean water (Coachman and Barnes 1961). Using approximate figures (Fig. 2) from a work in preparation, of the 175 species known to occur in the Canadian Arctic, 160 are in temperate waters of the Atlantic. Half of the 160 extend into the Pacific as well. In distinct contrast, no more than 3 arctic species are found in the Pacific but not the Atlantic. The remaining 12 species have a more confined distribution, of which some are restricted to the Arctic, whereas others extend into the Bering Sea or along the Labrador coast.

In all probability there would be a greater numerical affinity between the Canadian Arctic and Atlantic (or Pacific) floras, but for the fact that only a small number of species are capable of enduring the rigorous arctic environment. Several physical conditions seem to be most effective as limiting agents. The conditions in themselves are not necessarily unique to the Arctic, but their distribution in time (prolonged) and space (extensive) is a distinctive feature. Depending upon a species' level of tolerance for intensifying polar growth conditions, it could be completely excluded or its range of establishment could be restricted to widespread.



FIG. 3. Rocky shore, near low tide, with dark patches of *Ulothrix*, *Blidingia*, *Urospora* and *Rhizoclonium*, among others. Westbourne Bay, opposite Ongalaota Island, southern Baffin Island, 26 July 1967.

Proceeding east to west in the Canadian Arctic, the algal communities increasingly tend to occur as small and widely scattered units. This is partly due to substrate limitations for, except in the region bordered by Baffin Bay and Hudson Strait (Fig. 3), exposed bedrock and large boulders are very infrequent. The shores down to the bottom of deep channels are more often of unconsolidated, small-sized material: cobbles, pebbles (Fig. 4) and, especially where there is a freshwater discharge, silt or clay (Fig. 5). Whatever shape or form the flow of water is from land (that is, river, stream or diffuse seepage from a wet low-lying area), the adjacent shore over a wide area to the bottom of deep water is characteristically muddy. These areas have no attached growth, and their extensive and frequent occurrence effectively isolates the benthic communities to the available pockets of rocky material.

But the distribution of some species goes beyond the normal requirement of a suitable substrate. For example, at the M'Clure Strait and Amundsen Gulf portions of Banks Island, viable unattached communities were found lying on the silt and clay bottoms of calm bays. Examination of the specimens collected indicated that their loose accumulation was probably due to both transport by currents and *in situ* growth. Some of the identified forms included a dwarf *Fucus* species, *Desmarestia aculeata* (L.) Lamour., *Sphacelaria plumosa* Lyngb., *Halosaccion ramentaceum* (L.) J. Ag., *Phyllophora truncata* (Pall.) Newr. & Tayl. and *Chaetomorpha melagonium* (Web. & Mohr) Kütz. There were 3 environmental conditions common to the different bays: low temperatures, low salinities and one or more freshwater inflows. The low salinity was more likely a limiting factor, but the low temperature and apparently ample transport of nutrients from



FIG. 4. Cobble and pebble shore with ice-pushed ridge, south shore of Cape Fisher in Hecla and Griper Bay, Melville Island, 16 August 1968.



FIG. 5. Muddy shore just south of Depot Island in Hecla and Griper Bay, Melville Island, 16 August 1968.

land probably contributed a great deal to the survival and growth of the unattached populations.

Dunbar (1968) has emphasized the problem of nutrient replenishment and its significance over temperature and light in affecting the production of phytoplankton in the Arctic. Nutrient supply seems to be just as important for the establishment and production of the benthic algal communities. It is even possible that the absence of an algal community in an otherwise suitable habitat could be directly related to an inadequate supply of nutrients.

Large tides and waves, two effective ways of transporting nutrients in shallow depths, are localized and generally seasonal owing to ice hindrance. According to the Canadian Hydrographic Service (1971), Hudson Strait and the southeast coast of Baffin Island (particularly Frobisher Bay and Cumberland Sound) have the highest tides, with a mean range of 3.1 to 9.2 m. Other areas having relatively large mean tides are western Hudson Bay (to 4.2 m.) and eastern Ellesmere

Island (to 2.9 m.). For most of the central and all the western sections of the Canadian Arctic, the mean tidal amplitude is within the somewhat negligible range of 0.03 m. to 1.0 m. Shallow water agitation caused by wave action also tends to diminish in the same westward direction. This is primarily because of the increasing amount of ice cover (Figs. 6 and 7), which protects the water against wind stress for most of the year. Even after ice break-up in the brief summer season, the presence of pack ice can effectively dampen wave formation (Shapiro and Simpson 1953).

Vertical transport of nutrients from deep water is also hampered by arctic conditions. The upper (from 0 to 200 m. depending on the sill depth) Arctic Ocean water filters through the western channels of the Archipelago and eventually mixes with the warmer water of Baffin Bay. Bailey (1957) has recorded the summer temperature and salinity of the surface water layer (0 to 20 m.) in the western part of the Archipelago to be -1.0 to 2.2°C . and 4.1 to 27.4‰. At the opposite Baffin Bay side, he noted a deeper surface layer (0 to 75 m.), in which the temperature ranged between 2.0 and 6.4°C . and the salinity was from 31.0 to 32.5‰. The considerable salinity variation between the two regions seems to be a seasonal phenomenon, resulting from differences in ice concentration and subsequent ice melt. For example, in M'Clure Strait, during a year when the ice cover was 90 per cent or more, Collin (1962) recorded salinities of a normal 31.5‰ in winter to a low of less than 5.0‰ in summer. The formation of the brackish water layer extended down to the 10 to 20 m. depth, and it persisted until the return of freeze-up in September. To what extent the brackish layer increases water stability is not known, but its occurrence during the growing season can only aggravate the problem of nutrient replenishment.

Thus ice cover not only has a dampening effect on wind-generated water movement, but it also deters vertical mixing between water layers by density gradients. As shown in Figs. 6 and 7, ice conditions become increasingly severe towards the western and northern sections of the Canadian Arctic. This is because of the prevailing low air and water temperatures in these areas.

The overall pattern of algal distribution can be related to this largely longitudinal difference of physical conditions. Nearly 95 per cent of all the known Canadian Arctic species grow in the eastern section along Baffin Bay and into Hudson Strait. But in the western parts, where the environment is much more rigorous, the number of species is only about 40 per cent of the total. Many of the species in the southeastern section, being ill-adapted extensions of a predominantly North Atlantic flora, are probably just below the threshold of being eliminated from the Arctic. Their absence in colder parts of the Archipelago is an indication of their present marginal existence.

There are, however, some species that are able to live underneath a 10-month-old, perhaps even longer lasting, mantle of thick ice. These species apparently are able to tolerate prolonged dark periods and a probably life-long immersion in water that is below 0°C . Such conditions prevailed in one of the most extreme habitat locations sampled, which was the channel between Brock Island and Mackenzie King Island.

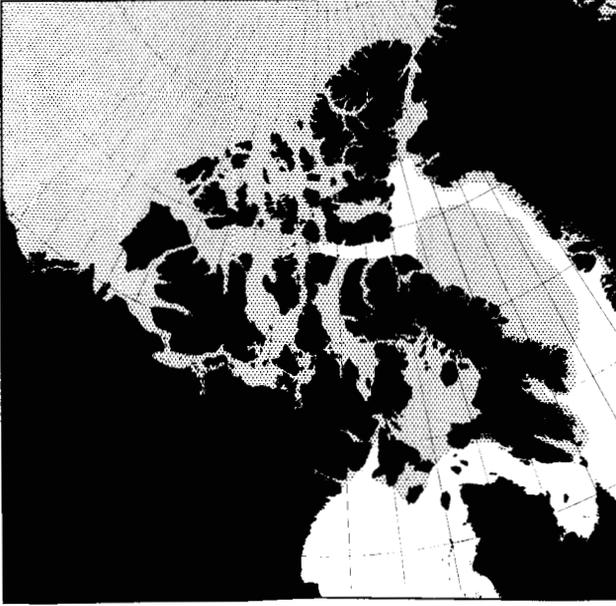


FIG. 6. General winter sea-ice cover (stippled) of both consolidated pack ice and continuous ice sheet. Adapted from Canadian Hydrographic Service (1970) data.



FIG. 7. Summer extent of 70 to 100 percent ice cover (stippled) during a favourable year. Adapted from Canadian Hydrographic Service (1970) data.

Bordering the Arctic Ocean, the habitat is in an area that has a solid cover of ice through most of the year (Black 1965; Lindsay 1969). Even during a recorded year (1962) of minimum ice cover, the ice around the islands north of M'Clure Strait did not break up until early August, after which time a moving ice cover persisted to the following month, when young ice formed and consolidated the floes (Black 1965). In August of 1968 there was a small patch of open water between the above-mentioned islands of Brock and Mackenzie King.

It was the only significant disruption in a solid mantle of ice that extended from Prince Patrick Island to beyond Borden Island in the north, and as far east and west as one could see while airborne between the two islands. According to Black (1965), the channel is a polynia, or an area of recurring open water.

The disrupted portion was about 4 by 7 km., within which was a 40 per cent cover of ice floes that was being moved northward by a slight current. Temperature measurements of the surface water varied from -1.4 to -1.0°C . within a 3-hour period. The Brock Island channel shore was composed of small cobbles which, typical of unconsolidated beach material, were pushed by ice into ridges (as in Fig. 4, also Owens and McCann 1970). The cobbles extended below the waterline, where they gradually mixed with a black clay-like sediment. A fuzzy coating of diatoms, other kinds of unicellular algae and unbranched filamentous forms, such as *Ulothrix*, were on the submerged cobbles. Colonization by these ephemeral, fast-growing plants (Lee 1966) can evidently take place only after the cobbles are no longer ice-bound and subsequently are little disturbed by pack ice.

Dredging was done from about 40 m. off the Brock Island shore at depths of 7 to 12 m. where the substrate consisted of small boulders, cobbles and from pebbles to clay. Several drags disclosed the presence of a robust, well-established community of animals (including bryozoans, hydroids, annelids, sea urchins and molluscs) and such algae as *Giffordia ovata* (Kjellm.) Kylin, *Omphalophyllum ulvaceum* Rosenv., *Sphacelaria arctica* Harv., *Desmarestia viridis* (O. F. Müll.) Lamour., *Laminaria solidungula* J. Ag., brown crust spp., *Spongomorpha* sp., *Phycodrys rubens* (L.) Batt., melobesioid spp. and *Turnerella pennyi* (Harv.) Schm., within which were cells of *Chlorochytrium inclusum* Kjellm. Indicative of the community's extreme arctic habitat are the small number of species and appreciable proportion of "arctic-type" species (the most obvious ones are *Omphalophyllum ulvaceum*, *Sphacelaria arctica*, *Laminaria solidungula* and *Turnerella pennyi*).

The intertidal zone of most of the western Canadian Arctic is generally uninhabited. As in the subtidal region, the intertidal substratum is most often made



FIG. 8. Intertidal community, of which *Fucus* is the dominant alga, on pebbles and cobbles strewn on mud. At Cape Dorset settlement, southern Baffin Island, 30 July 1967.

up of loose particles that range from small cobbles to fine clay. But even where a stable rocky substrate is available, as in certain parts of Amundsen Gulf, the few species that do occur form very sparse populations. Optimum intertidal growth, in terms of number of species and density, takes place in the warmer southeastern part of the Canadian Arctic, from Baffin Bay to Hudson Strait (Fig. 8). Here a representative intertidal community includes the green algal genera *Enteromorpha*, *Blidingia*, *Ulothrix*, *Urospora*, *Rhizoclonium* and *Codium*; the brown algae *Fucus*, *Ralfsia*, *Pseudolithoderma*, *Petroderma*, *Litosiphon*, *Sphacelaria* and *Pilayella*; and the red alga *Rhodochorton* (see also Wilce 1959; Ellis and Wilce 1961). Both the number of species and development of populations dwindle beyond this region.

The related factors of heavy ice conditions, low salinity, and low air and water temperatures are the most plausible ones to consider in attempting to determine the reason for the limited northwestward penetration of intertidal species. As already mentioned, compared to the Baffin Bay and Hudson Strait shores, those of the northwest remain ice-bound for a longer, more often continuous, period. When the heavy ice formation breaks up, coincidental with the barring of the intertidal habitat is its immersion in the seasonally developed layer of brackish water.

Besides the colder water, the ice-free shore is subject to the lowest daily maximum air temperatures of the Archipelago. According to a 1951-1960 climatological data compilation (Thompson 1967), during July, the warmest month, the Prince Patrick Island and Borden Island region has mean daily maximum temperatures of 6.1 to 6.5°C., while from Frobisher Bay into Hudson Strait the same maximum reaches 12.0°C. Both sections have for the same month mean daily minima within the range of 0.9 to 1.4°C.

Scouring by ice movements has been overemphasized in the literature to the point of being meaninglessly stated to be the cause of the overall barren condition of the arctic intertidal habitat. The significance of ice scouring is that it is a disruptive agent subsequent to habitation. During a mild year, the intertidal zone in some sections of the colder northwestern part of the Archipelago may become available for colonization for 2 or 3 months after ice melt. Within this period of substrate exposure, scraping by ice floes, the severity of which varies locally in time and space, can hardly account for the widespread paucity of intertidal growth. At the Juan de Fuca Strait shore of British Columbia, denuded intertidal substrates were colonized by fast-growing green algal forms, such as *Ulothrix*, *Urospora* and *Enteromorpha*, within a period of less than 15 days (Lee 1966). These genera do colonize shores of the eastern section of the Canadian Arctic. Perhaps the prolonged low air temperature should be considered as one possible cause for the nearly complete lack of intertidal growth in the western section. Supplemented by the daily submergence in brackish and below 0°C. water, the possibility of colonization by any species seems remote.

To conclude, a comment on ecological development seems appropriate. A major generalization of biogeography is that the number of species tends to decrease towards the higher latitudes. Although poorly understood ecologically,

the change in diversity is at least indicative of a pattern of adaptation along environmental gradients. The low order of diversity of the arctic algal species, the way they are distributed, and the almost complete lack of endemics all point to a low level of adaptation. Perhaps the suggested incipient adaptation is a reflection of a high gradient of physiological stress brought on by a fluctuating and unstable environment (Dunbar 1968; Sanders 1968). The arctic algal communities may indeed be relatively young in the course of ecological evolution, just as Dunbar (1968) had postulated for the arctic ecosystem as a whole.

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