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ICE ALGAL INVESTIGATIONS: HISTORICAL PERSPECTIVE

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Abstract: Organisms that live in sea ice have been known and studied for over 150 years. The earliest studies were done on samples collected during voyages of exploration and are mainly lists of species. Experimental investigations began in the 1960s and, in the first 20 years, consisted primarily of pioneering studies on primary productivity, biomass, spatial and temporal distributions, and composition and abundance of the biota. By the 1980s, there were better techniques for measuring primary productivity and biomass and more emphasis was placed on physiological studies. Much of this work was done from shore-based stations. However, in the late 1970s, ice-breaking or ice-strengthened research vessels became available and since then, large, multi-disciplinary investigations, involving biologists, ice physicists, and chemists, have worked mostly in the marginal seas of polar regions, although Canadian and U.S. icebreakers crossed the Arctic Ocean via the North Pole in the summer of 1994. Drifting ice floe and ice island stations have provided information from the central Arctic Ocean since the 1930s, and in 1992 from the Weddell Sea.

1. History before 1900

Ice algal investigations began in the early to mid 1800s, often during voyages of discovery. There was great interest in natural phenomena and naturalists, or medical doctors who doubled as naturalists, often accompanied these voyages. The botanist, Joseph HOOKER (1847) gave the first description of ice algal populations from the Antarctic:

"The Waters and the Ice of the South Polar Ocean were alike found to abound with microscopic vegetables belonging to this Order (Diatomaceae)."

Later, in describing where and how his samples were collected, HOOKER said: "Ice encloses *Diatomaceae*: they are deposited on the already formed ice by the waves, or frozen into its substance during calm weather, when the upper stratum of water rapidly congeals. .... The Pancake-ice was often seen a few hours after a calm, covering leagues of ocean, and uniformly stained brown from the abundance of these plants. It was taken in buckets, and when removed from the water appeared perfectly pure and colourless. On melting, however, it deposited a pale red cloudy precipitate, ..., consisting wholly of *Diatomaceae*. This precipitate was bottled on the spot, and proved more rich in species than any of the other collections. The specimens were also the best preserved;...."

In the Arctic, SUTHERLAND (1852) found small cavities containing "a greenish slimy-looking substance" that gave out a "fetid smell" after a few days exposure to air. He wrote that "the vital action going on in such masses, ..., would maintain a temperature a little above the surrounding medium, which would easily produce the small cavities that attracted our notice." SUTHERLAND was apparently the first person to describe organisms other than diatoms from the ice when he looked at decayed ice and saw a "brownish, slimy substance ... teeming with animal life and minute vegetable forms of very great beauty." He also reported a summer ice flora (see below).

Also in the Arctic, Robert BROWN (1868) supplied a good early description: "In June 1860, whilst the iron-shod bows of the steamer I was on board of crashed its way through among the breaking-up floes of Baffin's Bay among the Women's Islands, I observed that the ice thrown up on either side was streaked and discoloured brown; and on examining this discolouring matter I found that it was almost entirely composed of the siliceous moniliform *diatom* I have described as forming the discolouring matter of the iceless parts of the icy sea" (*i.e., Melosira arctica*).

Most of the early papers were taxonomic in nature, with EHRENBERG (1841, 1853) providing the first taxonomic information on diatoms collected from sea ice based on samples collected by HOOKER and SUTHERLAND. These early papers were primarily lists of species found in various places and descriptions of new species, sometimes with some natural history based on personal observations, as in the case of SUTHERLAND's report (1852).

In the Arctic, the same species were found in sea ice collected across the Arctic Basin. Thus, NANSEN (1898) reasoned that there must be some passage or current between Bering Strait and Greenland. As a result, ice diatoms provided some of the impetus for the First Norwegian North Polar Expedition on the FRAM. The best and most extensive early description of the ice algal community and its ecology is that of GRAN (1904) based on samples collected by Dr. BLESSING during the FRAM expedition. Diatoms were found as free-floating lumps and masses between ice floes, on the ice foot at the bottom of ice floes, in holes in the bottom of freshwater melt ponds not connected with the underlying seawater, and in newly formed ice. NANSEN (1906) described "infusoria and flagellates" and bacteria and their habitats beginning with observations from the East Greenland Sea in 1882 and Denmark Strait in 1888.

2. History since 1900

In the first half of this century, a number of investigators mentioned ice algae and USACHEV's papers from the 1930s and 40s reviewed previous work, especially that of Russian investigators (USACHEV, 1938, 1949). Freshwater diatoms and green and bluegreen algae were reported from ice that probably formed in the Yenisey River (USACHEV, 1938). Twenty-four diatom species that developed on the lower surface of the ice and occurred in all his Arctic samples were described as cryophiles (USACHEV, 1949). Further, the ice communities consisted of benthic and littoral diatoms and were different from planktonic communities consisting of centric planktonic diatoms (*e.g., Chaetoceros, Rhizosolenia,* and *Thalassiosira* spp.). Also in the 1930s, the Russians started their long series of North Pole drifting stations.

In the Antarctic, a number of scientific expeditions provided information, including the German Antarctic Expedition of 1901–1903 (HEIDEN and KOLBE, 1928) and the British DISCOVERY cruises with the work of HART (1934, 1942) and HENDEY (1937), but observations on ice algae were incidental to research on phytoplankton.

The International Geophysical Year (IGY) of 1957–58 brought renewed interest in polar regions and the beginning of experimental studies on ice algae. APOLLONIO (1961, 1965) showed the effects of snow depth and light levels on chlorophyll concentrations in the ice and pointed out that ice algae were a concentrated, potential source of food for herbivorous zooplankton in the spring, well before phytoplankton were available for food in the water column. ENGLISH (1961, pers. commun.) pioneered diving under the ice at the U.S. Drifting Station Alpha and may have been the first to describe amphipods grazing on an ice community, a phenomenon also seen by APOLLONIO (1965).

In 1962, HOSHIAI and KATO published their ecological notes on the diatom community of Antarctic sea ice. They found 21 species of diatoms, many of them centrics, determined their vertical distribution in the ice, and said that most of the species were common to both the ice and water column, especially in pack ice regions, thus beginning comparisons between the ice and water column communities that continue to the present time. During this period, MEGURO (1962) studied what he called plankton ice found in a layer of snow 15–20 cm thick located at the snow-ice interface and infiltrated with seawater containing algal cells.

Also in the early 1960s, BUNT and WOOD (BUNT, 1963; BUNT and WOOD, 1963) wrote their classical papers on Antarctic ice algae and first used the term *epontic* for the ice community. The term *sympagic* is now preferred because it indicates a relationship with ice (WHITTAKER, 1977; CAREY, 1985; HORNER *et al.,* 1992). In a long series of papers, BUNT and his colleagues (*e.g.,* BUNT, 1964a, b, 1968a, b; BUNT and LEE, 1970, 1972) reported on seasonal primary production, ecology, and physiology, finding that the ice algae were shade-adapted.

In the Arctic, MEGURO *et al.* (1966, 1967), working in the Chukchi Sea, suggested that cells were frozen into the ice when it formed and probably survived by producing cysts. They thought that grazing did not occur within the ice, but only after the ice algae were released into the water column.

In the 1970s, ACKLEY and co-workers (ACKLEY *et al.,* 1979) studied ice properties in the Antarctic, and suggested a model for the formation of an interior ice community. Moreover, they related characteristic assemblages to particular localities in the ice and suggested the terms surface, interior, and bottom for those assemblages, terms that are still recommended today (HORNER *et al.*, 1992).

In the Arctic, GRAINGER (1977, 1979) studied nutrient cycles and primary production at Frobisher Bay. ALEXANDER, HORNER and their co-workers followed the annual cycle of production, biomass, and species and pioneered the *in situ* measurement of primary production in the Chukchi Sea off Barrow, Alaska (HORNER and ALEXANDER, 1972; CLASBY *et al.*, 1973; ALEXANDER *et al.*, 1974; MATHEKE and HORNER, 1974; ALEXANDER, 1974; GRANT and HORNER, 1976).

By the 1980s, a new group of investigators began studying the ice communities. In the Antarctic, SULLIVAN and colleagues worked at McMurdo Sound (*e.g.*, PALMISANO and SULLIVAN, 1983, 1985; PALMISANO *et al.*, 1985; MCGRATH GROSSI *et al.*, 1987; SULLIVAN *et al.*, 1985; ARRIGO *et al.*, 1993) and in the marginal ice zone of the Weddell Sea (*e.g.*, SULLIVAN *et al.*, 1988; COMISO *et al.*, 1990; LIZOTTE and SULLIVAN, 1991, 1992); HOSHIAI and his co-workers continued their investigations at Syowa (*e.g.*, HOSHIAI, 1985; SASAKI and HOSHIAI, 1986; WATANABE and SATOH, 1987); MCCON-

VILLE studied ice algae at some of the Australian stations (MCCONVILLE, 1985; MCCONVILLE *et al.*, 1985), and LIGOWSKI worked in the South Shetland Islands (LIGOWSKI, 1987, 1991; LIGOWSKI *et al.*, 1992). In the Arctic, the U.S. dropped out of investigations at shore-based stations with the closure of the Naval Arctic Research Laboratory at Barrow, but fortunately, investigations persisted in the Canadian Arctic with continuing studies at Frobisher Bay (GRAINGER and HSIAO, 1982, 1990; GRAINGER *et al.*, 1985a; HSIAO, 1980, 1983, 1988, 1992), Hudson Bay (*e.g.*, LEGENDRE *et al.*, 1981, 1987, 1991, 1992; GOSSELIN *et al.*, 1985, 1986; MAESTRINI *et al.*, 1986; MICHEL *et al.*, 1988, 1993; TREMBLAY *et al.*, 1989; LEVASSEUR *et al.*, 1994), Resolute (*e.g.*, COTA, 1985; COTA *et al.*, 1987, 1990; HARRISON *et al.*, 1990; SMITH and HERMAN, 1991, 1992; SMITH *et al.*, 1988, 1990; STURGES *et al.*, 1992; WELCH *et al.*, 1991), and elsewhere (*e.g.*, IRWIN, 1990; DE SÈVE and DUNBAR, 1990, 1991).

There were many cruises in polar regions during the 1980s and early 1990s. In the Antarctic, the U.S. had cruises on icebreakers and research vessels in the Ross and Weddell Seas. Much of this work was on ice-edge phenomena, but GARRISON (*e.g.*, GARRISON and BUCK, 1985, 1989, 1991; GARRISON *et al.*, 1987; GARRISON and WATANABE, 1991; GARRISON and CLOSE, 1993) and SULLIVAN (*e.g.*, SULLIVAN *et al.*, 1988; LIZOTTE and SULLIVAN, 1991, 1992) also studied algae in the pack ice. The first drifting floe station in the Antarctic, ISW-1, was occupied by Russian and U.S. investigators from February to June 1992 (FRITSEN *et al.*, 1994; MELNIKOV, 1994).

In the Arctic, the Norwegian PRO MARE ecosystem investigations in the Barents Sea included ice algal work (*e.g.*, SYVERTSEN, 1991; HEGSETH, 1992; SYVERTSEN and KRISTIANSEN, 1993). The importance of polynyas in polar ecosytems became known and an international group of investigators worked in the Northeast Water polynya off the northeast coast of Greenland in 1992 and 1993. And lastly, there was the Canada/ U.S. transect across the Arctic during the summer of 1994 (ANONYMOUS, 1994).

Perhaps the greatest single push for polar research in general, but also ice algal studies, was the 1982 commissioning of the German research vessel POLARSTERN that carries out multi- and interdisciplinary investigations in both polar regions. Many new scientists were brought into the field, for example during the European Polarstern Studies (EPOS) cruises of 1988–89 (*e.g.*, HEMPEL, 1989; HEMPEL *et al.*, 1989; RIEBESELL *et al.*, 1991; papers in Polar Biology 12(1, 2), 1992). Many cruise and scientific reports and scientific papers have been written from these journeys, some on ice algae (*e.g.*, BARTSCH, 1989) or with ice algal components (*e.g.*, BATHMANN *et al.*, 1992; SPINDLER *et al.*, 1993).

3. Kinds of Research

Research on ice algae has been variable and wide-ranging. Studies have been conducted by biologists, physicists, chemists, and geologists, with most of the earlier work being done by biologists. Investigations have included taxonomy, ecology, physiology, productivity, chemical composition, and ice structure.

One of the first factors to consider is the character of the ice itself. This work has been done mostly by ice physicists, but lately biologists and physicists are working together to determine physical features of the ice environment that influence the biology (*e.g.*, LANGE *et al.*, 1989; SPINDLER, 1990; WEISSENBERGER *et al.*, 1992; ACKLEY and SULLIVAN, 1994).

An old question with regard to the algae, and one that is still important, is how do the cells get into the ice? Both HOOKER (1847) and BROWN (1868) commented on this, but the initial formation and development of the ice communities is still not known with certainty. It may involve physical concentration as the ice forms (ACKLEY, 1982; GARRISON *et al.*, 1983), flooding (MEGURO, 1962), deformation (ACKLEY, 1985), or other processes (ACKLEY *et al.*, 1979).

What kinds of algae live in the ice? At least 10 taxonomic classes of algae are present, including pennate and centric diatoms, autotrophic and heterotrophic dinoflagellates, autotrophic and heterotrophic flagellates from several classes, euglenoids, and choanoflagellates (HORNER, 1985).

Where do the algae live in the ice? Early investigations dealt with the bottom few centimeters of the ice, but we now know that cells live throughout the ice and in a variety of habitats (*e.g.*, SYVERTSEN, 1991; HORNER *et al.*, 1992; ACKLEY and SULLIVAN, 1994).

Seasonal studies have been important. Spring is the time most studied because that is when the bottom ice communities are dominant, but populations are present in the ice at all times of the year. In the Arctic, APOLLONIO (1985) pointed out the summer community with observations on *Melosira arctica*, a community that was already known to SUTHERLAND (1852) in 1852 and BROWN (1868) who saw the moniliform diatom during his 1860 cruise. Is there a summer ice community similar to this in the Antarctic? In the Antarctic, an autumn bottom ice community, present from February to October, has been described from Syowa Station by HOSHIAI (1985) and WATANABE and SATOH (1987). In the Weddell Sea pack ice, FRITSEN *et al.* (1994) observed an autumn bloom from February to June in the so-called freeboard, or porous, layer just under the water surface. GARRISON and CLOSE (1993) and BARTSCH (1989) described winter blooms having carbon, chlorophyll *a*, and cell abundances similar to communities found in other seasons. GARRISON and CLOSE suggested that since this is the time of rapid ice formation, it may be the time when cells first become established in the ice.

The ice algae need nutrients and these come from ice desalinization, biological regeneration *in situ,* and mixing with the adjacent water column (*e.g.*, MEGURO *et al.*, 1967; COTA *et al.*, 1987). Nutrients must be supplied to relatively thin, dense layers of cells and thus, availability varies both seasonally with ice growth and over shorter time scales due to hydrodynamic forcing such as tides and internal waves (COTA *et al.*, 1991). Nutrient limitation may occur toward the end of a bloom (COTA *et al.*, 1987; GOSSELIN *et al.*, 1990). Unfortunately, nutrient concentrations and fluxes have not been measured yet in the actual algal microenvironment (COTA *et al.*, 1991) and new technology is needed to determine these changes on small scales of meters to millimeters.

Light has been called the most important environmental factor controlling the initiation and early growth of the ice algae (COTA *et al.*, 1991). While the cells are adapted to the relatively low light levels at the bottom of the ice, they are also able to adapt to changes in irradiance over periods of days, so are not an obligate shade flora (COTA and SMITH, 1991b).

Temperature effects are variable for both ice algae and high latitude phytoplankton, but many species have optimum temperatures higher than ambient for photosynthetic carbon assimilation. However, production and growth rates are low and consistent with both low temperature and irradiance levels (COTA and SMITH, 1991a).

A number of investigators have found that ice communities have tremendous spatial variability-both vertically and horizontally (*e.g.*, POULIN *et al.*, 1983; MCGRATH GROSSI *et al.*, 1987; COTA and SMITH, 1991a). This may be in terms of biomass, production, or species presence and abundance, but the variability and scales of variability have not been adequately studied.

We now know that no one factor is responsible for biomass accumulation in the ice, and that many factors including latitude, water depth, nutrient availability, local climate, hydrographic regime, ice type, and loss terms (*e.g.*, grazing, respiration, sinking) all influence the ice community (COTA *et al.*, 1991).

What is the fate of the ice algae? A number of suggestions have been made. They may initiate the spring phytoplankton bloom in the water column or be some unknown contribution to the planktonic system. To some extent, this may depend on water depth and loss factors. For example, in the Bering Sea when the ice edge is over deep water in cold years, the zooplankton community is able to ingest a wide range of particle sizes and more of the ice edge production is grazed. However, when the ice edge is receeding or during warmer years when it is over shallow water, the zooplankton population cannot utilize all the organic material and it sinks to the bottom (NIEBAUER *et al.*, 1981). Often, however, the ice algae and the phytoplankton are clearly separated floristically, temporally, and spatially (HORNER, 1984). Cells may rapidly sink to the bottom and be eaten by benthic invertebrates or be incorporated into the sediments where they are sometimes used as indicators of past climatological conditions (SANCETTA, 1981). Also, cells may dissolve during sinking, especially if, as is often stated, they are weakly silicified especially at the end of a bloom; and they may be grazed either in the ice or in the water column.

One of the biggest problems is still sampling. And, as with other factors affecting ice algal communities, this one depends on season, location, ice conditions, and parameters being measured. A number of methods to collect, prepare samples for analysis, and for productivity measurements have been described and most work for the area where they were used, but might not work elsewhere. However, because of this variety of methods, it is often difficult to compare values between locations and investigators. Moreover, many investigators still do not describe their methods adequately (HORNER, 1990; HORNER *et al.*, 1992; COTA and SMITH, 1991a).

Ice algae are known also from lower latitudes in the northern hemisphere, *e.g.*, the Baltic and Oslofjord in Europe (HASLE and SYVERTSEN, 1990; NORRMAN and ANDERSSON, 1994), Gulf of St. Lawrence in North America (DE SÈVE and DUNBAR, 1990, 1991), and Lake Saroma, Japan (HOSHIAI and FUKUCHI, 1981).

The earliest papers on ice algae were primarily taxonomic and they are still being written, *e.g.*, the Polar Diatom Manual (MEDLIN and PRIDDLE, 1990) with sections on ecology and taxonomy. Individual papers are also still abundant with new species being described, *e.g.*, MEDLIN and HASLE (1990)

And finally, where do we go from here? Many questions are left to be answered. We need to look at the available data, identify gaps, and make comparisons between communities and polar regions. A beginning are the papers by COTA *et al.* (1991) and COTA and SMITH (1991a, b). The biggest problem involves sampling and devising methods to work at the scales necessary to determine production, biomass, salinity, and nutrient levels in the microenvironment of the algae. Spatial distributions are still a question. What causes large differences over small areas? What is the relative importance of the various loss factors? How much grazing actually occurs within the ice? What is the role of the nano-and meiofauna in the ice? Can remote sensing be used to detect ice populations? Obviously there are still many unanswered questions, and despite nearly 10 years of new and very intensive research in a variety of places, many of the unanswered questions are the same ones posed in 1985 (HORNER, 1985).

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