

## THE SIGNIFICANCE OF AUTUMNAL SEA ICE BIOTA IN THE ECOSYSTEM OF ICE-COVERED POLAR SEAS

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**Abstract:** The autumnal sea ice proliferation occurs at Syowa Station. The algal cells produced support the ice meiofauna and possibly planktonic and benthic consumers. However, the autumnal bloom of ice algae has received little attention from polar biologists during long-term history of sea ice biota research. The geographical distribution, and ecological importance and function of the autumnal ice algal community is reviewed and compared with the spring ice community.

### 1. Introduction

The importance of ice algae as one of the primary producers in the ecosystems of ice-covered sea has been comprehensively recognized (ALEXANDER, 1974; HORNER, 1985; KNOX, 1994). Recently, the function of ice algae and phytoplankton in the geochemical cycle of carbon in the polar seas has been examined in relation to the global change in natural environments (LEGENDRE *et al.*, 1992). To increase the understanding of the physiology and role of ice algae and phytoplankton in the carbon cycle, the photosynthetic activity and other physiological processes of algae have been intensively investigated (SMITH and SAKSHAUG, 1990). However, such basic problems as the spatial extent, the seasonal change and ecological role of ice algae in the ice-covered waters remain to be more thoroughly investigated.

Although the spring-summer blooms of ice algae have attracted the interest of many scientists due to their relatively large biomass, the autumnal blooms have received less attention. It seems, however, that autumnal ice algae play a key role in the ice-covered coastal ecosystem. To fill the gap in the present knowledge of the sea ice biota, we here review the papers on the geographical distribution of autumnal ice algal communities and the reports dealing with their role as the food resource for the copepods living in the sea ice, and compare these data with the results obtained during investigations in the vicinity of Syowa Station (69°00' S, 39°35' E). The distribution of ice algae and sea ice meiofauna and feeding of meiofauna on the ice algae has been assumed for a long time but actual data to verify the relationship are not always sufficient. Differences in the methods used for research, as well as the seasons and locations of studies makes it difficult to compare and the evaluate the available data. Accordingly, our attempt to review the reports dealing with sea ice copepods in the polar oceans is a first step toward future development of an ecological study of sea ice biota.

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## 2. Sea Ice as Habitat of Ice Biota in the Vicinity of Syowa Station

The surface community of ice algae develops at the interface of snow and sea ice in the ice floes in the drifting ice zone, while the bottom community occupies the lowermost part and undersurface of the sea ice in the fast-ice field south of 68°S between 30°E and 45°E (MEGURO *et al.*, 1992). Syowa Station is situated at an island named East Ongul surrounded by the fast-ice field. Usually the major part of the fast-ice field persists in the summer, but part of the ice field melts locally and small open water areas are formed here and there in mid-summer. However, the fast-ice field breaks up in late summer to autumn at intervals of several to ten years. The break-up of fast-ice rarely occurs in mid-winter. Thus, we are able to observe the developmental process of the ice algal community in the new ice from an early stage. Freezing of open water usually begins in mid-February. The sea ice thickness is about 30 cm by late March but does not grow remarkably until mid-April. Notable growth of the ice occurs between mid-April and mid-September, when the ice thickness is between 100 and 150 cm. Thereafter, the growth of the ice is extremely slow. The ice algal blooms in the lowermost layer of sea ice occur both in autumn and in spring-summer. Occasionally, a surface community is formed at the snow and ice interface with the infiltration of sea water (WATANABE and SATOH, 1987).

## 3. Autumnal Proliferation of Ice Algae at Syowa Station

In late March 1967, an autumnal bloom of ice algae was observed at the bottom part of new ice 38 cm thick; the bottom 2 cm layer was stained brown by the densely concentrated algal cells ( $< 300 \text{ mg} \cdot \text{chl.}a \text{ m}^{-3}$ ) (HOSHIAI, 1969). The color of this layer gradually became light, extending upward and downward, but it remained as a colored band until mid-January 1968. The second bloom occurred in late December at the bottom of ice 107 cm thick. The autumnal occurrence of the brown layer at the bottom of sea ice in 1968 was reported by NARUSE *et al.* (1971). Similarly in late March 1970, a brown layer was observed at the bottom part of new ice 30 cm thick. The algal biomass was peaked at  $994 \text{ mg} \cdot \text{chl.}a \text{ m}^{-3}$  on April 16. However, the brown color gradually diminished with time and faded out by October. The spring-summer increase of ice algae began in late September and a brown layer became visible at the bottom of ice 148 cm thick in November. The highest value of ice algal biomass was  $5320 \text{ mg} \cdot \text{chl.}a \text{ m}^{-3}$  on December 12. The standing crop of ice algae at the peak of autumn and spring-summer was  $30 \text{ mg} \cdot \text{chl.}a \text{ m}^{-2}$  and  $35 \text{ mg} \cdot \text{chl.}a \text{ m}^{-2}$ , respectively (HOSHIAI, 1981a). WATANABE and SATOH (1987) reported an autumnal bloom occurring at the bottom of new ice greater than 50 cm thick that formed in early May 1983 after the break-up of the fast-ice field.

The autumnal increase of ice algae occurred not only in new ice but also in ice that remained during the summer (HOSHIAI, 1981a; WATANABE and SATOH, 1987). According to HOSHIAI (1981a), light, but visible, brown and yellow layers were formed at the bottom of these ice of 70 cm and 140 cm thick, respectively. In general, relatively higher concentrations of chlorophyll *a* were detected from the bottom layer, even though there

was no colored band.

#### 4. Factors Controlling Autumnal Proliferation of Ice Algae

As the natural conditions in which the autumnal bloom of ice algae occurs, HOSHIAI (1981b) suggested that the solar radiation of 150 to 250 cal cm<sup>-2</sup> day<sup>-1</sup> must be supplied for two to three weeks and that the undersurface of the sea ice must be stable with only extremely gradual changes of melting or accretion during the period. The stability of the undersurface of sea ice 30 cm thick, under which the sea water temperature was at the freezing point, was actually kept at air temperatures between -5°C and -10°C. The maximum snow depth was about 10 cm.

Similar conditions were found at Toetoko (44° 11' N, 143° 45' E) in Saroma Ko lagoon, Hokkaido, Japan, in February 1980, and the bloom of ice algae occurred in the bottom layer of the sea ice 35 cm thick (HOSHIAI and FUKUCHI, 1981). On February 20, 1992, KUDOH *et al.* (1995) discovered a brown layer at the bottom of sea ice about 35 cm thick at Sakaeura in Saroma Ko lagoon when solar radiation of 6000 kW m<sup>-2</sup> (≅ 143 cal cm<sup>-2</sup> day<sup>-1</sup>) to 10000 kW m<sup>-2</sup> (≅ 240 cal cm<sup>-2</sup> day<sup>-1</sup>) was supplied on the sea ice surface. The sea ice thickness of 35 cm did not change from the beginning of February, and the snow depth was less than 40 cm.

#### 5. Autumnal Ice Algal Bloom at Other Antarctic Stations

BUINITSKY (1977) discovered a dense accumulation of diatom cells (1954 cells ml<sup>-1</sup>) at the bottom of sea ice of 35 cm thick on April 20, 1968, at Mirny Station (66° 33' S, 93° 01' E). GRUZOV (1977) also observed the bottom of sea ice several centimeters thick was stained by diatoms in autumn between February 1970 and March 1972 in the same area. Although they noted the importance of the autumnal community of ice algae, the stress of their research was on the spring-summer community due to the high biomass and possible ecological effects of the latter community.

Autumnal bloomings of ice algae were reported from Casey Station (66° 17' S, 110° 32' E) by McCONVILLE and WETHERBEE (1983) and from Davis Station (68° 35' S, 77° 58' E) by PERRIN *et al.* (1987). PERRIN *et al.* (1987) observed two peaks of ice algal biomass in 1982. The first peak (140 × 10<sup>4</sup> cells l<sup>-1</sup>) appeared at the bottom layer of new sea ice 26 to 68 cm thick in April to May and the second (160 × 10<sup>4</sup> cells l<sup>-1</sup>) at the bottom layer of sea ice 152 to 194 cm thick in October to December. It is interesting that the four stations where the autumnal ice algal community was observed are situated in a zone between 66° S and 69° S latitude.

In comparing the profile of the fast ice core taken in summer 1972 at McMurdo Station (77° 15' S, 166° 40' W) with that of the 1967 overwintered core at Syowa Station (69° 00' S, 39° 35' E), HOSHIAI (1972) showed that the McMurdo core had only one brown layer 20 cm thick at the bottom of the sea ice, while the Syowa core had two brown layers. Since then, there have been no detailed investigations to determine if the autumnal blooming of ice algae occurs at McMurdo, although, GARRISON *et al.* (1986) indicated the possible presence of an autumnal algal increase in this area. LIGOWSKI (1987) reported that pack ice colored by diatoms drifted on to the seashore of Admiralty

Bay (62° S, 58° 30' W), King George Island, during winter season between June and August 1983. Since the land-fast ice was not formed in the bay in this year, the location from which the drifting ice floes came could not be identified.

GARRISON and CLOSE (1993) reported that the algal biomass frequently concentrated in the bottom of ice floes of 30 to 50 cm thick from mid-June to early July in the region surrounded by 59° S, 61.5° S latitude and 40° W, 49° W longitude in the Weddell Sea. They ascribed this high biomass (more than 20  $\mu\text{g chl.}a\ l^{-1}$ ) to the winter growth of ice algae. In addition, FRITSEN *et al.* (1994) observed the autumnal ice algal communities formed in the freeboard layer in a drifting ice floe in February to June between 71.4° S and 65.8° S along 53° W longitude in the Weddell Sea.

## 6. Autumnal Ice Algal Bloom in the Arctic Waters

Although GRAN (1904) recorded that F. Nansen discovered a brown layer containing microorganisms at the bottom part of the probably new ice in mid-October 1893 at 78° 19' N, 126° 16' E and on October 15, 1894, at 81° N, 125° E, thereafter few reports of autumnal algal proliferation have been made in the Arctic. HSIAO (1980) recorded a dense aggregation of diatoms (485906 cells  $l^{-1}$ ) at the bottom of sea ice 50 cm thick in Eskimo Lakes (69° 35' N, 131° 20' W) on November 24, 1972. SCHELL and FUKUCHI (pers. commun.) detected chlorophyll *a* of 87.8 mg  $m^{-3}$  in a yellowish bottom layer of 31 cm thick sea ice probably newly formed near Narwhal Island, Alaska, (70° 25' N, 147° 29' W) on November 9, 1980. These facts seem to indicate the possibility of the ubiquitous presence of autumnal blooming of ice algae in the Arctic Ocean, particularly in the coastal waters. It should be noted that the latitudes of both Eskimo Lakes and Narwhal Island are approximately comparable with those of the Antarctic stations where the autumnal algal bloom was observed. This implies that there is a similarity in the physical and biological conditions in autumn in the corresponding localities of both polar oceans.

## 7. Feeding of Sea Ice Copepods on the Ice Algae in the Antarctic

In the Syowa Station area, a calanoid copepod, *Paralabidocera antarctica* and the three unidentified species of harpacticoid copepods continuously inhabit the sea ice (HOSHIAI and TANIMURA, 1986). The nauplius of *P. antarctica* appeared in the interstices between ice crystals of the brown layer in late March 1970. The stage composition of nauplii gradually progressed from April to June, followed by its steady state until September. Between October and December, the abrupt growth of nauplii to the copepodite stages occurred. The two growing periods of young *P. antarctica* coincided with the autumn and spring-summer blooms of ice algae. The autumnal algal community was thought to contribute to the autumnal growth and the winter survival of *P. antarctica*. Grown *P. antarctica* moved into the water column in December. The feeding of this copepod on the ice algae was confirmed by analysis of the gut contents (HOSHIAI *et al.*, 1987). The nauplius of *P. antarctica* were one of the major food items of young nototheniid fish, *Pagothenia borchgrevinki* (HOSHIAI *et al.*, 1991). Nauplii, copepodites and adults of harpacticoid copepods occurred in the sea ice between late March and December. Feeding of harpacticoids on the ice algae similar to that of *P.*

*antarctica* was suspected.

TUCKER and BURTON (1988) noted the relationship of two species of calanoid copepods, *P. antarctica* and *Stephos longipes*, to the sea ice at Davis Station. *P. antarctica* appeared just beneath the undersurface of sea ice in September 1982 and disappeared in December with the breaking-up of the sea ice. Although TUCKER and BURTON (1988) did not mention the behavior of the nauplii, we presume that juveniles of *P. antarctica* persisted mainly in the sea ice before September there as well as at Syowa Station. In April, abundant individuals of *S. longipes* and two species of cyclopoid copepods were collected just beneath of the newly formed sea ice in which ice algae were contained as reported by PERRIN *et al.* (1987). Cyclopoids disappeared in June, but *S. longipes* stayed until December. It is possible to suspect that *S. longipes* fed on ice algae which increased in autumn and were preserved in the sea ice.

Based on observations made in the summer of 1991 in the region surrounded by 70° S, 76° S latitude and 16° W, 33° W longitude in the Weddell Sea, KURBJEWIT *et al.* (1993) hypothesized the life cycle of *S. longipes*, stressing the close relation to the ice algae as food. The nauplii of *S. longipes* hatched in the ice in late November and December and grew to young copepodite stages by the end of December or the beginning of January. Then they moved into the top of the water column under the ice where they developed to the copepodite IV and V stages there by the end of March. These copepodites were thought to migrate into deeper water and overwinter there. MENSHENINA and MELNIKOV (1995) reported that *P. antarctica*, *S. longipes*, *Pseudocyclopina belgica* and harpacticoid copepods had a close relationship to the sea ice in the Weddell Sea, based on observations made on the USA-Russia Ice Station which drifted from 72° S, 51° W to 65° S, 53° W between February 11 and June 9, 1992. Also in March 1986, HOPKINS and TORRES (1988) observed *S. longipes* and a tisburyid harpacticoid in the sea ice in the region surrounded by 64.5° S, 66° S latitude and 42° W, 52° W longitude in the Weddell Sea. As mentioned in Section 5, recent studies also have shown the presence of the autumnal blooming in drifting ice floes in the Weddell Sea (GARRISON and CLOSE, 1993; FRITSEN *et al.*, 1994). However, in order to draw a picture of the complete life cycle of *S. longipes*, long term observations, preferably year-round, are required and must take into account the autumnal increase of ice algae.

With the above two calanoid copepods, harpacticoid copepods were reported as members of "the permanent groups of ice meiofauna" defined by HOSHIAI and TANIMURA (1986). DAHMS *et al.* (1990) distinguished two species of harpacticoid copepod, *Drescheriella glacialis* and *Harpacticus furcifer* as the regular members, out of four ice-associated harpacticoids, in the Weddell Sea. All naupliar and copepodite stages of *D. glacialis* were observed in the sea ice from July to September. Thus this species was thought to be reproductive through the winter, feeding on the diatoms in the ice (DAHMS and DIECKMANN, 1987). Here, we may also postulate that autumnal algal communities contributed to the growth of *D. glacialis*.

## 8. Coupling of Sea Ice Copepods with the Ice Algae in the Arctic

In the Arctic, the correlation between ice algae and copepods as one of the major components of the sea ice meiofauna has been mentioned (CAREY, 1985). Instead of the

calanoid copepods in the Antarctic, cyclopoid copepods, consisting of *Cyclopina glacilis* and its allied species, and harpacticoid copepods represent the sea ice copepod in the Arctic.

Young copepodite stages of *Cyclopina* sp. with a few adults appeared in the sea ice in February and continued to grow there until May. In June, *Cyclopina* sp. moved into the water under the ice before ice break-up (GRAINGER and HSIAO, 1990; GRAINGER and MOHAMMED, 1986). KERN and CAREY (1983) found that *Cyclopina glacilis* continuously reproduced at the ice-water interface between mid-April and the beginning of June. Two species of harpacticoid copepods, *Tisbe furcata* and *Harpacticus superflexus* also grew within the sea ice and on its undersurface from February to June (GRAINGER and HSIAO, 1990; GRAINGER and MOHAMMED, 1986). CROSS (1982) and GRAINGER and HSIAO (1990) reported copepods feeding on the ice algae. Although GRAINGER and HSIAO (1990) reported that abundant nauplii appeared at the ice-water interface in February, no information on the origin and the destination of nauplii was given. Also the dynamics of the *Cyclopina* population in autumn and winter are not known. Accordingly, we have to suggest that further investigations, in particular long-term, basic observations of sea ice biota are required to increase our understanding of the structure and function of sea ice biota in polar waters.

### 9. Autumnal Ice Algal Contributions to Organisms in the Outside of Sea Ice

Between April and November, the biomass of phytoplankton in the water column under the ice was extremely low (FUKUCHI *et al.*, 1984). During this period, however, the ice algal biomass was larger than that of the phytoplankton by one or two orders of magnitude (BUINITSKY, 1977; HOSHIAI, 1981a; WATANABE and SATOH, 1987). Algal cells contained in the bottom layer of sea ice were fed on by Antarctic krill, *Euphausia superba*, in winter in the Weddell Sea (MARSCHALL, 1988; DALY, 1990) and by an amphipod, *Paramoera walkeri* in winter at Molodezhnaya Station (67°40' S, 45°51' E) (RAKUSA-SUSZCZEWSKI, 1972). It appears that the growth curve of juvenile *P. walkeri* illustrated in this paper shows the possible contribution of autumnal ice algae to the growth of the amphipod. There has been no record of such direct feeding of animals on the ice algae in the Syowa Station area, except for observations of Antarctic krill on the undersurface of ice upturned by ships in summer.

The sedimentation of ice algae from the spring-summer community is comprehensively known (SASAKI and HOSHIAI, 1986). In addition, MATSUDA *et al.* (1987) reported that organic particles suspended in the upper layer of the water column contained fresh algal cells during winter, while degraded or inactive cells were the main components of organic matter collected with a sediment trap in a deeper layer. The fresh algal cells were thought to be the fall-out of ice algae.

### 10. Concluding Remarks

The autumnal sea ice biota has not received reasonable attention in comparison with the spring-summer biota, even though the autumnal community plays an important role as a major primary producer between autumn and spring in the Antarctic Ocean.

Fortunately, the recent increased knowledge about the autumn and winter ecology in the Antarctic Ocean makes it possible to review the austral autumnal ice biota. However, as mentioned in the before sections, information and data on the autumn and winter ecology in the ice-covered water of the northern hemisphere is so limited that a systematic synthesis of ecological events during winter is impossible. In order to improve this situation, long-term observations, if possible year-round, at relevant sites in the Arctic are required. Following this initial stage of sea ice biota research, coordinated investigations on the comparable topics between both polar oceans are desirable in order to enhance and broaden our understanding of polar ecosystems.

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