Development of Arctic sea-ice organisms under graded snow cover

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In May 1988, the short-term response of sea-ice organisms to manipulated changes in snow cover (no snow cover, natural snow cover, natural snow cover + black foil) was investigated in one ice floe located in the East Greenland Current northwest of Svalbard over a period of three weeks. Autotrophic organisms (flagellates and diatoms) were concentrated in the lowermost 30 cm of the floe. In the field without snow cover, the highest diatom concentrations were observed, consisting nearly entirely of pennate forms, together with a maximum bacterial abundance. The community of larger protozoa and smaller metazoa was dominated by ciliates. Under natural conditions the flora consisted of both flagellates and diatoms, while turbellaria were the dominating animals. In the darkened field, the organism concentrations decreased with time. The results indicate that brine drainage, induced by changes in ice temperature, can reduce concentrations of ice organisms over short time scales.

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Introduction

Sea ice is a characteristic feature of polar regions. It covers $7–14 \cdot 10^6$ km^2 of the Arctic Ocean (Walsh & Johnson 1979) and offers a unique habitat for a highly diverse biocoenosis. First reports about diatoms associated with ice floes were given by Ehrenberg (1841). Nansen (1906) was the first to discuss trophodynamic interactions between ice diatoms, protozoa, crustacea, fish and seals.

In Arctic sea-ice algal, cells were mostly found concentrated in layers at the bottom of the ice floes or as ice-associated mats dominated by *Melosira arctica* (Horner 1985). In contrast to results from the Antarctic (e.g. Ackley et al. 1979), no interior communities were observed in Arctic sea ice. A variety of invertebrates has been collected from the bottom layer communities dominated by organisms belonging to the meiofauna size range (Carey 1985), but very few quantitative estimates are given. The structure of the cryopelagic food web and its importance for pelagic organisms are therefore not fully understood. In the Arctic most investigations have been carried out in coastal shelf areas due to the relatively easy accessibility of these sites. Based on the occurrence of gammarid amphipods, Carey (1985) described four different regional community types: three fast ice communities over different water depths and one multi-year ice community over deeper water, highlighting the lack of studies in deep water areas.

Experiments using graded snow cover to simulate different light regimes have been performed both in the Arctic (Apollonio 1961) and Antarctic (Grossi & Sullivan 1985; Palmisano et al. 1985a, b; Sullivan et al. 1985; Grossi et al. 1987; Palmisano et al. 1987) to study the effects of light on the photoadaptation and development of ice algae and to follow the response in abundance and diversity of the bacterial assemblages. In the Arctic, Apollonio (1961) observed a decrease in chlorophyll concentration following the removal of a natural snow cover from ice floes. He concluded that increased heat absorption by the ice algae and changes in the ice structure as a result of the increased light intensities lead to a release of the algae from the bottom layer. As a second possible mechanisms for the chlorophyll *a* reduction he proposed physiological inhibition of the algae due to unnaturally high light intensities. On the other hand studies in the Antarctic showed an enhanced development of both algae and bacteria in terms of biomass and activity as a result of reduced snow cover.

Our study was located between Greenland and Svalbard in the western part of the Fram Strait, where the major outflow of polar water and multi-year ice floes from the Arctic Basin takes place (Tschernia 1980). We followed the development of the ice community in one ice floe during a period of three weeks under three different in situ light regimes in order to test whether reduced snow cover inhibits or promotes growth of ice organisms, and to determine which mechanisms are responsible for the observed differences between the results of Apollonio (1961) and Antarctic researchers.

Material and methods

The investigation was carried out during R/V POLARSTERN expedition ARK V/1 in May 1988. The icebreaker was moored to an ice floe (SAFE Island) within the East Greenland Current and drifted for three weeks in the area between 80°12′ to 80°52′N and 0°20′W to 5°24′E (Hoeber et al. 1989). Three experimental fields (N, L, D) of 10 m^2 each were set up close to each other in a homogeneous part of SAFE Island and treated in different ways to evaluate the influence of light on the development of the ice organisms. Field N (Natural) was not manipulated in any way and served as a control, while the snow cover was removed regularly from field L (Light). Field D (Dark) was darkened with a 0.5 mm thick black foil. To avoid heating of the ice by light absorption of the foil, it was covered by a layer of snow.

Light intensities were evaluated after coring with a spherical 4 π-LI-COR quantum radiometer in and below the ice after removal of the ice core.

Duplicate ice cores (less than 10 cm apart) were taken from each field every 4th day beginning on 5 May until 24 May 1988, using 3′ SIPRE ice augers. Sections of ice were cut with a stainless steel saw. The temperature of the ice was measured directly after coring in 5 cm intervals.

Sections of the first core were melted in the dark at 2°C and analysed within 24 hours for determination of salinity and pigment concentration (chlorophyll *a*. phaeopigments). The pigment concentrations were measured with a Turner fluorometer according to Evans & O'Reilly (1966). The salinity of the melted cores was measured with a WTW LF 191 conductometer. The structure of the ice cores was determined from vertical thin sections of the ice core.

The second core was cut in 10 cm long segments which were melted in 3 liters of 0.2 µm filtered seawater to avoid osmotic stress on the ice organisms during the melting procedure (Spindler & Dieckmann 1986; Garrison & Buck 1986). Subsamples of 100 ml from the three deepest segments of the core were fixed with borax-buffered formalin (end-concentration 1% formaldehyde) and filtered on 0.2-µm irgalan-black stained Nuclepore filters after staining the organisms with DAPI (Porter & Feig 1980). Counts of bacteria, auto- and heterotrophic flagellates and diatoms were made with a Zeiss epifluorescence microscope under UV (filter set 487701) or blue light excitation (filter set 487709). Ciliates and metazoa were concentrated from the total sample volume using 20 µm mesh and live-counted under a dissecting microscope.

One additional core was taken from each field on 24 May to estimate the accuracy of the determined organism concentations. The average discrepancy of the results from one core to the average of both was 19.5% (range: 5.2–33.3%). These values fall in the range for the statistical error which is expected by individual counts below 100 units per species (HELCOM 1983). Horizontal patchiness of the ice oganisms in our experimental area could therefore be neglected for the purposes of this study.

Results

Ice structure

The ice thickness in the sampling site showed only small variations between 164–171 cm, and an average natural snow cover of 27 cm was measured. The ice cores consisted entirely of congelation ice; only the upper 10 cm contained snow ice, frazil ice or a mixture of these 3 different ice textures (Lange & Eicken pers. comm.).

Light

As a result of daily differences of the cloud cover the absolute surface light intensities ranged between 2000–4500 $\mu E \cdot m^{-2} \cdot s^{-1}$. The available light intensities inside and below the ice as percentage of the surface irradiance (Fig. 1) showed no time dependency. Under natural conditions

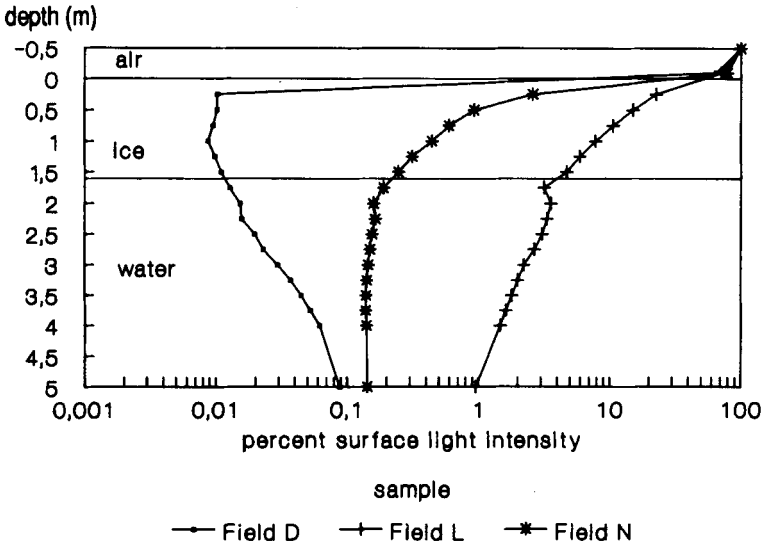

Fig. 1. Average percentages of surface light in and below the ice in fields N, L, and D during the investigation.

(field N) an average of 0.24% (4.4–10.1 $\mu E \cdot m^{-2} \cdot s^{-1}$) of the surface irradiance reached the bottom of the ice floe. In field L 4.71% (105–150 $\mu E \cdot m^{-2} \cdot s^{-1}$) and in the darkened field D only 0.01% (0.3–0.4 $\mu E \cdot m^{-2} \cdot s^{-1}$) was measured at the ice-water interface. The differences in the snow cover were still reflected in the measurements 5 m below the ice.

Temperature

Three major fluctuations of the air temperature occurred during the 3-week investigation period (Fig. 2). First there was a warming period with the temperature rising from below −18°C to 0°C. The second sampling of ice cores took place at the end of this warming period (9 May). The temperature subsequently dropped to between −6 and −12°C. During this time two samples were taken (13 May and 17 May). Toward the end of the investigation temperatures increased to above −6°C. Ice samples were taken two times (21 May, 24 May) during this period.

The variations of air temperature were reflected in the ice (Fig. 3), however, with different magnitudes in the fields N, L, and D. On 5 May the ice temperature in the upper 80 cm was below −7°C. During the first warming period a steep increase was observed. Without insulating snow cover (field L), the ice temperature rose to above −5.2°C in the entire core and even above −2°C in the upper 5 cm. The disturbed snow cover in field D resulted in a faster response to variations of the air temperature than in field N, but in a slower response than in the exposed field L: this demonstrates the effect of snow cover on the heat exchange between ice and atmosphere. As a consequence of the subsequent decrease in air temperature (11 May–20 May), the ice temperature in field L again dropped to below −5°C, but only in the upper 30 cm. The increase in air temperature toward the end of the investigation showed effects in fields L and D: the ice core temperatures in the upper 80 cm had increased from below −7°C to more than −3°C in field

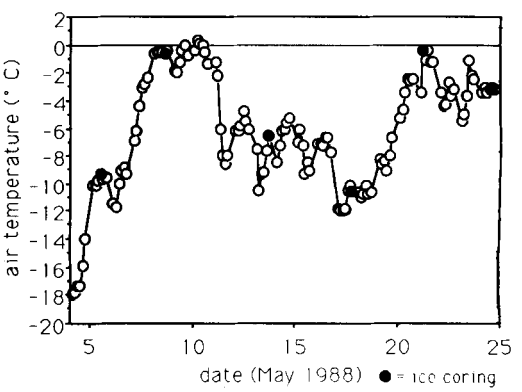

Fig. 2. Fluctuations of the air temperature during the investigation (● = ice coring date).

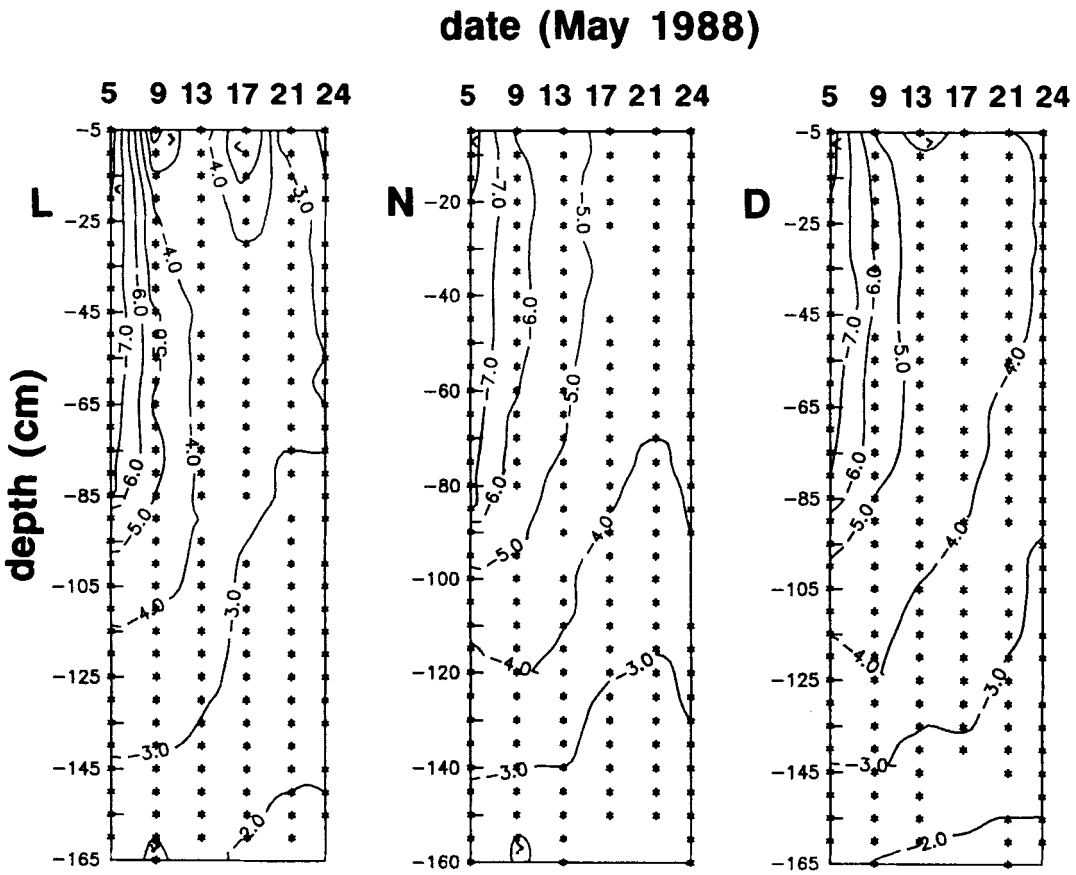

Fig. 3. Fluctuations of the ice temperature (°C) during the investigation (5 May–24 May 1988) in fields L, N, and D.

L, −4°C in field D and −5°C in field N. The temperature in the bottom 20 cm of the ice remained almost constant in all three fields.

Salinity

Changes in salinity (Fig. 4) correspond to the fluctuations in temperature, the largest changes occurring in field L. Between 5 May and 13 May salinity dropped from more than 10‰ to values below 6‰. The same was observed in fields D and L, but with less variation and an increasing time lag between changes in air temperature and salinity. In these two fields the salinity remained above 7‰. In the lowest 20 cm of the ice the measured fluctuations were small (2.9–4.9‰) and were not related to time or air temperature. The relation of the total salt content in the upper 80 cm of the core to the total salt content of the core (Fig. 5) demonstrates the drainage of salt from the upper half of the ice floe to the lower parts during the first 8 days of the study. During this period the ratio decreased from an initial value of 59% in all fields to 46% and 51% in fields L and D, while remaining more or less constant in field N. This phenomenon, together with the decrease in the integrated salt content of the ice, indicates drainage of brine from the upper decimetres of the floe through the ice into the water column during this period.

Pigments

A distinct maximum of chlorophyll *a* was observed in the lowermost 10 cm of all cores collected, but showed large temporal changes (Fig. 6). In field L the concentration dropped from initially 1.45 mg · m^{-3} to values below 0.7 mg

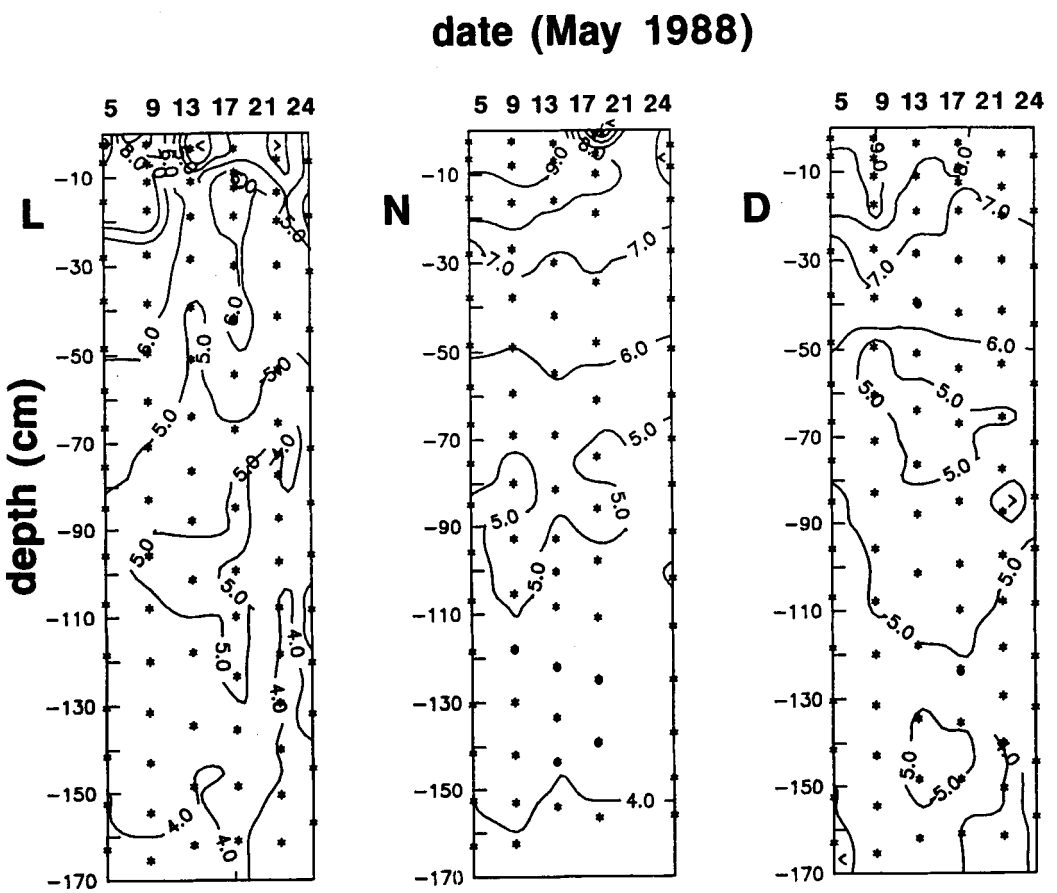

Fig. 4. Fluctuations of the salinity (‰) during the investigation (5 May–24 May 1988) in fields L, N, and D.

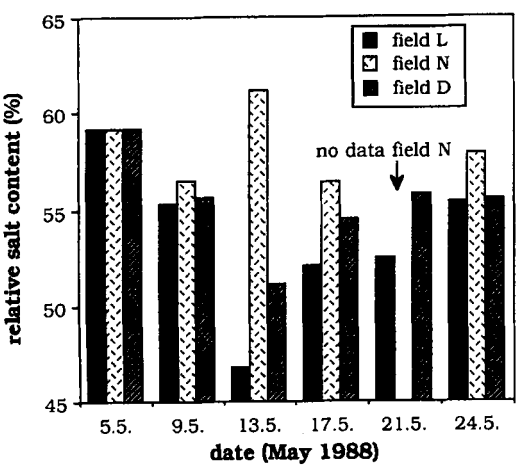

Fig. 5. Relation of the salt content (%) in the upper 80 cm to the total salt content of the core during the investigation.

chl $a \cdot m^{-3}$. The same changes were found in fields D and N. A period of increasing chlorophyll *a* concentrations followed the initial decrease. On 21 May the values exceeded 1.1 mg chl $a \cdot m^{-3}$ in fields L and D with a maximum of 1.93 mg chl $a \cdot m^{-3}$ in field L. At the end of the study a sharp decrease to values below 0.5 mg chl $a \cdot m^{-3}$ was observed only in field L, while the concentrations in fields N and D remained above 0.8 mg chl $a \cdot m^{-3}$.

The ratio of phaeopigments to chlorophyll *a* is shown in Fig. 7. Values below 0.5 were characteristic for the lower portion of the ice floe in all three fields, while values above 1.5 dominated in the upper decimetres. The decrease of this ratio during the cooler period (11 May–20 May) in upper parts of fields L and D was due to increasing chlorophyll *a* values with a maximum of 0.08 mg

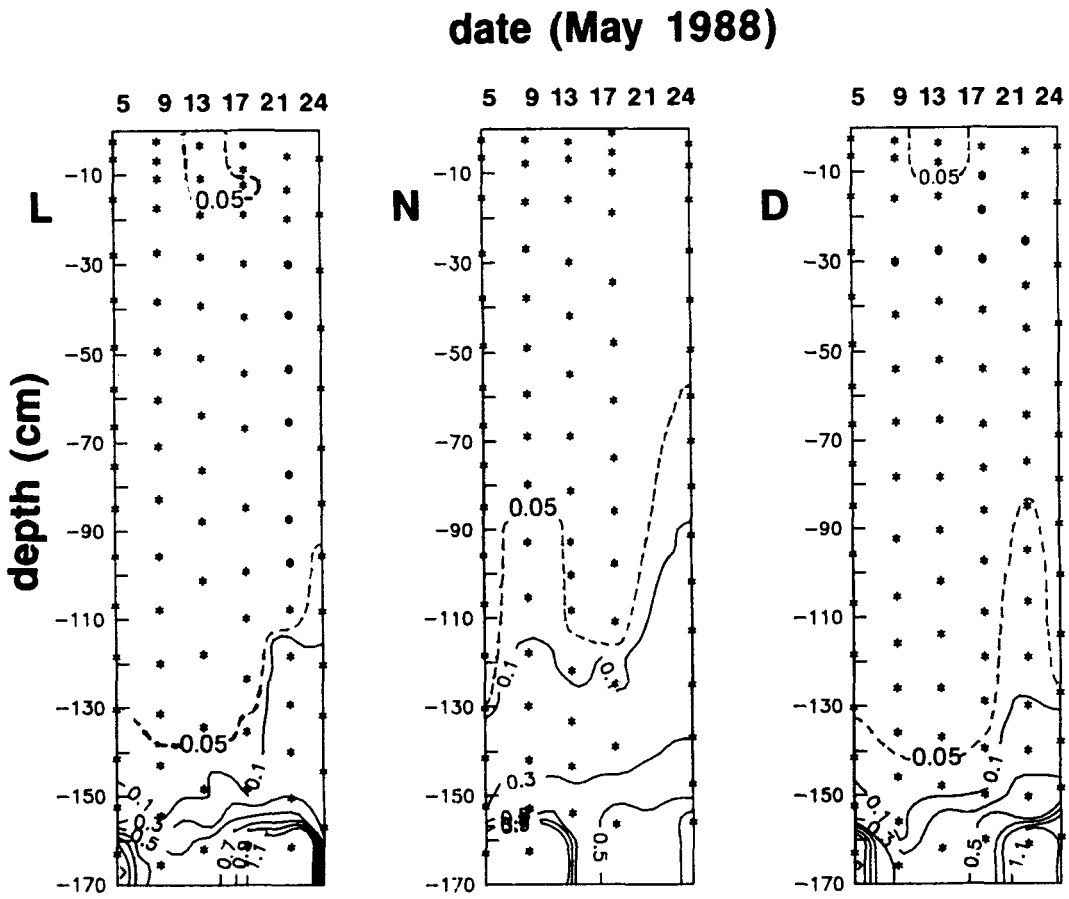

Fig. 6. Fluctuations of the chl *a* content (mg·m^{-3}) during the investigation (5 May–24 May 1988) in fields L, N, and D.

chl *a*·m^{-3} at the top of field L on 13 May in contrast to concentrations of 0.01 mg chl *a*·m^{-3} in the same level at the beginning and the end of the investigation.

Bacteria, autotrophic and heterotrophic flagellates, diatoms

Bacteria, diatoms, autotrophic and heterotrophic flagellates had their maximum abundance in the lowest 10 cm of the floe (Table 1). This distribution pattern was very distinct for the autotrophic organisms (diatoms, autotrophic flagellates), while bacteria and heterotrophic flagellates were distributed more homogeneously in the lower 30 cm of the floe.

The development of the sea ice community in the three fields N, L, and D is shown in Fig. 8. In the fields L and D, the cell numbers decreased until 13 May; no data were available from field N on 9 May due to loss of the samples.

Under natural light conditions (field N) the abundance of diatoms and autotrophic flagellates increased slowly after 13 May. The generation times for these two groups were estimated using an exponential growth model leading to a doubling time of $t_g = 9.6$ d ($N_t = N_0 \cdot e^{0.072 \cdot t}$, N = cells·ml^{-1}, t = time (d), $r^2 = 0.59$) for diatoms and 19.3 d ($N_t = N_0 \cdot e^{0.036 \cdot t}$, $r^2 = 0.34$) for autotropic flagellates. The density of heterotrophic organisms (bacteria, heterotrophic flagellates) showed no significant variation during the investigation.

The enhanced light availability in field L resulted in a strong proliferation of diatoms. Highest densities of 15,000 diatoms·ml^{-1} were

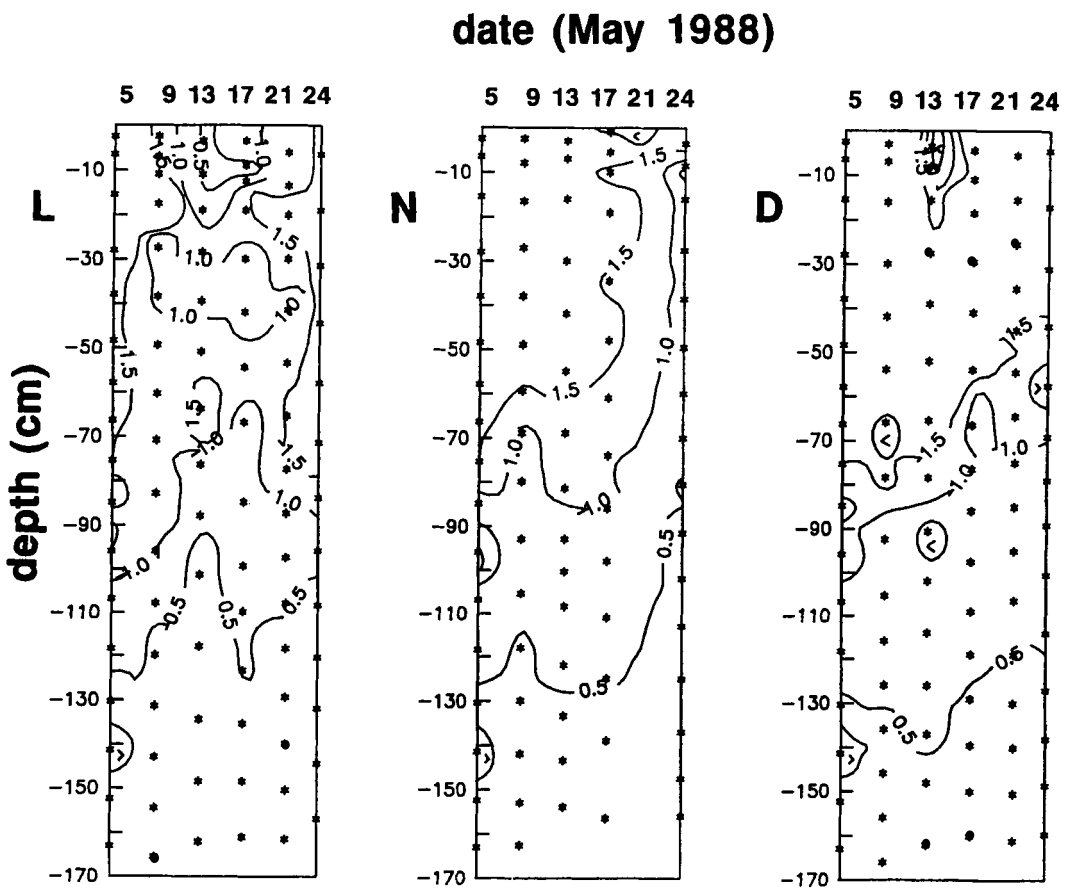

Fig. 7. Fluctuations of the ratio of phaeopigments to chl *a* during the investigation (5 May–24 May 1988) in fields L, N, and D.

reached on 24 May in the lowest 3 cm of the floe. The increase followed an exponential growth curve ($N_t = N_0 \cdot e^{0.22 \cdot t}$, $r^2 = 0.94$) with a generation time of 3.2 d. The contribution of centric forms to the total number was below 1%. The dominating pennate cells belonged to the genus *Fragillariopsis*. On the last sampling day the chlorophyll autofluorescence was very weak, indicating a senescence of the diatoms. Coinciding with the diatom peak, the bacteria attained their maximum ($1.2 \cdot 10^6$ cell $\cdot$ ml^{-1}) on the last sampling day, a large fraction being attached to the diatom cells.

In contrast to the diatom population the auto-

Table 1. Average abundances of bacteria ($10^3 \cdot$ ml^{-1}), diatoms (cells $\cdot$ ml^{-1}), autotrophic and heterotrophic flagellates (cells $\cdot$ ml^{-1}) in the lowermost decimetres of the studied ice floe under natural light conditions (field N) during the whole investigation period.

Depth (cm)	Bacteria ($10^3 \cdot$ ml^{-1})	Autotrophic flagellates (cells $\cdot$ ml^{-1})	Diatoms (cells $\cdot$ ml^{-1})	Heterotrophic flagellates (cells $\cdot$ ml^{-1})
140–150	364 ± 226	304 ± 56	162 ± 69	39 ± 27
150–160	223 ± 46	533 ± 120	277 ± 129	276 ± 375
160–170	344 ± 51	1416 ± 361	1028 ± 395	327 ± 385

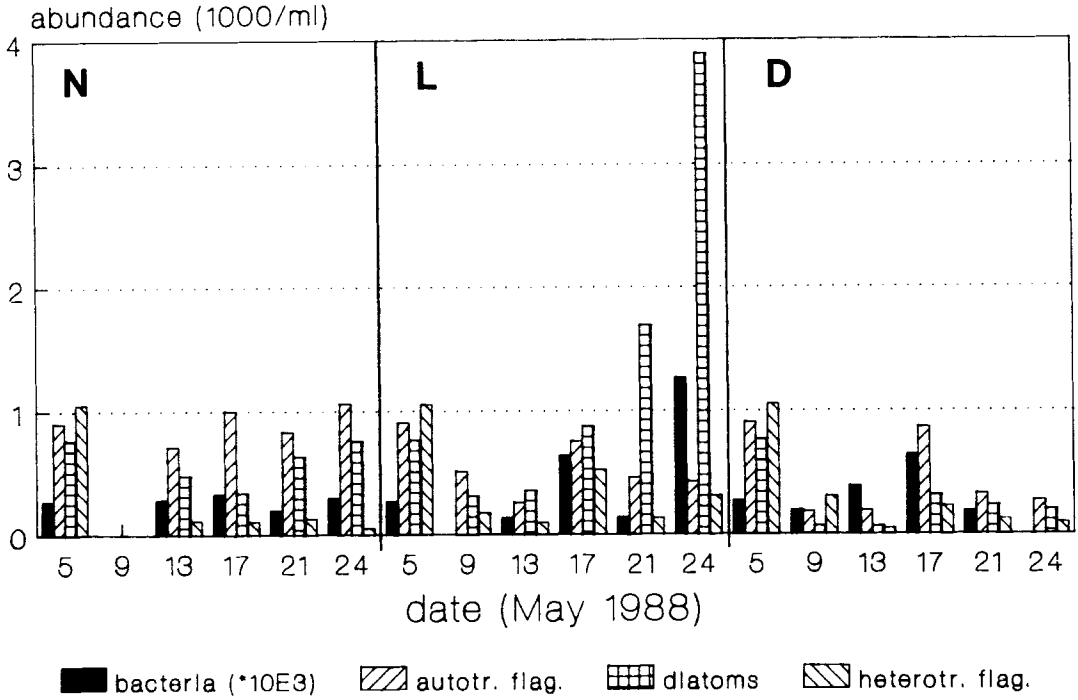

Fig. 8. Fluctuations of the average abundances ($1000 \cdot ml^{-1}$) of bacteria, autotrophic and heterotrophic flagellates, and diatoms in the lowermost 20 cm of the ice in fields N, L, and D.

trophic and heterotrophic flagellates did not show a constant increase with time.

The lowest concentrations of all organism groups were observed in the darkened experimental field D. A decrease of the cell densities occurred during the first 8 days and after 17 May. The chlorophyll *a* autofluorescence of the diatoms was very intense at the end of the study, indicating a high chlorophyll *a* content per cell.

Ciliates and metazoa

A rich and highly diverse community of ciliates and small metazoa (Fig. 9, Table 2) lived inside the ice, with more than 95% of all organisms found in the lowest 20 cm of the floe.

Under natural light conditions (field N) the community was dominated by ciliata (29% of all organisms) and acoelic turbellaria (51%). During

Table 2. Average abundances (organisms $\cdot m^{-3}$) of ciliates and metazoa in the three ice fields during the entire investigation period: cil. = ciliata; nem. = nematoda; turb. = turbellaria; rotat. = rotatoria; naup. = copepoda: nauplii; copep. = copepodites; harpact. = harpacticoids.

Field	cil.	nem.	turb.	rotat.	naup.	copep.	harpact.	Sum
L	20300	500	4350	500	300	50	150	26,150
	(78%)	(2%)	(17%)	(2%)	(1%)	(<1%)	(<1%)	
N	8600	1450	15140	200	3900	50	250	29,600
	(29%)	(5%)	(51%)	(<1%)	(13%)	(<1%)	(<1%)	
D	4300	250	9250	50	1000	0	150	15,000
	(29%)	(2%)	(62%)	(<1%)	(7%)	(0%)	(1%)	

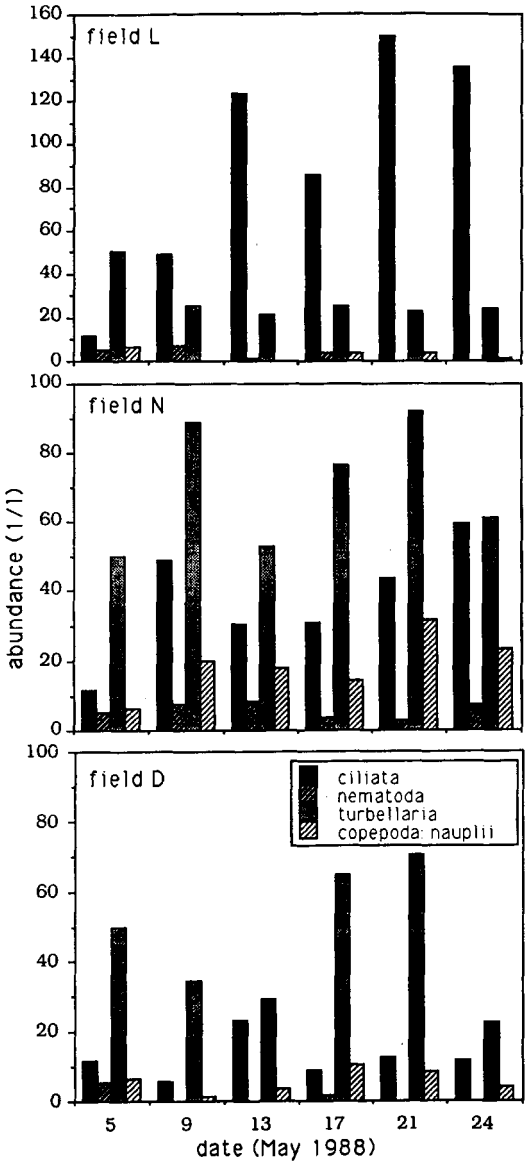

Fig. 9. Fluctuations of the average abundances ($l \cdot^{-1}$) of ciliates and metazoa in the lowermost 20 cm of the ice in fields N, L, and D.

the first 4 days, the concentrations of these groups increased and remained afterwards more or less constant. Nauplii (13%), copepodites (<1%), adult harpacticoids (<1%), rotatoria (<1%) and the nematode *Theristus melnikovi*, TSCHESUNOV 1986 (5%) were regularly found in lower densities.

A different community developed under enhanced light intensities (field L). It was dominated by ciliata (78%), especially of the genus *Didinium*. In contrast to field N, nauplii (1%) were nearly absent, while the number of turbellaria (17%) remained constant after an initial decrease.

The darkened field D had a similar community to field N, but concentrations were lower. Ciliata (29%) and turbellaria (62%) were the numerically dominating organism groups, exhibiting large fluctuations during the period of investigation.

Discussion

The occurrence of biomass maxima in the lower decimetres of ice floes is well known both from the Antarctic and the Arctic (see Horner 1985 for review). Most of the Arctic studies focused on the lowermost 2–20 cm of the ice, coloured by ice algae (Apollonio 1961; Kern & Carey 1983; Legendre et al. 1987; Smith et al. 1987; Smith et al. 1989a), while results from measurements throughout the whole ice cores in distinct strata are only available from Antarctic sites (Garrison et al. 1986), with the exception of the study from Hsiao (1980) in the Canadian Arctic.

Our data clearly show that the highest concentrations of a viable ice flora and fauna occur in the bottom part of the ice floe. Estimates of the algal standing crop (mg chl $a \cdot m^{-2}$) from various Arctic regions (Table 3) show that the algal development in early spring starts in the middle of April and lasts until the beginning of May (Horner & Schrader 1982; Smith et al. 1989a). The absolute values are mostly an order of magnitude higher than those observed in our study. The neritic location of the other areas studied could be indicative of higher initial populations of algae inside the fast ice in connection with increased nutrient supply, e.g. by tidal mixing during the growth season (Cota et al. 1987). Moreover, our study area was the most northern one, and therefore the growth season had probably started later than in the other regions, and the biomass maximum was not reached.

The slight increase in chlorophyll *a* concentrations in the upper decimetre of ice fields L and D between 9 May and 17 May to values exceeding $0.08\,mg \cdot m^{-3}$ and the resulting decrease in the ratio of phaeopigments to chlorophyll *a* are the first clear indications of growing surface ice communities reported from the Arctic

Table 3. Chlorophyll *a* content (mg·m^{-2}) of Arctic sea ice from different areas: (p) = pack ice, (f) fast ice.

Author	Region	Ice thickness (cm)	Time	Chlorophyll *a*
Clasby et al. (1973)	Chukchi Sea	155–170 (f)	May–June	3.0–30.5
McRoy & Goering (1974)	Bering Sea	200–300 (p)		0.3–3.0
Grainger (1979)	Frobisher Bay	200 (f)	January	0.4
			March	1.6
			May	4.6
Booth (1984)	Davis Strait	100–160 (p)	April–May	0.0–9.6
Horner & Schrader (1982)	Beaufort Sea	?	April	0.0–2.4
			May (early)	1.2–8.3
			May (late)	14.4–26.5
Smith et al. (1989a)	Barrow Strait	170–190 (f)	April	<10.0
			May	100.0
Gosselin et al. (1986)	Hudson Bay	75–215 (f)	April	0.1–22.9
		90–160 (f)	May	1.1–39.7
This study	Fram Strait	164–171 (p)	May	0.1–0.4

pack ice. Only Booth (1984) has given a description of brownish coloured ice surfaces, but he proposed that algal cells of pelagic origin were entrapped in the ice surface by the flushing of the ice with seawater and subsequent freezing. In fast ice of the Canadian Arctic, Hsiao (1980) found high densities of algae on the ice surface; these had developed from trace amounts of chlorophyll *a* after the ice had formed in late winter. He measured a maximum of 2.27 mg chl $a \cdot m^{-3}$ at the end of May. During the short period of our study the biomass increase was restricted to the relatively warm period in the middle of the investigation period. Sea ice temperature largely influences the habitat of sea ice organisms by controlling the salinity inside the brine pockets and channels. Using the equations of Assur (1958) for the calculation of the salinity within the brine channels and pockets from the ice temperature data, a strong decrease from values above 120‰ to those below 100‰ (field D) and 70‰ (field L) occurred between the first two sampling dates. Studies of the influence of salinity on the activity of ice algae have shown that high salinities above 90–100‰ inhibit the growth and physiology of ice algae (Kottmeier & Sullivan 1988; Bartsch 1989). On the other hand the results of Bartsch (1989) showed the capability of ice algae to survive extended periods of high salinities and to regain growth when transferred to lower salinities. It can thus be assumed that the development of ice algae in the upper decimetres of the Arctic sea ice was controlled by ice temperature and brine salinity during periods of our experiment.

In contrast to the large fluctuations of the temperature at the top of the ice floe, the conditions at the bottom were rather constant. Only minor fluctuations were observed, ranging from −1.8°C to −3°C. The resulting calculated brine salinities of 32–52‰ are not expected to inhibit algal growth (Kottmeier & Sullivan 1988; Bartsch 1989). The sharp drop of chlorophyll *a* and organism concentrations observed in the fields L, D, and N during the first week corresponds with the observations made by Apollonio (1961). He found a decrease of algal standing crop from 89.6 to 16.6 mg chl $a \cdot m^{-2}$ (averages) within 7 days during June under very similar ice and snow conditions. This phenomenon was interpreted as a reaction of the ice algae to increased light levels as well as to changes in the physical structure of the ice. He concluded that physiological inhibition is the main cause of pigment loss in sea ice. Smith et al. (1989a) monitored the chlorophyll *a* changes in the lowest 3–4 cm of annual ice floes in Barrow Strait from April to May. Their Fig. 1A depicts a distinct decrease of the chlorophyll *a* concentrations between the end of April and the middle of May, first in ice without snow cover and later in ice areas with thicker snow cover. In ice without snow, the algal biomass dropped from 40 mg chl $a \cdot m^{-2}$ to values below 20 mg chl $a \cdot m^{-2}$, while values remained more or less near this level or even increased in areas with thicker snow cover (2–12 cm). Smith et al. (1989a) concluded that self-shading was the major mechanism which initiated the decrease in chlorophyll *a* in the ice without snow cover. However, they did not explain

the existence of an even higher biomass under lower light intensities.

Taking into account our results on the temporal fluctuations of the total salt content of the ice, we propose a new mechanism which leads to short time changes of organic biomass: the decrease in the chlorophyll *a* concentrations corresponds to the outflow of brine from the upper decimetres of the floe into the water column. Gravity drainage by flushing appears to be the dominant and most effective mechanism for removing salt from sea ice in early spring and summer when the surface temperatures increase (Weeks & Ackley 1982). Martin (1974) and Eide & Martin (1975) demonstrated that brine drainage processes are connected with oscillating sea water inflow into the ice as a result of convective instabilities, taking place in time scales of seconds to minutes. Eide & Martin (1975) proposed this mechanism as a pumping source of oxygen and nutrients into the ice. The results of our study indicate that brine drainage as a result of temperature changes in the ice can lead to a release of both algae and animals from the ice into the water. From this point of view the findings of Apollonio (1961) and Smith et al. (1989a) could be explained in the same way. Their measurements were derived in June and at the end of April, when similar meterological conditions as in our study area could be expected. Further field studies and experiments have to be undertaken to confirm our hypothesis of organism release by brine drainage. We would like to stress the importance of measuring abiotic and biotic parameters over the total thickness of the sea ice since changes in upper parts may strongly influence species abundance and distribution in lower parts.

Following the initial chlorophyll *a* decrease, the algal biomass in all three fields increased at different rates. The diatoms, as the dominant autotrophic group, showed highest growth rates (t_g = 3.9 d) in field L under light intensities over 100 $\mu E \cdot m^{-2} \cdot s^{-1}$, while no growth in terms of cell numbers could be observed in field D (0.3–0.4 $\mu E \cdot m^{-2} \cdot s^{-1}$). Under natural light intensities (4–10 $\mu E \cdot m^{-2} \cdot s^{-1}$) intermediate growth rates were found for diatoms (t_g = 9.6 d) and autotrophic flagellates (19.3 d). The discussion in the literature on the effects of light on algal growth is extensive and enigmatic. Booth (1984) found light inhibition of in situ primary productivity at intensities >20 $\mu E \cdot m^{-2} \cdot s^{-1}$. According to Horner & Schrader (1982) light intensities of 2.3–9.3 $\mu E \cdot m^{-2} \cdot s^{-1}$ would be sufficient to initiate the spring development of ice algae. Cota (1985) observed a 65% higher increase of chlorophyll *a* in sea ice with moderate to heavy snow cover than under little or no snow cover. Similar results were reported by Smith et al. (1989a). On the other hand long term experiments using graded snow cover in McMurdo Sound, Antarctica revealed highest algal accumulation under snow cleared areas with light intensities over 100 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Grossi et al. 1987). Despite the major differences in the study areas (Arctic/Antarctic) the sampling intervals also differed between these studies. Grossi et al. (1987) took samples every 2–3 weeks, while Smith et al. (1989a) sampled on a weekly and Apollonio (1961) on a daily base. Thus the data from the Antarctic describe long term changes due to e.g. algal growth and not short-time events such as brine drainage processes. The differences between the observed reactions of Antarctic and Arctic ice organisms reflect, therefore, not only the different biological regimes but also differences in the methodology of the investigations.

The estimates of the ice aglal generation times given by Grossi et al. (1987) based on the chlorophyll *a* accumulation are with t_g = 2.4 d in the field without snow cover and t_g = 9.9 d with 25 cm snow cover almost identical to our results, based on the cell counts of diatoms. The difference in the growth estimates of the autotrophic flagellates in comparison to the diatoms can result from various factors. The higher motility of the flagellates could lead to increased exchange with the water column populations. Also selective grazing of herbivores in the ice or a better adaptation of the diatoms to the conditions inside the ice are possible explanations.

The chlorophyll *a* decrease in field L at the end of the investigation corresponded to low chlorophyll *a* autofluorescence of the diatom cells as seen in the epifluorescence microscope. At the same time the absolute number of diatoms reached a maximum with more than double as many cells compared to previous times and other light regimes. Thus, the chlorophyll *a* decrease was not a result of biomass reduction but of changes in the physiological state of the diatom population, probably as a result of high light intensities or of nutrient depletion. The highest densities of bacteria were also observed during that period. Smith et al. (1989b) found that bacteria grow actively in the bottom layer of Arctic

Table 4. Relative abundances of ciliates and metazoa in sea ice from different Arctic areas: cil. = ciliata; nem. = nematoda; turb. = turbellaria; rotat. = rotatoria; naup. = copepoda: nauplii; others include harpacticoids, copepodes, polychaetes, amphipods.

Author		Region	cil.	nem.	turb.	rotat.	naup.	others
Cross (1982)		Pond Inlet	—	59%	—	—	—	41%
Cross & Montagna (1982)		Stefanson S.	—	77%	—	—	—	23%
Kern & Carey (1983)		Beaufort Sea	—	47%	16%	—	—	37%
Grainger et al. (1985)		Frobisher Bay	<1%	51%	—	1%	45%	2%
This study	Field L	Fram Strait	78%	2%	17%	2%	1%	<1%
	Field N		29%	5%	51%	<1%	13%	1%
	Field D		29%	1%	62%	<1%	7%	<1%

sea ice, in spite of the fact that algal populations are static or declining.

The standing stock of metazoa which was found in the pack ice clearly differed from other observations. The studies of Cross & Montagna (1982), Kern & Carey (1983) and Grainger et al. (1985) from the European sector of the Arctic were made in shallow areas with water depths below 50 m, making interactions between benthic and sympagic communities probable. Grainger et al. (1985) stated that the major groups inhabiting sea ice are representatives of meroplanktonic and not of holobenthic or pelagic groups. Sea ice fauna therefore seemed to be totally distinct from the dominant Arctic zooplankton. The dominance of organisms belonging to the meiofauna is well documented (Carey 1985). A direct comparison of our results with those from other investigations (Table 4) is restricted due to considerable differences in the methods used. Cross & Montagna (1982), Kern & Carey (1983), and Grainger et al. (1985) melted the ice cores directly, which led to an underestimation of fragile organisms such as protozoa (Garrison & Buck 1986). The occurrence of ciliates was only reported by Grainger et al. (1985), but in concentrations of 1 to 2 orders of magnitude lower than in our study (<1000 cells $\cdot m^{-2}$). Another major problem arises from the different mesh sizes used in the different investigations; smaller protozoa may be underestimated in those studies with 63–76 µm mesh size applied. In neritic regions nematodes and nauplii were dominating, while turbellaria and ciliates were numerically most important in the Fram Strait. These differences may result from the different methology used, especially for the ciliates. Other differences may result from adaptation of life strategies to the annual vs. multi-year ice cover. Organisms living in annual fast ice must at least live partly in the water column or in the benthos, while organisms living inside multi-year ice floes are not released, for at least a year, into the water column by melting processes. They must therefore be capable of completing their life cycle within the ice. Grainger & Hsiao (1990) gave the first accounts on trophic links between the ice organisms by analysing gut contents, but further studies are needed to understand the dynamics of the ice populations and their relation to their habitat on different spatial and temporal scales.

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