Polarforschung 65 (3): 111-116, 1995 (erschienen 1998)

Dark Survival of Marine Microalgae in the High Arctic (Greenland Sea)

By Qing Zhang[1], Rolf Gradinger[2*] and Michael Spindler[2]

Abstract: With the onset of winter, polar marine microalgae face total darkness for a period of up to 6 months. A natural autumn community of Arctic sea ice microalgae was collected for dark survival experiments from the Greenland Sea during the ARK-XI/2 expedition of RV Polarstern in October 1995. After a dark period of 161 days, species dominance in the algal assemblage changed from initially pennate diatoms to small phytoflagellates (<20 µm). Over the entire dark period, the mean algal growth rate was -0.01 day^{-1}. Nearly all diatom species had negative growth rates, while phytoflagellate abundance increased. Resting spore formation during the dark period was observed in less than 4.5 % of all cells and only for dinoflagellates and the diatom *Chaetoceros* spp. We assume that facultative heterotrophy and energy storage are the main processes enabling survival during the dark Arctic winter. After an increase in light intensity, algal cells reacted with fast growth within days. Phytoflagellates had the highest growth rate, followed by *Nitzschia frigida*. Further investigations and experiments should focus on the mechanisms of dark survival (mixotrophy and energy storage) of polar marine microalgae.

Zusammenfassung: Mit Beginn des Winters sind polare Mikroalgen einer Dunkelperiode von bis zu sechs Monaten ausgesetzt. Experimente zur Überlebensstrategie arktischer Eisalgen wurden im Rahmen der Polarstern-Expedition ARK-XI/2 im Oktober 1995 durchgeführt. Die häufigsten Algen zu Beginn des Experiments waren pennate Diatomeen. Nach der Dunkelperiode von 161 Tagen wurde die Algengemeinschaft von Phytoflagellaten <20 µm dominiert, die durchschnittliche Wachstumsrate der Algen betrug -0.006 Tag^{-1}. Während die meisten Diatomeenarten stark in ihren Häufigkeiten abnahmen, stieg die der Flagellaten teilweise sogar an. Die Bildung von Dauersporen wurde nur für max. 4,5 % aller Zellen und nur bei *Chaetoceros* spp. und Dinoflagellaten beobachtet. Vermutlich bilden fakultative Heterotrophie zusammen mit der Nutzung gespeicherter Energie die Hauptprozesse zum Überleben des arktischen Winters. Auf Erhöhung der Lichtintensität reagierten die Algen mit schnellem Wachstum innerhalb weniger Tage, wobei Phytoflagellaten die höchsten Wachstumsraten aufwiesen, gefolgt von *Nitzschia frigida*. Zukünftige Studien und Experimente sollten sich speziell mit den Mechanismen der Dunkelanpassung polarer Algen (Mixotrophie, Energiespeicherung) befassen.

INTRODUCTION

Polar marine ecosystems are characterized by strong seasonality and interannual variability of environmental factors, especially ice cover and irradiance. Sea ice covers 7 to 14 million km^2 of the Arctic Ocean and is a critical parameter in the modeling of environmental changes in polar areas (SPINDLER 1990). Microalgae in the water column and the sea ice are important primary producers of polar oceans (HORNER 1985, LEGENDRE et al. 1992, ARRIGO et al. 1997). Diatoms are often dominant and may contribute more than 90 % to the total microalgal abundance. The seasonal development of polar marine microalgae is mainly controlled by abiotic parameters and the onset of algal growth in spring is controlled by the increase of available light after the dark polar winter (PALMISANO & SULLIVAN 1983). In the Arctic Ocean primary production is characterized by a single pulse during the short summer season. Consequently polar organisms must have adapted their life cycles to overcome the dark period.

Numerous studies at Antarctic, Arctic and sub-Arctic sites have demonstrated that light is the principle factor limiting the onset and early development of bottom ice algal blooms (COTA & SMITH 1991, SMITH et al. 1993). During a later phase, nutrients, especially silicate, become limiting because of high algal growth due to high levels of *in situ* irradiance and slow nutrient replacement by e.g., tidally-driven exchange processes (GOSSELIN & LEGENDRE 1990).

During the polar winter, microalgae face total darkness for a period of up to 6 months (PALMISANO & SULLIVAN 1983). Although survival of a proportion of the ice diatom community is essential to „seed" the annual spring bloom (MATHEKE & HORNER 1974, KUOSA et al. 1992), dark survival strategies have received little attention. BUNT & LEE (1972) observed that four Antarctic sea ice microalgae were still viable after a dark period of 3 months. PALMISANO & SULLIVAN (1983) found that up to 100 % of the population of three lab-cultured polar sea ice diatoms (two from Antarctica, one from the Arctic) were capable of growing again autotrophically after a dark incubation of 5 months at -2 °C. Formation of resting spores has been suggested as an overwintering strategy in sea ice diatoms (PALMISANO & SULLIVAN 1985). Conversely, SYVERTSEN (1991) pointed out that resting spores play no important role in winter survival of Arctic ice algae.

The ARK-XI/2 expedition of RV *Polarstern* to the Greenland Sea from 22 September to 29 October 1995 allowed us to study the natural autumn community of Arctic sea ice microalgae in a state prior to the dark winter period. The goal of the present study was to follow the survival of Arctic marine microalgal species during a dark period of 23 weeks (161 days) followed by incubation in the light for 30 days.

MATERIALS AND METHODS

Ice material was collected at 79° 02' N, 2° 59' W in the Greenland Sea on 08 October 1995. The daylength was about 8 h and decreased by about 30 min each day. Grease ice was collected with a bucket and melted in 0.2 µm-prefiltered seawater (volu-

[1] Qing Zhang, Second Institute of Oceanography, State Oceanic Administration, Hangzhou 310012, Peoples Republic of China

[2*] Dr. Rolf Gradinger and Michael Spindler, Institute for Polar Ecology, Kiel University, Wischhofstr. 1-3, Geb. 12, D-24148 Kiel, Germany

Manuscript received 06 October, 1997; accepted 05 December, 1997

me ratio 1:1) at 1 °C in the dark. After melting, larger zooplankton was removed with a 64 µm gauze. The water was put into fifty 50 ml Corner polystyrene tissue culture vials and kept in the dark at 1 °C for 23 weeks (161 days). Samples were shaken manually twice a day in the dark. After the dark incubation period, cultures were pured into larger vials (125 ml) and put into a light incubator with 1.6 µmol m^{-2} s^{-1} irradiance and 12L:12D light cycle at a temperature of 1 °C. Fifty ml filtered (0.2 µm) seawater, which had been collected at the sampling location and stored in darkness at 1 °C, was added to each vial as an additional nutrient source.

Two vials were fixed during the dark period every 7 days during the first five weeks, every 14 days in the following 18 weeks and every 5 days during the light period with borax-buffered formalin (1 % final concentration). Algal abundances were determined with the Utermöhl technique according to HELCOM (1988) using a Zeiss Axiovert 135 inverted light microscope. For species determination we followed MEDLIN & PRIDDLE (1990) although we are aware of recent changes of the names of certain taxa. Algal growth rate, μ_t, was calculated:

$$\mu_t=(\ln N_{t2}-\ln N_{t1})/(t_2-t_1),$$

where N_{t_1} and N_{t_2} represent the cell abundance (cells/ml) at time t_1 and t_2, respectively.

RESULTS

Algal composition and abundance

The algal assemblage in the grease ice was dominated by pennate diatoms (Table 1, Fig. 1 and 2), e.g., *Nitzschia frigida* Grunow (17 %) and *Nitzschia cylindrus* (Grunow) Hasle (16 %), accompanied by *Nitzschia pellucida* Karsten (12 %), the centric diatom *Chaetoceros gracilis* Schütt (11 %) and phytoflagel-

Dark period (days)	0	7	14	21	28	35	49	63	77	91	105	119	133	147	161
Actinomonas sp.	-	5.5	4.2	3.0	2.5	3.8	2.9	2.0	-	2.0	-	2.0	-	4.4	-
Bacterosira fragilis	3.0	4.4	4.1	-	3.1	2.3	-	-	-	-	-	-	-	-	3.6
Chaetoceros gracilis	11.2	7.3	6.8	8.6	9.5	3.0	6.0	5.9	7.4	9.5	17.1	4.1	7.2	8.0	11.7
Chaetoceros simplex	-	2.9	4.6	7.2	9.8	2.4	-	2.0	3.7	5.6	3.4	5.3	9.1	5.5	6.3
Coscinodiscus sp.	-	-	-	-	-	-	-	-	-	-	-	-	2.4	-	-
Navicula algida	2.3	-	-	-	-	-	-	-	-	-	-	-	-	2.9	-
Navicula cuspidata	3.7	-	-	-	-	-	-	-	-	-	-	2.0	-	4.4	-
Nitzschia arctica	5.3	3.6	12.4	10.5	4.3	11.7	3.2	8.5	-	2.9	-	-	5.8	2.2	-
N. closterium	2.8	3.3	-	-	-	-	-	-	-	-	-	-	-	-	2.7
N. cylindrus	15.6	13.5	9.3	7.4	7.1	8.9	7.3	5.7	-	7.2	6.0	2.0	7.7	8.0	4.9
N. frigida	**16.5**	**17.1**	8.8	3.6	2.1	4.4	-	-	-	-	-	-	2.9	2.2	-
N. pellucida	11.9	8.7	**12.5**	10.9	**15.3**	9.6	7.1	8.3	2.9	2.9	-	4.9	7.2	3.6	5.8
N. pseudodelicatissiuma	2.1	3.6	-	-	-	-	-	-	-	-	-	-	3.8	-	-
N. pseudonana	2.7	4.0	3.6	3.6	3.4	4.1	2.8	-	-	3.6	5.1	2.8	2.9	-	-
N. seriata	-	-	-	-	-	-	-	-	-	2.0	-	-	2.4	-	-
Nitzschia spp.	9.6	6.5	5.0	5.2	10.1	9.2	3.7	3.3	2.6	3.9	2.6	2.8	6.7	4.4	2.2
Phytoflagellates (<20µm)	-	3.6	8.9	8.7	10.1	**17.9**	**46.6**	**41.4**	**76.1**	**47.1**	**32.5**	**56.1**	**29.3**	**27.6**	**50.7**
Phytoflagellates (>20µm)	6.0	8.0	10.4	**23.1**	12.9	15.8	11.7	5.7	-	5.9	23.1	4.1	6.7	16.7	6.3
Chaetoceros spp. (spores)	-	0.4	0.8	0.3	-	-	-	-	-	-	-	-	-	-	-
Dinoflagellate cysts	-	-	0.2	0.3	0.9	0.9	0.5	2.6	0.4	1.3	-	4.5	1.0	-	-
Sum of *Nitzschia* spp.	68.3	62.9	56.4	45.2	48.2	51.6	28.1	37.0	8.5	25.5	21.4	17.9	40.4	26.9	18.8
Sum of diatoms	92.7	88.4	80.7	68.2	77.0	66.3	41.7	52.9	22.1	47.1	44.4	39.8	63.9	55.6	43.0
Sum of phytoflagellates	7.3	11.6	19.3	31.8	23.0	33.7	58.3	47.1	77.9	52.9	55.6	60.2	36.1	44.4	57.0
Total abundance	225.6	55.0	123.0	187.0	65.2	164.6	123.2	183.6	108.8	122.4	46.8	98.4	83.2	55.0	89.2

Light period (days)	161	166	171	176	181	186	191
Actinomonas sp.	-	-	-	-	-	-	2.2
Bacterosira fragilis	3.6	-	-	-	-	-	-
Chaetoceros gracilis	11.7	-	2.9	2.9	2.7	3.3	5.6
Chaetoceros simplex	6.3	-	3.6	3.8	2.5	4.6	5.2
Navicula cuspidata	-	-	-	-	-	-	2.6
Nitzschia arctica	-	-	3.4	2.7	2.2	-	-
N. closterium	2.7	-	-	-	-	-	-
N. cylindrus	4.9	-	-	-	-	2.3	6.9
N. frigida	-	-	-	2.0	-	-	-
N. pellucida	5.8	-	-	2.4	-	-	4.8
Nitzschia spp.	2.2	-	2.5	-	-	-	5.2
Phytoflagellates (<20µm)	**50.7**	**90.5**	**72.6**	**74.7**	**74.2**	**79.8**	**56.7**
Phytoflagellates (>20µm)	6.3	2.8	8.4	4.7	6.8	3.3	6.9
Sum of *Nitzschia* spp.	18.8	3.8	10.9	10.9	11.9	7.8	20.3
Sum of diatoms	43.0	6.7	19.0	20.6	18.9	16.9	36.4
Sum of phytoflagellates	57.0	93.3	81.0	79.4	81.1	83.1	63.6
Total abundance	44.6	235.4	176.8	180.4	251.2	122.8	92.4

Tab. 1: Relative abundance (%) of taxa comprising more than 2.0% (except spores) and total abundance (cells/ml) of the algal assemblage. Dominant taxa for each day are in bold.

Tab. 1: Relative Zusammensetzung (%) der Phytoplanktongemeinschaft mit Taxa, die über 2.0% (außer Sporen) der Gesamtzahl beitrugen. Dominante Taxa am jeweiligen Tag sind fett gedruckt.

Taxa	Dark period (days)				Light period (days)			
	0-35	35-105	105-161	0-161	0-5	0-20	0-30	20-30
Chaetoceros gracilis	-0.046	0.007	0.005	-0.005	-0.262	0.013	0.000	-0.027
Nitzschia cylindrus	-0.025	-0.024	0.008	-0.013	0.000	0.039	0.036	0.029
Nitzschia frigida	-0.047	-0.031	-0.012	-0.028	0.277	0.150	-0.100	-0.139
total *Nitzschia* spp.	-0.017	-0.031	0.009	-0.014	0.014	0.064	0.027	-0.047
total diatoms	-0.019	-0.024	0.011	-0.011	-0.039	0.045	0.019	-0.035
small phytoflagellates	0.067	-0.009	0.019	0.017	0.449	0.105	0.028	-0.127
total phytoflagellates	0.035	-0.011	0.012	0.007	0.431	0.104	0.028	-0.124
total algae	-0.009	-0.018	0.012	-0.006	0.333	0.086	0.024	-0.100

Tab. 2: Mean growth rates (μ, day^{-1}) of the algae during the dark period and after exposure to light.

Tab. 2: Mittlere Wachstumsraten (μ, Tag^{-1}) der Algen während der Dunkel- bzw. Hellphase.

lates (7 %). Total cell abundance at the beginning of the experiment was 226 cells/ml, in which diatoms accounted for 93 %.

During the dark phase, the abundance of the algae gradually decreased. At the end of the dark period, total algal abundance was 89 cells/ml, being 40 % of the initial abundance. The relative algal composition also changed to small phytoflagellates (<20 μm; 51 %), *Chaetoceros gracilis* (12 %) and *Chaetoceros simplex* (6 %) as main taxa. *Nitzschia* spp. only accounted for 19 % of the total algal abundance.

The addition of filtered sea-water during the onset of the illuminated phase resulted in a 50 % reduction of cell concentrations (Fig. 2). In the light, algal abundance increased in the first 20 days from 45 cells/ml to 252 cells/ml, mainly due to the growth of small phytoflagellates (<20 μm). At day 181, small phytoflagellates, large phytoflagellates (>20 μm), *Chaetoceros gracilis* and *Chaetoceros simplex* dominated the algal community with 74 %, 7 %, 3 %, and 3 %, respectively. At that time, *Nitzschia* spp. contributed 12 % to the total algal assemblage.

During the last 10 days of the light period from day 181 to day 191, the total algal abundance decreased to 92 cells/ml. At the end, small phytoflagellates still dominated the algal assemblage contributing 57 %, accompanied by large phytoflagellates (7 %), *Nitzschia cylindrus* (7 %), *Chaetoceros gracilis* (6 %), and *Chaetoceros simplex* (5 %).

Growth rates

Over the entire dark period of 161 days, the mean algal growth rate was -0.01 day^{-1}. Nearly all diatom species had negative growth rates, only phytoflagellates had positive growth rates of 0.02 day^{-1} for cells <20 μm and 0.01 day^{-1} for larger phytoflagellates (Table 2).

In the first 5 weeks of the dark period, small phytoflagellates grew at a rate of 0.07 day^{-1}, while all diatom species had negative growth rates. In the middle of the dark period from day 35 to day 105 (week 5 to 15), abundance of small phytoflagellates increased at a rate of 0.03 day^{-1} from day 35 to day 77, and then decreased at a rate of -0.06 day^{-1} to day 105. The mean growth rate of small phytoflagellates from day 35 to day 105 was -0.01 day^{-1} (Table 2 and Fig. 2).

During the first 5 days of the light phase, the algal community grew at a rate of 0.33 day^{-1}. Small phytoflagellates displayed the highest growth rate (0.45 day^{-1}), followed by *Nitzschia frigida* (0.28 day^{-1}) (Table 2, Fig. 2). During the first 20 days of the light period, algal abundance increased with a mean growth rate of 0.09 day^{-1} with *N. frigida* having the highest rate of 0.15 day^{-1}, followed by small phytoflagellates at 0.11 day^{-1}. In the last 10 days of the light period however, nearly all algal species had negative growth rates.

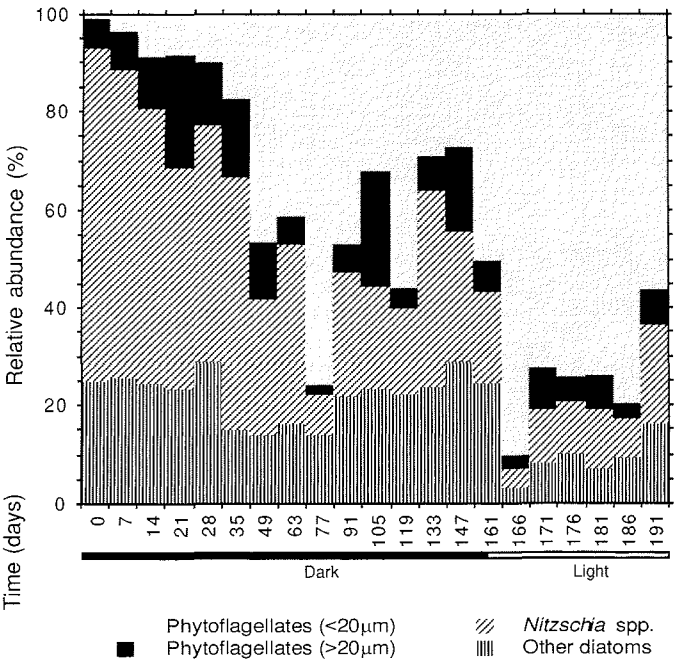

Fig. 1: Relative composition (%) of algae during the experiment.

Abb. 1: Relative Zusammensetzung (%) der Algengemeinschaften während des Experiments.

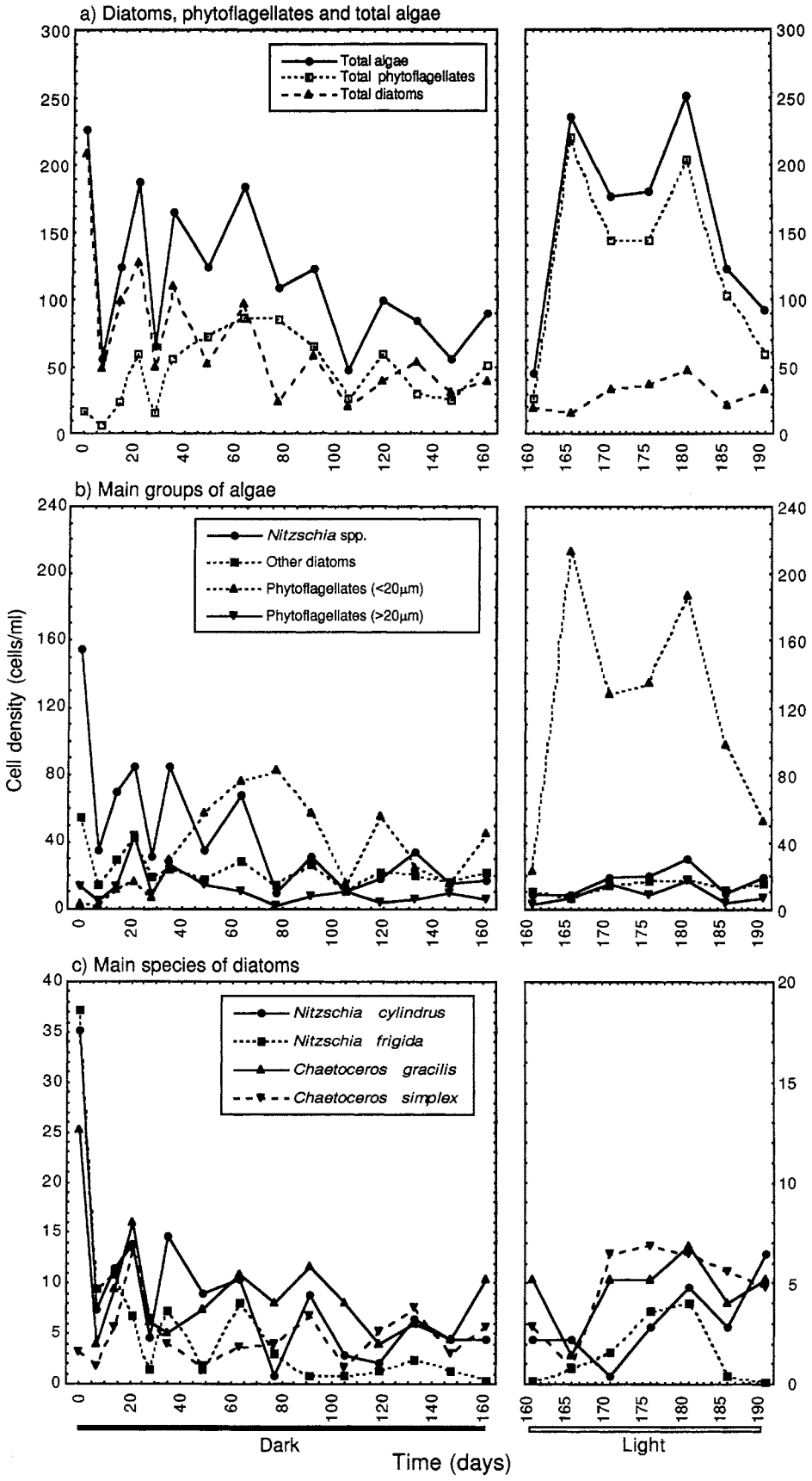

Fig. 2: Changes of the abundance of algae: a): Diatoms, phytoflagellates and total algae, b): dominant algal taxa and c): dominant diatom taxa. Note the changes of scale within the cell density-axis between a), b) and c), and the dark and light periods.

Abb. 2: Veränderungen der Häufigkeiten der Algen: a) Diatomeen, Phytoflagellaten und Gesamtalgenzahl, b) dominante Algentaxa und c) dominante Diatomeentaxa. Beachte die verschiedenen Ordinatenskalen in a-c) bzw. für die dunklen und hellen Perioden.

Resting spores

Resting spore formation was only observed for dinoflagellates and *Chaetoceros* spp. during the dark period (Tab. 1). The resting spores of *Chaetoceros* were found together with normal cells between the second and fourth week of darkness. Spores of dinoflagellates were observed during the entire dark period. Resting spores accounted for only a small proportion of the assemblage throughout the dark period (minimum of 0.4 % of all cells at week 2 to maximum of 4.5 % in week 11). Resting spores of the genus *Chaetoceros* accounted for 1.1 % of all *Chaetoceros* cells at week 1, 6.7 % at week 2 and 2.0 % at week 3.

DISCUSSION

The experiments clearly demonstrate the potential of Arctic marine microalgae to survive long periods in the dark. After the 161 day period of darkness we still found 40 % of the initial organism abundance and 64 % of the initially observed species. Although we tried to exclude grazers from our vials by prescreening through a 64 µm gauze, micrograzers such as heterotrophic flagellates and ciliates were present in our samples and the estimated growth rates are therefore underestimations of the true values.

To survive long periods of darkness, marine microalgae have at least three survival strategies: facultative heterotrophy, storage and utilization of energy reserves at a reduced metabolic rate, and resting spore formation. These are not considered to be mutually exclusive and may vary in importance between species (Palmisano & Sullivan 1985). Little attention has been paid to the physiological and biochemical mechanisms of winter survival in sea ice microalgae. Previous studies on dark survival were based mostly on data from clonal cultures (Bunt & Lee 1972, Palmisano & Sullivan 1982, 1983, Palmisano et al. 1987, Peters & Thomas 1996a, b). In such experiments, competition between algal species and temporal evolution of the algal assemblages were not considered. Prior studies on Arctic, temperate and Antarctic diatoms demonstrated their ability to utilize dissolved organic material (DOM) for nutrition (Allen 1970, 1971, White 1974, Palmisano & Sullivan 1982), but Horner & Alexander (1972) considered this process to be insignificant. In our investigation we observed that flagellated taxa survived better than diatoms during the dark period. The ability to use organic sources as DOM or bacteria to sustain their growth is well documented for many pelagic flagellated species (e.g., McKenzie et al. 1995, Andersson et al. 1989) but has not been studied on taxa found in the ice. The net growth of flagellates during the dark period of our experiment suggests that facultative heterotrophy (grazing on bacteria, uptake of DOM) plays an important role in the dark survival of Arctic marine flagellates. Therefore future studies should focus on the seasonal varying role of mixotrophy within the ice food web.

The storage of energy in the form of lipid droplets or carbohydrates has been observed in many diatoms (Barrett et al. 1995, Fahl & Kattner 1993, Nichols et al. 1988). Microscopical live observations on ice algae during our expedition (Gradinger, unpubl. data) showed, that many diatom and flagellated cells contained large amounts of storage products. Although we did not quantify the amount and composition of storage products, we assume, that this mechanism is of great significance for the dark survival of Arctic algae. Combined with energy storage, reduction of cellular metabolism (Peters & Thomas 1996a) will allow for survival of algal cells during the dark polar winters.

Many algal groups (e.g., diatoms and dinoflagellates) have evolved specific cell types and stages to survive unfavourable environmental conditions (Fryxell 1994). During our study, we observed resting spore formation in only two taxa (*Chaetoceros* spp., dinoflagellates) while most of the cells remained unchanged. Our findings are consistent with Antarctic (Palmisano & Sullivan 1985) and Arctic (Syvertsen 1991) studies where spore formation also was rarely reported. Also Peters & Thomas (1996a) observed no spore formation for three Antarctic diatoms species during a dark period of 10 months. Consequently we assume that resting spores play no important role in winter survival of most ice algae.

The response to light after the 161 day period of darkness was different for flagellates and diatoms. Phytoflagellates attained a fast growth rate of 0.43 day^{-1} during the first 5 days, while the cell abundances of most diatom species were still declining, some even at a higher rate than during the period of darkness. The ability of algae to adapt to the increasing light intensity within hours is consistent with other culture experiments which showed that photoadaption from low to high light intensities occurs within hours (Smith & Sakshaug 1990). Algal cells are thus able to sustain a photosynthetic active apparatus for months in the darkness, which allows for carbon assimilation immediately after reintroduction to light (Peters & Thomas 1996a). The lag phase to resume growth is probably longer for diatoms than for flagellated taxa (our study, Peters & Thomas 1996 a,b).

Due to the difficult accessibility of Arctic waters during winter/early spring, only a limited amount of field data on ice algal development during that season is presently available. Studies on ice algal growth during late spring in May 1988 (Gradinger et al. 1991) revealed growth rates of 0.08 day^{-1} for diatoms and 0.04 day^{-1} for autotropic flagellates in the lowermost 30 cm of an ice floe under similar light conditions during a period of 20 days. These results are in accordance with those from our investigation (Table 2). The fastest growth rate of a sea ice diatom was recorded for *Nitzschia cylindrus* with 0.28 day^{-1} under "summer" conditions in a clonal culture by Palmisano & Sullivan (1982), which is similar to the maximum growth rate for a diatom species (*Nitzschia frigida*) in our experiment. The general decrease of algal cells after 20 days in the light might have occurred due to nutrient exhaustion, as was the case in field observations from the Canadian Arctic (Gosselin & Legendre 1990).

In conclusion our results demonstrate the ability of algae to survive long periods of darkness and to react to increased light levels within days. Further investigations and experiments should

focus on the mechanisms to explain such observations in respect to energy storage and utilization by algae and the role of mixotrophy and species competition.

ACKNOWLEDGMENTS

We thank J. Ikävalko, T. Mock, I. Werner and the crew of RV *Polarstern* for their help during the expedition ARK-XI/2. This study was carried out within the frame of the Cooperation Program between the German Federal Ministry of Education, Science, Research and Technology (BMBF) and the State Science and Technology Commission of China. Helpful comments of G. Dieckmann, R. Horner and C. Krembs significantly improved this contribution. This study was partially supported by the Deutsche Forschungsgemeinschaft (DFG Gr 1405/1-1). Q. Zhang is grateful for support from BMBF for his stay at the Institute for Polar Ecology of Kiel University and the opportunity to participate in the Arctic expedition of RV *Polarstern*.

References

Allen, M. B. (1970): Metabolic activities of phytoplankton associated with Arctic sea ice.- Sci. Rep., R70-1. Inst. Mar. Sci., Univ. Alaska, Fairbanks.

Allen, M. B. (1971): High latitude phytoplankton.- Ann. Rev. Ecol. Syst. 2: 261.

Andersson, A., S. Falk, G. Samuelsson & Å. Hagström (1989): Nutritional characteristics of a mixotrophic nanoflagellate, *Ochromonas* sp.- Microb. Ecol. 17: 251-262.

Arrigo, K. R., D. L. Worthen, M. P. Lizotte, P. Dixon & G. Dieckmann (1997): Primary production in Antarctic sea ice.- Science 276: 394-397.

Barrett, S. M., J. K. Volkman, G. A. Dunstan & J. M. Leroi (1995): Sterols of 14 species of marine diatoms (Bacillariophyta).- J. Phycol. 31: 360-369.

Bunt, J. S. & C. C. Lee (1972): Data on the composition and dark survival of four sea-ice microalgae.- Limnol. Oceanogr. 17: 458-461.

Cota, G. F. & R. Smith (1991): Ecology of bottom ice algae. II. Dynamics, distributions and productivity.- J. Mar. Syst. 2: 279-295.

Fahl, K. & G. Kattner (1993): Lipid content and fatty acid composition of algal communities in sea-ice and water from the Weddell Sea (Antarctica).- Polar Biol. 13: 405-409.

Fryxell, G. A. (1994): Planktonic marine diatom winter stages: Antarctic alternatives to resting spores.- Mem. Calif. Acad. Sci. 17: 437-448.

Gosselin, M. & L. Legendre (1990): Light and nutrient limitation of sea-ice microalgae (Hudson Bay, Canadian Arctic).- J. Phycol. 26: 220-232.

Gradinger, R., M. Spindler & D. Henschel (1991): Development of Arctic sea-ice organisms under graded snow cover.- Polar Research 10: 295-307.

HELCOM (1988): Guidelines for the Baltic monitoring programme for the second stage.- Baltic Marine Environm. Prot. Comm., Helsinki. 249 pp.

Horner, R. A. & V. Alexander (1972): Algal populations in Arctic sea ice: an investigation of heterotrophy.- Limnol. Oceanogr. 17: 454-458.

Horner, R. A. (1985): Ecology of sea ice microalgae.- In: R.A. HORNER (ed.), Sea Ice Biota. CRC Press, Boca Raton. pp.83-103.

Kuosa, H., B. Norrman, K. Kivi & F. Brandini (1992): Effects of Antarctic sea ice biota on seeding as studied in aquarium experiments.- Polar Biol. 12: 333-339.

Legendre, L., S. F. Ackley, G. S. Dieckmann, B. Gulliksen, R. Horner, T. Hoshiai, I. A. Melnikov, W. S. Reeburgh, M. Spindler & C. W. Sullivan (1992): Ecology of sea ice biota. 2. Global significance.- Polar Biol. 12: 429-444.

Matheke, G. E. M. & R. Horner (1974): Primary production of the benthic microalgae in the Chukchi Sea near Barrow, Alaska.- J. Fish. Res. Board Can. 31: 1779-1786.

McKenzie, C. H., D. Deibel, M. A. Paranjape & R. J. Thompson (1995): The marine mixotrophic *Dinobryon balticum* (Chrysophyceae): phagotrophy and survival in a cold ocean.- J. Phycol. 31: 19-24.

Medlin, L. K. & J. Priddle (1990): Polar marine diatoms.- British Antarctic Survey, Natural Environment Research Council, Cambridge. 214 pp.

Nichols, P. D., J. K. Volkman, A. C. Palmisano, G. A. Smith & D. C. White (1988): Occurrence of an isoprenoid C25 diunsaturated alkene and high neutral lipid content in Antarctic sea-ice diatom communities.- J. Phycol. 24: 90-96.

Palmisano, A. C. & C. W. Sullivan (1982): Physiology of sea-ice diatoms. I. Response of three polar diatoms to a simulated summer-winter transition.- J. Phycol. 18: 489-498.

Palmisano, A. C. & C. W. Sullivan (1983): Physiology of sea ice diatoms. II. Dark survival of three polar diatoms.- Can. J. Microbiol. 29: 157-160.

Palmisano, A. C. & C. W. Sullivan (1985): Growth, metabolism, and dark survival in sea ice microalgae.- In: R.A. HORNER (ed.), Sea Ice Biota. CRC Press, Boca Raton. pp. 131-146.

Palmisano, A. C., J. B. SooHoo, R. L. Moe & C. W. Sullivan (1987): Sea ice microbial communities. VII. Changes in under-ice spectral irradiance during the development of Antarctic sea ice microalgal communities.- Mar. Ecol. Prog. Ser. 35: 165-173.

Peters, E. & D. N. Thomas (1996a): Prolonged darkness and diatom mortality. I: Marine Antarctic species.- J. Exp. Mar. Biol. Ecol. 207: 25-41.

Peters, E. & D. N. Thomas (1996b): Prolonged nitrate exhaustion and diatom mortality: a comparison of polar and temperate *Thalassiosira* species.- J. Plankton Res. 18: 953-968.

Smith, R. E. H., J. F. Cavaletto, B. J. Eadie & S. G. Wayne (1993): Growth and lipid composition of high Arctic ice algae during the spring bloom at Resolute, Northwest Territories, Canada.- Mar. Ecol. Prog. Ser. 97: 19-29.

Smith, W. O. Jr. & E. Sakshaug (1990): Polar phytoplankton.- In: W.O. SMITH, JR. (ed.), Polar Oceanography. Part B. Chemistry, biology and geology. Academic Press, San Diego. pp. 477-525.

Spindler, M. (1990): A comparison of Arctic and Antarctic sea ice and the effects of different properties on sea ice biota.- In: U. BLEIL & J. THIEDE (eds.), Geological History of the Polar Oceans: Arctic versus Antarctic, Kluwer Academic Publishers, Dordrecht, pp. 173-186.

Syvertsen, E. E. (1991): Ice algae in the Barents Sea: types of assemblages, origin, fate and role in the ice-edge phytoplankton bloom. - Polar Research, 10:277-287.

White, A. (1974): Growth of two facultative heterotrophic marine centric diatoms.- J. Phycol. 10: 292-300.