ARCTIC
VOL. 37, NO. 3 (SEPTEMBER 1984) P. 234-243

The Epontic Algal Community of the Ice Edge Zone and Its Significance to the Davis Strait Ecosystem

J.A. BOOTH[1]

ABSTRACT. The ice algae community in the dynamic outer edge zone of the Davis Strait pack ice was investigated in April-May 1978. Surveys of the epontic community were made using a remote camera system, a fibrescope, an ice corer, and *in situ* C^{14} incubation chambers. The undersurfaces of the floes were generally flat, containing slight undulations and small depressions of up to 10 cm. In the bottom few centimetres a transition was noted from hard ice to more fragile, but still firm, crystalline ice.

Epontic flora was highly patchy and almost entirely restricted to the bottom few centimetres of the floes. Average concentration in the bottom 6 cm of ice was 10.24 mg chl $a \cdot m^{-3}$. The pack ice bloom occurred in April and May with a peak occurring in May. The maximum primary production rates of 2.4 mg $C \cdot m^{-2} \cdot d^{-1}$ occurred at a light intensity of 1.8 $\mu E \cdot m^{-2} \cdot s^{-1}$. Photosynthesis appeared to be inhibited at light levels above 20 $\mu E \cdot m^{-2} \cdot s^{-1}$. The dominant genera of the epontic flora were *Navicula, Nitzschia,* and *Pleurosigma*; species composition of the epontic algal community differed significantly from that of the plankton. Two other ice algae communities were noted; a "sandwich" community in the middle of an ice floe, dominated by *Asteromphalus hookeri* and *Thalassiosira gravida*; and a floe surface community which was on one occasion observed being seeded from the plankton.

The total contribution of the epontic algae to the primary production of the Davis Strait was estimated to be approximately 7×10^7 g $C \cdot y^{-1}$, or less than 1% that of the phytoplankton. The contribution may still be important, however, as it precedes the phytoplankton bloom and is the only algal concentration under heavy pack ice.

Key words: Davis Strait, pack ice, epontic, primary production, ice algae

RÉSUMÉ. L'auteur a étudié en avril et mai 1978 la communauté d'algue glaciale dans la zone dynamique des abords extérieurs de la banquise de détroit de Davis. Des levées de la communauté épontique furent effectués à l'aide d'une caméra télécommandée, d'un fibroscope, d'un carottier glacial et de chambres d'incubation au C^{14} *in situ*. La surface inférieure de la banquise était plate d'ordinaire, avec de légères ondulations et de petites dépressions d'au plus 10 cm. Dans les quelques centimètres du fond, on nota une transition de la glace dure à une glace cristalline plus fragile mais toujours ferme.

La flore épontique était très inégale et était presque entièrement restreinte aux quelques derniers centimètres inférieurs de la banquise. La concentration moyenne des derniers 6 cm de glace était de 10.24 mg chl $a \cdot m^{-3}$. La floraison de la banquise se produisait en avril et en mai, l'activité maximale se déployant en mai. Les taux de production primaire de 2.4 mg $C \cdot m^{-2} \cdot d^{-1}$ avaient lieu sous une intensité de lumière de 1.8 $\mu E \cdot m^{-2} \cdot s^{-1}$. La photosynthèse semblait être entravée par des niveaux de lumière de plus 20 $\mu E \cdot m^{-2} \cdot s^{-1}$. Les genres dominants de flore épontique était la *Navicula*, la *Nitzchia* et la *Pleurosigma*; la composition par espèce de la communauté d'algue épontique différait de façon significative de celle du plancton. On nota deux autres communautés d'algue glaciale: une communauté "sandwich" dans le milieu d'un iceberg, dominée par *Asteromphalus hookeri* et *Thalassiosira gravida*, et une communauté de surface de banquise qui fut sujète observation en train d'être ensemencée par le plancton.

La contribution totale de l'algue épontique à la production primaire du détroit de Davis est évaluée à environ 7×10^7 g $C \cdot y^{-1}$, ou à moins de 1% de celle du phytoplancton. La contribution peut toutefois être d'une valeur importante, puisqu'elle précède la floraison du phytoplancton et constitue la seule concentration d'algue sous la banquise épaisse.

Mots clés: détroit de Davis, banquise, production primaire, algue glaciale

Traduit pour le journal par Maurice Guibord.

INTRODUCTION

During the winter and spring months ice covers more than 60% of the surface of Davis Strait. Phytoplankton biomass is low in the water column beneath the ice with chlorophyll *a* standing stocks of 0.002 to 0.01 $g \cdot m^{-2}$ (MacLaren Marex, 1979a). As only 3-4% of the incident radiation penetrates to the underside of the floes (MacLaren Marex, 1979b), primary production of phytoplankton in this area would also be expected to be low. It may, however, be supplemented by algae growing in association with the sea ice.

Sea ice algal communities have been reported from both the Arctic and Antarctic oceans (see review by Horner, 1976). The productivity of ice algae has been measured in Antarctic pack ice (Burkholder and Mandelli, 1965; Bunt, 1968), Bering Sea pack ice (McRoy and Goering, 1974), Chukchi Sea fast ice at Barrow, Alaska (Clasby *et al.*, 1973), and nearshore ice off Godhavn, Greenland (Andersen, 1977). In all areas except the sea ice off Godhavn, the ice algae not only contribute a significant proportion of the total annual primary production of the region but also are the only concentration of algae available to grazers during the late winter-early spring months. The ice algae off Godhavn are a short-lived phenomenon, contributing only about 0.015% of the total annual production. However, Andersen (1977) felt that the algae in the sea ice could act as an inoculum for the spring phytoplankton bloom when the ice melts.

A primary objective of the present study was therefore to document the presence of sea ice algae in Davis Strait and measure its distribution, biomass, and productivity to compare with concurrent measurements being made on the phytoplankton (MacLaren Marex, 1979a,b). A secondary objective was to describe the taxonomic composition of the ice algae to give some insight into its origin, fate, and relationship with the phytoplankton community. Physical and chemical analyses of the ice environment were also made to explore factors which may control the distribution and productivity of the ice algae.

[1]MacLaren Plansearch Limited, 1000 Windmill Road, Dartmouth, Nova Scotia, Canada B3B 1L7. *Present Address:* Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia, Canada V9R 5K6

METHODS

A total of 17 stations was occupied in the outer edge of the Davis Strait pack ice during April and May, 1978. These stations were situated between 60° and 64°N and restricted to the outer 50 km of the pack ice (Fig. 1). At each station, the local pack was described and the degree of ice cover estimated. Up to three floes were sketched, photographed, and measured. Physical characteristics such as rafting, cracking, erosion, snow depth, and drift pattern were described.

Access holes were bored on each of the chosen floes using a motorized ice auger. The bottom of the floe was observed using an Olympus model 1F11D2-10 industrial fibrescope with a 3 m probe. Photographs of the underside of the ice floe were obtained with a camera coupled to the fibrescope and with a surface-operated Nikonos II camera lowered through the auger hole. The Olympus fibrescope-camera setup had the advantage of allowing the investigator to observe the area being photographed; however, the resolution of the photograph was limited by the size of the optical fibres.

Quantitative samples of the interior and undersurface of each floe were collected, using an S-9000-T SIPRE geostat corer (7.5 cm diameter) with carbide tips. For the final 15 cm of the core, the corer was rotated by hand to avoid excessive pressure on the last few centimetres of fragile ice which might cause sample loss from the bottom of the core. Both direct observation with the fibrescope of the floe bottom during coring and subsequent examination of the bottom section of the core showed that sample loss through coring was not a problem such as had been reported elsewhere (Alexander, 1974; Meguro *et al.*, 1967).

Eight cores were taken from each floe; two from each of two sites near the floe edge and four from a site in the centre. As the ice flora was restricted almost entirely to the bottom of the floe, the bottom 6 cm of six cores were sectioned off, melted at 25°C, and individually retained for analysis of chlorophyll *a*, nutrients, salinity, and taxonomic composition of the biota. Sections of the upper portion of one of the cores were retained for analysis of salinity, chlorophyll *a*, and nutrients. The bottom 1-cm section was taken from the seventh core to estimate the amount of plant material and nutrients present at the lower ice surface. The eighth core was kept frozen intact for reference.

On each floe a 5-L Niskin bottle was lowered through the central access hole and a sample of water was taken at the level of the water/ice interface for qualitative taxonomic and chemical comparison with the ice samples.

On six of the floes, the bottom 5-cm sections of two 7.5 cm diameter ice cores were divided in two longitudinally and placed in semi-circular plexiglass incubation chambers (Fig. 2). One half of each core was placed in a clear chamber, the other in an opaque chamber. Each chamber was then inoculated with 3 ml ($\sim$ 15.0 μCi) prefiltered $NaH^{14}CO_3$, filled with a measured amount of filtered sea water, and sealed with a watertight lid. At no time was the bottom section of the ice core exposed to direct sunlight. The chambers were suspended for four hours under an undisturbed ice surface at least 1 m from any auger or core holes, with the core sections in their original orientation. All incubations were conducted between 0930 and 2045 hours.

During the incubation period, the total amount of photosyn-

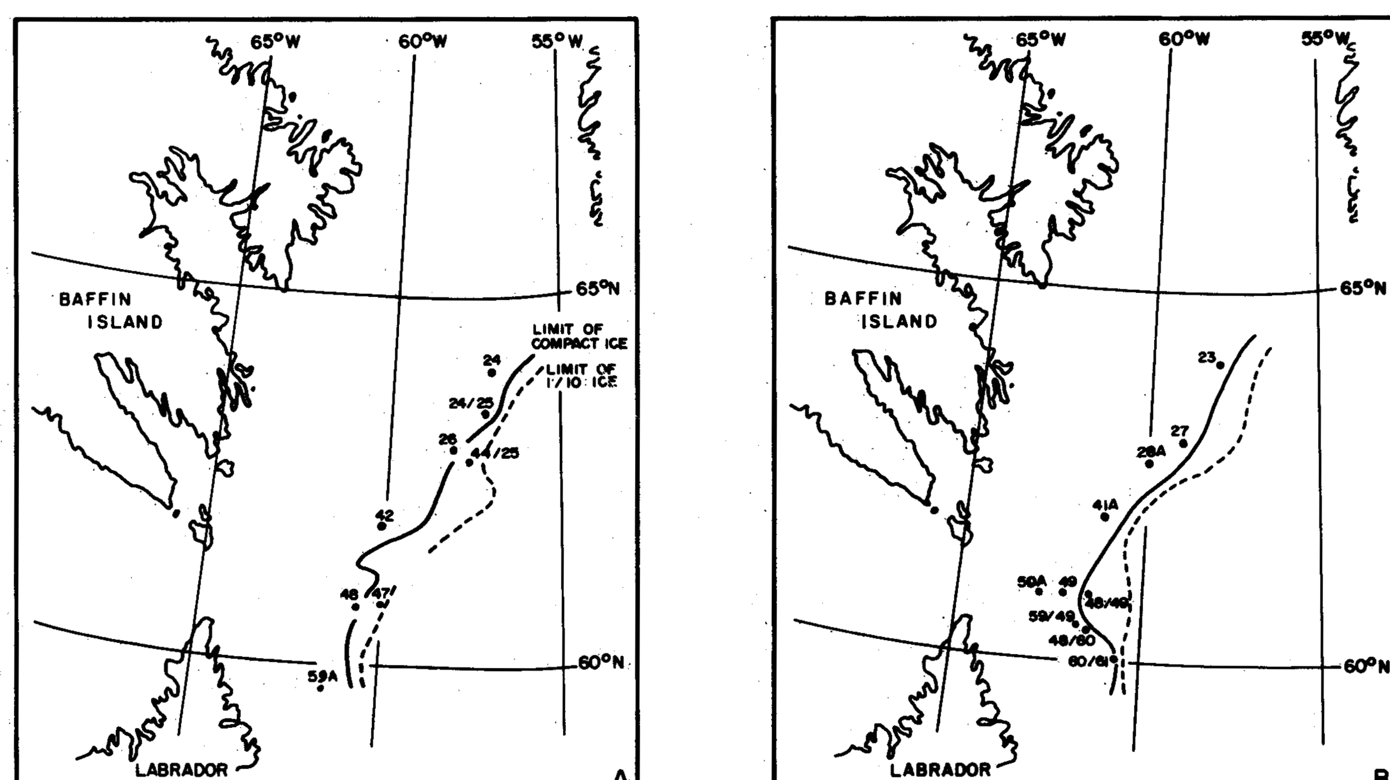

FIG. 1. Station positions, Davis Strait, April 1978 (A) and May 1978 (B).

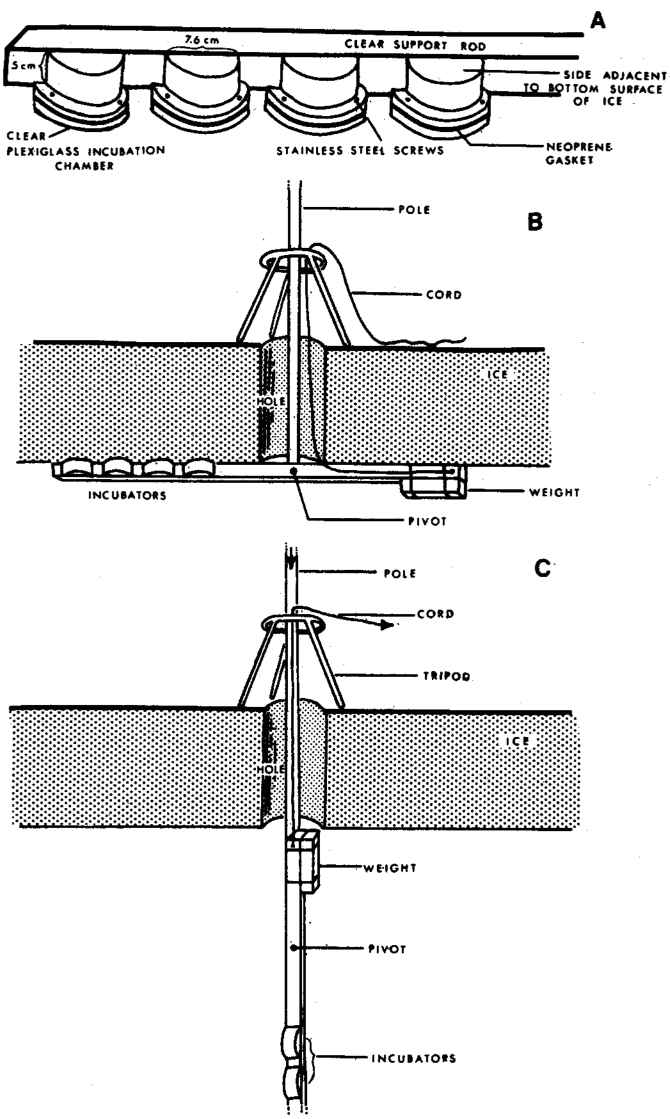

FIG. 2. Ice-core incubation chambers used for productivity measurements. A: Plexiglass incubation chambers; B: Incubation chambers in position under ice; C: Retrieval of incubation chambers.

thetically active radiation (PAR) in the 400-700 μm wave band reaching the ice floe surface was measured using a Li-Cor quantum integrator. At the end of the incubation, the PAR was measured below the ice floe in the exact spot that the chambers had been suspended and compared with that reaching the ice floe surface to determine the percentage penetration. The average PAR reaching the incubators under the floe throughout the incubation period was then estimated from the average PAR at the surface of the floe and the fraction of that PAR which reached the bottom of the ice. Although the presence of ice algae on the undersurface of the floe would diminish the amount of light reaching the incubation chamber, this would be accounted for in the light measurement.

After incubation, the core sections were transferred to 300-ml glass jars, and were fixed with 1 ml 0.4% HgCl. Cores were melted slowly in the dark and then filtered through 0.45 μm Millipore membrane filters. The filters were then stored in glassine envelopes in a desiccator at −20°C. At the end of the cruise the filters were acid-fumed, dissolved in fluor, and counted on a liquid scintillation counter. The scintillation fluor consisted of equal parts toluene and ethylene glycol monoethyl ether with 8.4 $g \cdot L^{-1}$ PPO and 0.16 $g \cdot L^{-1}$ POPOP. Primary productivity rates measured during the experiment were converted to daily rates assuming a 12-hour day, which was roughly the time period each day when measurable light could be detected below the floes.

Nutrient concentrations (nitrate, nitrite, phosphate, and silicate) of melted ice cores were measured using a Technicon Auto-Analyser II. Salinity measurements were made using a Guildline 8400 Autosal Salinometer or standard titrations. Samples for chlorophyll analysis were filtered through glass fibre filters (Gelman A/E). Chlorophyll *a*, *b*, and *c* and phaeophytin concentration were measured using the fluorometric and trichromatic techniques (Yentsch and Menzel, 1963: Holm-Hansen *et al.*, 1965; Jeffrey and Humphrey, 1975; Jensen, 1978).

A 50-ml subsample of the bottom 6 cm of core samples was preserved in Lugol's solution and counted using the standard Utermöhl inverted microscope technique (Utermöhl, 1958). Pennate diatoms were examined under a phase contrast microscope at 1000× magnification after the subsamples were cleared of all organic matter using the technique of Hasle and Fryxell (1970), and mounted on styrax mounting medium (Czarnecki and Williams, 1972).

Preliminary data and ancillary information for this study are contained in MacLaren Atlantic (1977) and MacLaren Marex (1979a,b).

RESULTS AND DISCUSSION

Davis Strait Pack Ice

Three zones of ice coverage are typical of the Davis Strait study area: a relatively heavy corner of pack ice extending east from the Canadian coast; a highly dynamic edge zone; and open water. The location and extent of ice cover 1/10 or greater during the study is illustrated in Figure 1. The ice cover encountered during this study was slightly greater than average for the area (U.S. Naval Oceanographic Office, 1968). Sampling and experiments carried out in this study were limited to the ice edge zone.

The dynamic nature of the ice coverage in the area was evident throughout the cruise, but particularly in the edge zone. This zone was characterized by long "strings" of ice floes extending out from the main pack into open water. Within hours the combined effect of wind and current could significantly alter the type of coverage at a given location. The mobility of individual floes was evident particularly on one occasion when a displacement of 21 km was noted over an 18-h period.

Most of the floes observed had flat top surfaces, though on some floes rafting had occurred around part or all of the circumference. Floes were generally covered with a thin crusty layer of snow and occasionally snowbanks of up to 40 cm were observed, usually in the lee of projecting rafted ice. In several cases, all or part of the floe surface had been washed over by waves, transforming the snow cover into ice.

The underside of most floes was relatively flat with a smooth bottom-edge. On a small scale, the bottom surface features varied from slight undulations to small depressions of up to 10 cm in depth. When viewed at close range, floe bottoms had a glassy appearance and were pocked with the ends of tiny smooth-edged brine channels.

The internal structure of the ice consisted of brine channels from top to bottom. Several times, larger pockets of soft ice or slush with high salinity levels were encountered while coring. The "slush" layer reported from the Antarctic pack ice (Bunt and Lee, 1970) and to a much lesser extent in Arctic fast ice (Horner, pers. comm. 1978) was absent; however, there was a transition within the bottom 2-3 cm from hard ice to a more fragile crystalline ice as had been reported elsewhere in the Arctic (Alexander *et al.*, 1974; Hsaio, 1980). Stalactites reported to occur under fast sea ice (Green and Steele, 1975; Lewis and Milne, 1977) were not observed.

The average mean thickness of the 34 floes studied was 125 cm; floe mean thicknesses ranged from 32 to 265 cm. The single longest core was 355 cm. The majority of the floes were between 100 and 160 cm thick with no rafting. It seemed likely that thicker ice was formed by rafting of two floes.

Distribution and Productivity of the Ice Algae

Visual examination of the underside of the ice floes by camera and fibrescope revealed a highly patchy distribution of epontic flora on any one floe (Fig. 3). This patchiness was reflected in the range and variance of the chlorophyll concentration over a floe (Table 1).

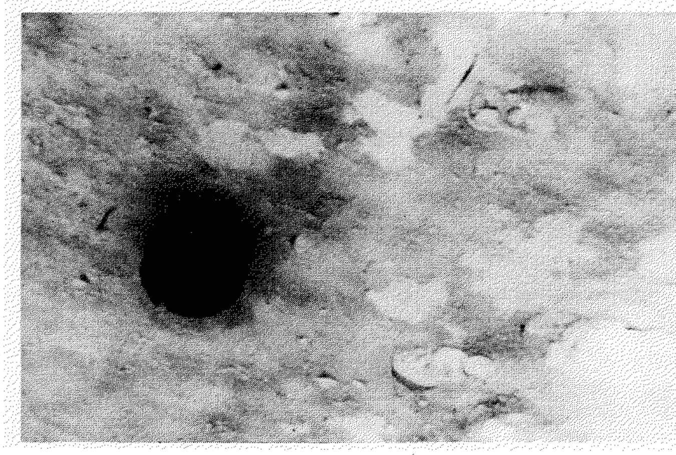

FIG. 3. Photograph of epontic community (dark areas) of the bottom surface of an ice floe taken with Nikonos camera. Black object is 7.5-cm diameter tip of ice corer.

Although there was no statistical difference between the mean epontic chlorophyll concentrations of the study floes, certain trends were discernible. Epontic chlorophyll concentrations tended to decrease from south to north during both April and May, presumably in response to latitudinal variation in available light. The epontic bloom was in the early stages of development in April; the only area with a high mean chlorophyll concentration was just south of 60°N on 16 April at Station 59A. In May there was an overall increase in epontic chlorophyll concentrations, the highest concentrations again being found in the southwest portion of the Davis Strait pack

TABLE 1. Concentration of chlorophyll *a* ($mg \cdot m^{-3}$) in bottom 1 and 6 cm of floe ice and in water directly below the floe, Davis Strait, April and May 1978

			Bottom 6 cm of ice core					Bottom 1 cm of ice core		Water directly below floe	
Station	Date	n^f	Mean value	Standard deviation	Maximum value	Minimum value	n^c	Mean value	n^c	Mean value	samples (N)
59A	78.04.16	1	45.14	37.4	86.33	13.35	4				
47	78.04.20	2	0.49	0.48	1.42	0.03	7	0.28	1	—	
48A	78.04.21	2	7.46	6.51	17.02	0.96	12			0.19	2
42	78.04.22	1	0.41	0.26	0.83	0.18	6	4.46	1	0.71	1
26	78.04.25	2	3.50	5.49	2.19	0.24	14	21.96	2	12.73	2
24	78.04.27	2	9.33	7.00	27.89	0.46	12	29.30	2	27.46	2
24/25	78.04.28	1	1.44	1.80	5.13	0.61	6	1.14	1	12.75	1
Total for April		11	7.63	14.29			61				
23	78.05.04	3	13.75	9.48	31.64	0.54	17	38.82	2	10.08	3
27	78.05.06	3	3.30	4.45	18.20	0.23	18	21.85	2	7.22	2
28A	78.05.07	3	1.37	1.16	4.55	0.33	19	6.82	2	10.35	3
41A	78.05.09	3	4.38	5.15	18.37	0.29	18	66.10	3	7.71	3
49	78.05.11	3	8.01	4.79	19.87	2.08	18	159.96	3	8.34	3
50A	78.05.12	3	24.58	23.31	68.34	3.95	16	281.30	3	0.41	3
48/49	78.05.13	3	0.65	0.52	5.70	0.14	18	0.69	3	7.80	2
60/61	78.05.15	2	10.14	6.35	18.00	1.41	12	46.20	2	3.12	2
49/59	78.05.16	3	41.86	42.38	160.43	7.69	15	204.78	3	6.20	2
48/60	78.05.17	1	3.54	0.01	3.54	3.53	2		—		
Total for May		27	10.32	15.89			151				

n^c = number of ice cores sampled
n^f = number of ice floes sampled

ice. In both months concentrations of chlorophyll *a* increased with distance from open water. By the end of the sampling period (late May), the ice algae bloom had begun to "slough off" the melting ice floes in the southern area, indicating that the bloom was approaching termination.

As reported in other areas of the Arctic (Clasby *et al.*, 1973) the epontic algal community in the Davis Strait pack ice was almost entirely restricted to the bottom few centimetres of the ice floes. From 50 to 100% of the chlorophyll *a* in the bottom 6 cm of cores was found in the lowest 1 cm of the ice (Table 1) with a maximum concentration of 467 mg chl $a \cdot m^{-3}$ measured from the bottom 1 cm of one core. The average concentration of chlorophyll *a* in the bottom 6 cm of Davis Strait pack ice over the April-May period was 10.24 mg chl $a \cdot m^{-3}$ which, on an areal basis, is equivalent to 0.61 mg chl $a \cdot m^{-2}$. This biomass is lower than that reached by the more northern epontic algal communities in the fast ice around Barrow, Alaska and Devon Island, Canada, but was similar to the chlorophyll *a* biomasses recorded in young (< 10 days old) ice at Godhavn, West Greenland, during the early stages of the epontic bloom in Bering Sea ice, and under fast ice in Frobisher Bay (Table 2). In contrast, Antarctic ice algae communities have a biomass of chlorophyll *a* almost an order of magnitude higher than that observed in this study (Table 2).

The daily primary production rate of the epontic community in Davis Strait ranged from 0.003 to 2.36 mg $C \cdot m^{-2} \cdot d^{-1}$ (Table 3). The maximum daily production was one to two orders of magnitude less than the maximum rates recorded from the sea ice communities of the Antarctic pack ice and the fast ice of the Chukchi Sea (Table 4). However, rates were similar to those recorded in 8- to 10-day-old sea ice along the west coast of Greenland at Godhavn, and in the Bering Sea pack ice during the early stages of the epontic bloom in April (Table 4). Areal primary production rates measured in the water column under sea ice in the Bering Sea and at Godhavn, West Greenland, were of a similar order of magnitude to that of the epontic algae, whereas in the Chukchi Sea at Barrow, Alaska, they were an order of magnitude lower (Table 4). Under ice, plankton production rates were not measured in Davis Strait; however, the low light levels under the ice (Table 5) indicate that production would be low.

The Davis Strait epontic algae were adapted to low light levels as shown by the ratio of primary productivity to chlorophyll *a* concentration (P/B) which was two to three orders of magnitude lower at light intensities of greater than 20 $\mu E \cdot m^{-2} \cdot s^{-1}$ than at intensities of less than 4 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Table 3). However, even the P/B ratios measured at the lower light intensities (0.02 to 0.26 mg $C \cdot (\text{mg chl } a)^{-1} \cdot h^{-1}$) were low in

TABLE 2. Concentration and biomass per m^2 of epontic chlorophyll *a* in the Davis Strait and other polar communities

Location	Community	Thickness of ice (cm)	Thickness of algal layer (cm)	Chlorophyll *a* concentration ($mg \cdot m^{-3}$)	Chlorophyll *a* biomass ($mg \cdot m^{-2}$)	Source
Arctic						
Jones Sound Devon Island	epontic land fast ice	165-120	3.5	403 (30-1460)	12 (3-23)	Apollonio, 1965
Barrow, Alaska Chukchi Sea	epontic land fast ice	200-400	5-30	120 (10-427)	24	Meguro *et al.*, 1967
Godhavn, West Greenland	epontic young ice	30-45	5	<0.34	<0.5	Andersen, 1977
Barrow, Alaska Chukchi Sea	epontic land fast ice	155-170	2-4	74.0-762	2.96-30.49	Clasby *et al.*, 1973
Frobisher Bay, Baffin Island	epontic land fast ice	200	5-8	(0-300)	0.023-7.58	Hsiao, 1980
Davis Strait	epontic pack ice	100-160	1-6	10.24 (.03-467)	0.61 (.002-9.63)	this study
Bering Sea	epontic pack ice	200-300			0.34-2.97	McRoy and Goering, 1974
Antarctic						
McMurdo Sound	epontic pack ice	400-500	30-100	250	125*	Bunt, 1964; Bunt and Wood, 1963
McMurdo Sound	epontic	240	20		—	Hoshiai, 1972
Palmer Peninsula	snow pack ice	—	30 (15-100)	300-400	105*	Burkholder and Mandelli, 1965
Lutzow-Holm Bay	snow	—	15-20	670	97	Meguro, 1962

*Estimated

TABLE 3. Rates of primary production and production per unit chlorophyll *a* (P/B) in the bottom 5 cm of Davis Strait pack ice, April-May 1978

Station No.	Floe	Replicate	Date	Average PAR $\mu E \cdot m^{-2} \cdot s^{-1}$	Average floe Chlorophyll *a* $(mg \cdot m^{-2})$	Primary production $(g\ C \cdot m^{-2} \cdot d^{-1})$	P/B (d^{-1})
24	1	A	78.04.24	36.0	0.463	0.014	0.029
		B				0.026	0.056
26	1	A	78.04.25	3.1	0.060	0.048	0.792
		B				0.015	0.255
28A	3	A	78.05.08	3.8	0.046	0.085	1.868
48A	1	A	78.04.21	20.5	0.631	0.003	0.005
		B				0.007	0.011
49	1	A	78.04.11	2.6	0.323	0.365	1.130
		B				0.618	0.191
60/61	1	A	78.05.15	1.8	0.755	2.361	3.127
		B				0.974	1.290

TABLE 4. Maximum rates of primary production and primary production per unit chlorophyll *a* (P/B) in the Davis Strait and other polar ice and plankton communities

Location	Maximum Primary Production $(mg\ C \cdot m^{-2} \cdot d^{-1})$	P/B $g\ C \cdot (g\ chl\ a)^{-1} \cdot h^{-1}$	Source
Ice Community			
Barrow, Alaska	55-179*	0.7	Clasby *et al.*, 1973
Godhavn, W. Greenland	0.05-2.0	0.2-0.6	Andersen, 1977
Bering Sea	4.8	0.1-0.8	McRoy and Goering, 1974
Antarctic (snow community)	190	2.6	Burkholder and Mandelli, 1965
Antarctic (epontic community)	46*	0.06-0.2	Bunt and Lee, 1970; Bunt, 1968
Davis Strait	2.4*	0.0004-0.3	present study
Plankton Community			
Barrow, Alaska: under ice	7.2*	—	Matheke and Horner, 1974
Barrow, Alaska: summer	286*	—	Matheke and Horner, 1974
Godhavn, W. Greenland: under ice	0.05-0.9	0.4-1.3	Andersen, 1977
Bering Sea: at ice fron	89	0.04	McRoy and Goering, 1974
Bering Sea: under ice	21	0.4	McRoy and Goering, 1974
Antarctic: around ice during epontic bloom	0.6-8.9	0.6-2.6	Burkholder and Mandelli, 1965
Davis Strait: pre-spring bloom open water	210	0.8-1.4	MacLaren Marex, 1979a
Davis Strait: spring bloom	2256	0.4-0.5	MacLaren Marex, 1979a
Davis Strait: August	54	0.1	MacLaren Marex, 1979a

*Assuming 12-h day when only hourly rates were given in literature.

comparison to other polar plankton and ice algae communities (Table 4). The actual rate of primary production by the epontic algae in the Davis Strait pack ice may, however, be somewhat higher than the rates measured. The degree of penetration of ^{14}C into the firm bottom ice of the Davis Strait pack ice is undoubtedly less than that in the loose slush of the Antarctic (Bunt and Lee, 1970) or the soft bottom of the Chukchi Sea at Barrow, Alaska (Clasby *et al.*, 1973).

Maximum primary production was measured at an average PAR of 1.8 $\mu E \cdot m^{-2} \cdot s^{-1}$ and may have been inhibited at high light levels. In the epontic community at Point Barrow, Alaska, light levels of 2.8 and 11.4 $\mu E \cdot m^{-2} \cdot s^{-1}$ were required to initiate primary production (Alexander *et al.*, 1974). In the Antarctic, Bunt (1974) reported initiation of primary production of epontic algae at 1.15 $\mu E \cdot m^{-2} \cdot s^{-1}$, light satuaration at 2.3 $\mu E \cdot m^{-2} \cdot s^{-1}$, and inhibition at 23 to 230 $\mu E \cdot m^{-2} \cdot s^{-1}$. Epontic algae thus form a shade-adapted community which can fix inorganic carbon at very low light intensities. Although light may have limited algal growth under some snow-covered floes where only 0.09-7.5% of incident PAR was transmitted (Table 5), these measurements do not include light absorbed by the algae, which can amount to 16% of the surface light (Matheke and Horner, 1974); the actual amount of light reaching the epontic algae may thus have been higher.

The salinity values of melted sections of floe ice cores usually decreased from top to bottom. Average salinity values in the top, middle, and bottom sections of the ice floes were 7.04, 5.83, and 5.35‰ respectively. When ice forms, salt is rejected from the pure crystal structure and trapped in brine pockets and channels between the ice crystals. Alexander *et al.* (1974) reported a salinity range of 20-39‰ for interstitial sea ice brine at Barrow, Alaska, whereas Lewis and Milne (1977) measured salinities of 62-68‰ in brine dripping from old sea stalactites. If a median value of 50‰ is taken for the salinity

TABLE 5. Photosynthetically active radiation (PAR) beneath the ice and percent attenuation in the Davis Strait pack ice, April-May 1978

	% of incident PAR	PAR ($\mu E \cdot m^{-2} \cdot s^{-1}$)
Ice Algal Bloom Present		
under ice with snow	0.09 - 7.66	0.32 - 27.2
under ice without snow	1.67 - 8.92	5.94 - 31.7
Ice Algal Bloom Absent		
under ice with 4-18 cm snow	1.43 - 9.36	5.08 - 33.3
under ice without snow	3.04 - 13.5	10.8 - 48.0

of the interstitial brine in Davis Strait sea ice, then the brine would constitute approximately 7-10% of the volume of the melted ice core.

Nutrient concentrations showed no consistent vertical gradients in the ice cores but tended to be both higher and more variable in the bottom 6 cm. The nutrient concentrations recorded in Table 6 are those measured in the melted bottom 6-cm core sections, and thus the concentrations seen by the algal cells in the interstitial brine could be 10-15 times these values. Nutrients did not appear to be a limiting factor to primary production.

Species Composition

The flora in the bottom 6 cm of the ice consisted of two components (Table 7): attached forms, mainly pennate diatoms; and non-attached forms frozen into the ice matrix or in free suspension in brine pockets. At stations where the epontic bloom had commenced the pennate diatoms were overwhelmingly dominant. A similar type of two component epontic flora has been described for the Antarctic (Bunt and Wood, 1963), Chukchi Sea (Alexander *et al.*, 1974), West Greenland (Vanhoffen, 1897), and East Greenland (Barents and Polar seas)(Gran, 1904).

The non-attached component of the ice flora consisted mainly of non-viable neritic phytoplankton (mostly centric diatoms) and their spores which were probably frozen into the ice the previous fall. A large (80-100 μm) "euglenoid-type" flagellate (Flagellate #1) was frequently observed as part of the epontic community, always appearing in a healthy state. This frozen-in planktonic component was dominant only at "prebloom" floes, e.g. at Station 42, Floe 1 (Table 7). On this floe 42% of the cells were *Chaetoceros* spores and the ice had a mean chlorophyll *a* concentration of only 0.41 $mg \cdot m^{-3}$.

Two other rarely observed ice algae communities were also noted in Davis Strait pack ice, in the middle and on the surface of the floes. The middle ice community was observed only

TABLE 6. Average concentrations of inorganic nutrients in the bottom 6 cm of Davis Strait pack ice, April-May 1978

Nutrients	Mean ($mg\text{-}at \cdot m^{-3}$)	Range ($mg\text{-}at \cdot m^{-3}$)
Nitrate-nitrite	6.8	0.9 - >30
Phosphate	0.6	0.02 - 3.1
Silicate	7.4	2.1 - 20.9

once at Station 44/25 on 4 April when a "sandwich" of brown ice containing viable algal cells was observed in a small decaying floe. *Asteromphalus hookeri* and the other dominant species of this community were not typical of other ice floes (Table 7) nor were they observed in surface water samples taken adjacent to the floe. It is probable that *in situ* development had occurred from a small planktonic "seed" population. Previous workers in the Antarctic (Buinitskiy, 1968; Hoshiai, 1972, 1977; Fukushima and Meguro, 1966; Ackley *et al.*, 1979) described the regular occurrence of a concentration of algae in the middle layer of the ice floe near the snow/ice interface. Ackley *et al.* (1979) called this the "interior community".

Seeding of the surface of the ice by planktonic algae was observed at Station 27 (Floe 2 on 6 May), when one edge of the floe was washed over by surrounding surface water. Samples of surface ice taken from the floe before and after the incident showed that planktonic algae had been frozen in the previously barren ice surface. This phenomenon has been described in Antarctic waters (Fukushima and Meguro, 1966), where it is thought to be a frequent and significant occurrence. In another instance, the surface of a honeycombed block of ice adjacent to Floe 2 at Station 60/59 was covered with large patches of a filamentous mat of *Melosira arctica.* The mat also contained large numbers of *Coscinodiscus* sp. and *Gymnodium* sp. The bottom flora of the floe was a completely different community dominated by *Nitzschia frigida* and *Pleurosigma angulatum*. Massive mucilaginous accumulations of *Melosira arctica* on the undersides of ice floes have been reported from the northern Barents Sea (Usachev, 1949). Brown ice surface, which did not result from overturned floes, was observed only twice on the present cruise, however, and this ice floe surface community is probably a rare and insignificant one in the Davis Strait. Without the insulation of snow or ice cover such as that found in the Antarctic (Meguro, 1962), the extreme cold, low salinity, and high light intensity of this habitat would make the survival of algae unlikely.

Phytoplankton sampled from directly below the ice and at nearby hydrographic stations had a species composition different from that of the epontic community (MacLaren Marex, 1979b). The only exception to this was at Floe 3, Station 49/59, on 16 May, where comparatively high numbers of apparently healthy epontic algae, typical of the local ice community, were collected from the water beneath the floe. The chlorophyll *a* concentration in the water below the floe was low at this time (0.36 $mg \cdot m^{-3}$) while in the bottom 6 cm of the ice it was very high and variable, ranging from 18.13 to 160.43 $mg \cdot m^{-3}$. It appears that the epontic algae were sloughing off the bottom of the floe into the water below.

The dominant genera of the Davis Strait pack ice epontic flora were *Navicula*, *Nitzschia*, and *Pleurosigma* (Table 7). Numerical analysis of the epontic algae community on five floes in "bloom" condition showed that the two dominant species, *Navicula transitans* var. *derasa* and *Nitzschia frigida* were also the most uniformly occurring species (Table 8). *Navicula transitans* var. *derasa*, *Nitschia delicatissima*, *N. frigida*, *N. grunowii*, and *Pleurosigma angulatum* were the

TABLE 7. Species composition of Davis Strait pack ice algae communities, April-May 1978 (D=Dominant; C=Common; P=Present)

Station	48A	42	44/25	26	26	23	49	49	49	49	50A	50A	50A	48/49	60/61	60/61	49/59
Floe	1	1	1	1	2	2	1	2	3	*	1	2	3	1	2	**	3
Date (Day/Month)	21/4	22/4	25/4	25/4	25/4	5/5	11/5	11/5	12/5	11/5	12/5	12/5	13/5	13/5	15/5	15/5	16/5
BACILLARIOPHYCEAE PENNALES																	
Amphiprora sp.							P	P	P								
Diploneis littoralis (Donkin) Cl.							C	C	C		P	P	P				
Licmophora sp.								P			P	P	P				
Navicula cluthensis Grun.								P			P						
N. crucigeroides Hust.							P	P	P			P	P				
N. directa (W. Sm.)Ralfs	P			P		P	P	P	P	P	P	C	C	D			
N. kjellmanii Cl.											P						
N. sibirica (Grun.)Cl.						P	C	P	C	P	C	C	C				
N. subinflata Grun.						P	P	P	C		P	P	P				
N. transitans var. *derasa* (Grun.)Cl.	D	P	P	P	D	D	D	D	D	D	D	P	P	D		P	
N. spp.		P			P	P	P	P	P			P	P	P	P	P	P
Nitzschia closterium (Ehrb.)W.Sm.						P	P	P	P								
N. cylindrus (Grun.)Hasle						P			P								
N. delicatissima Cl.				P		C	C	C	C			C	C			C	P
N. frigida Grun.	P	P		P	P	D	D	D	D	D		D	D	D	D	C	P
N. grunowii Hasle.		C	P		P	P			C							C	
N. longissima (Breb.)Ralfs							P		P								
N. seriata Cl.																	
N. sp. 1		C			P			P									
N. sp. 2							P	P	P								
Pinnularia sp.												P	P				P
Pleurosigma angulatum W.Sm.					P		C	P	C	C		C	C		D	P	D
P. sp.									P								
Thalassiothrix longissima Cl. and Grun.		P															
BACILLARIOPHYCEAE CENTRALES																	
Asteromphalus hookeri Cl.		C	D														
Chaetoceros atlanticus Cl.					P				P								
C. borealis Bail.		P	P														
C. decipiens Cl.		C	P														
C. septentrionalis (Grun.)Rattray		P			P	C	P	P	C			P	P				
C. spores		D	P														
Coscinodiscus sp.		P	P		P	P										D	
Detonula cystifera Gran.		P	P			P	P		P								
Eucampia greenlandica Cl.						P											
Melosira arcticum (Eheb.)Dickie																D	
Melosira arcticum spores				C		P		P	P								
Rhizosolenia hebetata (Bail.)Gran		C															P
Thalassiosira gravida Cl.	P		D		P	P		P	P	P							
T. nordenskioldii Cl.			P			P	P		P						P		
Unidentified				P			P	P	P						P		
CHRYSOPHYCEAE																	
Distephanus speculum (Eheb.) Haeckel		P														C	
Phaeocystis pouchetii (Har.) Lagerh									P								
DINOPHYCEAE																	
Exuviaella sp.																D	P
Gymnodinum sp.								P								C	
Gyrodinium sp.									P								
PRASINOPHYCEAE																	
Pyramimonas sp.																C	
OTHER																	
Flagellate #1							P	P	P			C	C				
Flagellates							P		P								
Spores		C			P	C											P

* ice flange next to St. 49 Floe 1
**from surface of floe 60/61

only epontic algal species which were also regularly observed in the plankton, though they were never abundant there. Many of the epontic algae were never found in the plankton samples; however, their occurrence on the floes was often sporadic (Table 7) indicating that they would be a rare element of the plankton and therefore easily missed in sampling.

The uniqueness of the epontic flora has been documented by other workers (Andersen, 1977; Bunt and Wood, 1963; Gran, 1904; Horner, 1976; Meguro *et al.*, 1967). The dominant genera and in some cases species are remarkably similar in different areas of the Arctic. This phenomenon has been previously noted (Usachev, 1949) and such species have been

TABLE 8. Abundance of dominant algae in the epontic community of selected ice floes, Davis Strait, April-May 1978

Station	49					49					49				
Floe	1					2					3				
Date	11/5					11/5					12/5				
Core	1	2	6	7	8	1	3	6	7	8	1	2	3	4	8
% Pennate diatoms	99.7	99.2	94.0	99.2	98.8	97.5	99.4	98.7	96.8	100	97.9	92.5	96.6	90.3	94.7
% *Navicula transitans*	42	24	46	53	65	20	8	30	63	79	51	47	70	37	42
% *Nitzschia frigida*	36	41	20	11	14	62	89	67	26	13	29	28	12	42	27
Total # cells$\cdot L^{-1} \times 10^6$	4.67	2.58	4.43	6.69	6.69	1.72	26.91	10.77	5.59	0.36	2.96	3.30	4.94	5.14	2.81

Station	24	42	23					28A				
Floe	2	1	2					2				
Date	27/4	22/4	5/5					7/5				
Core	4	3	1	2	3	7	8	1	3	6	7	8
% Pennate diatoms	90.6	30.9	96.2	76.7	93.2	98.0	88.2	93.3	97.8	93.8	95.6	96.8
% *Navicula transitans*	76	1	78	53	69	93	53	30	67	59	84	55
% *Nitzschia frigida*	9	0	15	0	0.3	4	28	60	30	31	11	40
Total # cells$\cdot L^{-1} \times 10^6$	3.52	4.20	5.92	0.78	2.67	12.08	2.52	5.38	4.95	5.16	6.21	8.43

termed "cryophiles". Ice species must be adapted to low light levels (Bunt, 1967; Alexander *et al.*, 1974), low temperature (Bunt *et al.*, 1966), and fluctuating salinity regimes (Grant and Horner, 1976), and to life on an inverted substrate.

CONCLUSIONS

Significance of the Epontic Community of the Ice Edge Zone

The total contribution of the epontic algae to the primary production of the Davis Strait may be only grossly estimated owing to the high spatial variability both of this community and of the pack ice. Since no sampling or experiments were carried out in the main pack zone (the major portion of the ice-covered area in the Davis Strait), estimates of biomass and productivity are presented for the ice edge zone only.

Total primary production in the 50-km edge zone of the pack ice was calculated from the estimates of total biomass of epontic chlorophyll *a* and the production rate per unit chlorophyll *a* (P/B) of the epontic algae. The total area of the 50-km strip along the edge of the pack was approximately 3.2×10^4 km^2 and average biomass of epontic chlorophyll *a* was 0.6 mg$\cdot$m^{-2}, giving a total ice-edge zone chlorophyll biomass of 2×10^7 g. The average ratio of P/B for the epontic algae was 1 g$\cdot$C$\cdot$(g chl *a*)$^{-1}\cdot$d^{-1}. Average daily production in the 50-km strip of the ice edge zone was therefore about 7×10^7 g C, with a possible maximum about three times higher.

Primary production of the plankton in the ice-free/loose pack area of Davis Strait in 1978 was 1.68×10^{10} g C in April and 4.74×10^{10} g C in May (MacLaren Marex, 1979a), two to three orders of magnitude greater than that of the epontic pack ice edge community at that time. On an annual basis this relative contribution would be even less, as epontic algal production probably only occurs for 2.5 months a year, from mid-March to the end of May.

Epontic algal production may make a larger contribution to total production in the nearshore fast-ice environment, or in the high Arctic where the open-water season is short and where phytoplankton production is limited accordingly. Grainger (1975) estimated that approximately 10% of the annual production in protected coastal embayments may be contributed by the epontic algae.

Although the contribution by the epontic community to the total primary production of the Davis Strait is probably small, other factors must be taken into consideration in an assessment of its relative significance in the ecosystem. The concentration of the community into dense, essentially two-dimensional patches increases its availability both to the grazers unique to this community and to the zooplankton in the water below. Epontic algae have been found in the guts and/or fecal pellets of grazers from both of these communities (MacLaren Marex, 1979b). As the epontic algae bloom develops before the phytoplankton bloom and is the only concentration of algae below heavy pack ice, it may extend the season of food availability to grazers in the area which can utilize it. The ice algal bloom, then, appears to provide a method by which both the period and quantity of plant production is increased and made available to higher trophic levels.

ACKNOWLEDGEMENTS

This study was sponsored by Esso Resources Canada Limited, Aquitaine Company of Canada Limited, and Canada-Cities Services Limited, as Project Number 127 of the Arctic Petroleum Operators' Association contribution to the Eastern Arctic Marine Environmental Studies program. The primary productivity studies were supported by the departments of Indian and Northern Affairs and Supply and Services.

The author gratefully acknowledges the assistance of David Stone, David Gillis, and Tom Windeyer in the preparation and carrying out of the studies as well as input from many MacLaren Marex Limited staff (too numerous to mention). Drs. Rita Horner, Glen Harrison, and especially David Stone provided valuable assistance in interpretation of results.

REFERENCES

ACKLEY, S.F., BUCK, K.R., and TAGUCHI, S. 1979. Standing crop of algae in the sea ice of the Weddell Sea region. Deep-Sea Research 26A:269-281.

ALEXANDER, V. 1974. Primary productivity of the nearshore Beaufort Sea, with reference to potential roles in ice biota. In: Reed, J.C. and Sater, J.E. (eds.). The Coast and Shelf of the Beaufort Sea. Washington, D.C.: The Arctic Institute of North America. 609-635.

______, HORNER, R., and CLASBY, R. 1974. Metabolism of Arctic Sea Ice Organisms. University of Alaska, Institute of Marine Science Report No. R74-4. 120 p.

ANDERSEN, O.G.N. 1977. Primary productivity associated with sea ice at Godhavn, Disko, West Greenland. Ophelia 16:205-220.

APOLLONIO, S. 1965. Chlorophyll in Arctic sea ice. Arctic 18:118-122.

BUINITSKIY, V.K. 1968. Effect of microscopic algae on the structure and strength of Antarctic sea ice. Okeanology 8:771-776.

BUNT, J.S. 1964. Primary productivity under sea ice in Antarctic waters. Antarctic Research Series 1:13-31.

______. 1968. Microalgae of the Antarctic pack ice zone. In: Currie, R.I. (ed.). Symposium on Antarctic Oceanography. Cambridge: Scott Polar Research Institute. 198-218.

______ and LEE, C.C. 1970. Seasonal primary production in Antarctic sea ice at McMurdo Sound in 1967. Journal of Marine Research 28:304-320.

BUNT, J.S., OWENS, O. van H., and HOCH, G. 1966. Exploratory studies on the physiology and ecology of a psychrophilic marine diatom. Journal of Phycology 2:96-100.

BUNT, J.S. and WOOD, E.J.F. 1963. Microalgae and sea ice. Nature 199:1254-1255.

BURKHOLDER, P.R. and MANDELLI, E.F. 1965. Productivity of microalgae in Antarctic sea ice. Science 149:872-874.

CLASBY, R.C., HORNER, R., and ALEXANDER, V. 1973. An *in situ* method for measuring primary production of Arctic sea ice algae. Journal of the Fisheries Research Board of Canada 30:835-838.

CZARNECKI, D.B. and WILLIAMS, H.D. 1972. A new mounting media for diatoms. Transactions of the American Microscopical Society 91:73.

FUKUSHIMA, H. and MEGURO, H. 1966. The plankton in ice as a basic factor of the primary production in the Antarctic Ocean. Antarctic Record 27:99-101.

GRAINGER, E.H. 1975. A marine ecology study in Frobisher Bay, Arctic Canada. In: Billingsley, L.W. and Cameron, T.W.M. (eds.). Energy Flow — Its Biological Dimensions. A summary of the I.B.P. in Canada, 1964-1974. Canadian Committee for the International Biological Programme, Royal Society of Canada. 319 p.

GRAN, H.H. 1904. Diatomaceae from the ice-flöes and plankton of the Arctic Ocean. The Norwegian North Polar Expedition 1893-1896. Scientific Results 4:1-74.

GRANT, W.S. and HORNER, R.A. 1976. Growth responses to salinity variations in four arctic ice diatoms. Journal of Phycology 12:180-185.

GREEN, J.M. and STEELE, D.H. 1975. Observations on marine life beneath sea ice, Resolute Bay, N.W.T. In: Proceedings of the Circumpolar Conference on Northern Ecology, 15-18 September 1975, Ottawa. National Research Council of Canada. 77-86.

HASLE, G.R. and FRYXELL, G.R. 1970. Diatoms: cleaning and mounting for light and electron microscope. Transactions of the American Microscopical Society 89:469-474.

HOLM-HANSEN, O., LORENZEN, C.J., HOLMES, R.W., and STRICKLAND, J.D.H. 1965. Fluorometric determinations of chlorophyll. Journal du Conseil Permanent International pour Exploration de la Mer 30:3-15.

HORNER, R. 1976. Sea ice organisms. Oceanography and Marine Biology Annual Review 14:167-182.

HOSHIAI, T. 1972. Diatom distribution in sea ice near McMurdo and Syowa Stations. Antarctic Journal 7:84-85.

______. 1977. Seasonal changes of ice communities in the sea ice near Syowa Station, Antarctica. In: Dunbar, M.J. (ed.). Polar Oceans. Proceedings of the Polar Oceans Conference, Montreal, 1974. Calgary: The Arctic Institute of North America. 307-318.

HSIAO, S.I.C. 1980. Quantitative composition, distribution, community structure and standing stock of sea ice microalgae in the Canadian Arctic. Arctic 33:768-793.

JEFFREY, S.W. and HUMPHREY, G.F. 1975. New spectrophotometric equations for determining chlorophyll *a*, *b*, *c*, and c_2 in higher plants, algae and natural phytoplankton. Biochemie und Physiologie Pflanzen 167:191-194.

JENSEN, A. 1978. Chlorophylls and carotenoids. In: Hellebust, J.A. and Craigie, J.S. (eds.). Handbook of Phycological Methods. Cambridge: Cambridge University Press. 59-70.

LEWIS, E.L. and MILNE, A.R. 1977. Underwater sea ice formations. In: Dunbar, M.J. (ed.). Polar Oceans. Proceedings of the Polar Oceans Conference, Montreal, 1974. Calgary: The Arctic Institute of North America. 239-246.

MacLAREN ATLANTIC LTD. 1977. Report on cruise 77-1. February 1977. Environmental Aspects of the Cruise to Davis Strait and the Labrador Coast. Arctic Petroleum Operators' Association Project Number 127-2. [APOA Information Service, P.O. Box 1281, Station M, Calgary, Alberta, Canada T2P 2L2.]

MacLAREN MAREX INC. 1979a. Primary Productivity Studies in the Water Column and Pack Ice of the Davis Strait, April, May and August, 1978. Ottawa: Department of Indian and Northern Affairs and Supply and Services Canada. 102 p. [Department of Indian and Northern Affairs, Offshore Environment Group, Ottawa, Ontario, Canada K1A 0H4.]

______. 1979b. Report on Cruise 78-1. Environmental Studies in the Pack Ice Zone of the Davis Strait. Arctic Petroleum Operators' Association Project Number 146-10. 271 p. [APOA Information Service, P.O. Box 1281, Station M, Calgary, Alberta, Canada T2P 2L2.]

MATHEKE, G.E.M. and HORNER, R. 1974. Primary productivity of the benthic microalgae in the Chukchi Sea near Barrow, Alaska. Journal of the Fisheries Research Board of Canada 31:1779-1786.

McROY, C.P. and GOERING, J.J. 1974. The influence of the ice on the primary production of the Bering Sea. In: Hood, D.W. and Kelley, E.J. (eds.). The Oceanography of the Bering Sea. Fairbanks: University of Alaska, Institute of Marine Science. 403-421.

MEGURO, H. 1962. Plankton ice in the Antarctic Ocean. Antarctic Record 14:1192-1199.

______, ITO, K., and FUKUSHIMA, H. 1967. Ice flora (bottom type): a mechanism of primary production in polar seas and the growth of diatoms in sea ice. Arctic 20:114-133.

U.S. NAVAL OCEANOGRAPHIC OFFICE. 1968. Oceanographic Atlas of the North Atlantic Ocean. Section III: Ice. U.S. Naval Oceanographic Office Publication Number 700. 165 p.

USACHEV, P.I. 1949. The microflora of polar ice. Institut Okeanologii Trudy 3:216-259. (Fisheries Research Board of Canada Translation Series 1305).

UTERMÖHL, H. 1958. The improvement of quantitative phytoplankton methodology. Mitteilungen Internationale Vereinigung für Theoretische und Angewandte Limnologie 9. 38 p. (Fisheries Research Board of Canada Translation Series 2713).

VANHOFFEN, E. 1897. Die fauna and flora Grönlands. Grönland Expedition der Gesellschaft für Erdkunde zu Berlin 1891-1893. Vol. 2(1):1-383.

YENTSCH, C.S. and MENZEL, D.W. 1963. A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. Deep Sea Research 1:221-231.