BERING SEA ICE DYNAMICS AND PRIMARY PRODUCTION

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Abstract: Sea ice communities in multi-year ice can accumulate a high algal biomass and develop a complex food web, and most higher trophic level biota of the regions north of 70 to 80°N depend on this for food. Further to the south, even within the seasonal sea ice zone, processes associated with the sea ice influence the biological regimes in important ways. For example, the biological spring is advanced on the order of weeks in the presence of sea ice, due to the development of populations of ice algae and subsequently, as the ice melts, the generation of an early spring bloom. In this paper, the influence of ice on the primary production regimes of arctic seas is discussed, with particular emphasis on the seasonal sea ice zone. Specific examples from recent work on the Bering Sea are included.

1. Introduction

Sea ice is a pervasive and physically-dominant component of the arctic marine environment, and plays an important role in its ecosystems. We even could say that arctic ecosystems as we know them today at all levels require sea ice. Sea ice strongly influences biological production regimes in arctic seas. For example, in the case of marine mammals the relationship with ice can be very clear. A polar bear hunting ringed seal on the pack ice depends on the ice, as does the seal which breeds in the ice and, in turn, its prey which lives under the ice. Although less readily visible, sea ice is no less important at the primary producer level. The primary production regimes of arctic seas have evolved to take advantage of sea ice. Arguably, the development of sea ice results in higher productivity in many parts of the northern seas than would be the case if there were no ice.

During the summer of 1994 a joint Canadian–U.S. scientific cruise used two icebreakers to traverse through the Bering Strait to the North Pole and back. Preliminary reports of the biological studies have been exciting. *Melosira arctica*, a prominent ice alga, was found in abundance at all latitudes all the way to the North Pole (P. WHEELER, pers. commun.). While this is new and exciting, it is perhaps not surprising. CAREY (1985) discussed the community of organisms found in multi-year ice, MEL'NIKOV and BONDARCHUK (1987) described large accumulations of *Melosira* under drifting arctic ice, and LØNNE and GULLIKSEN (1991a) have shown that high arctic multi-year ice supports a complex and persistent biological community. The ice community in seasonal sea ice, however, must recolonize each year. As a result, at least in the nearshore Beaufort Sea, the annual growth of ice algae is characterized only by a spring pulse, and a complex and persistent community dependent on the ice algae cannot

develop (CLASBY et al., 1973, 1976; LØNNE and GULLIKSEN, 1991a). This difference between seasonal and multi-year ice with respect to biological colonization is important. HORNER (1985) wrote "The distribution of ice algae in old sea ice, i.e., ice older than one year, is not known." The high Arctic has, of course, been largely inaccessible by any means which allowed quantitative sampling for ice algae. The significance of ice or the epontic algal community in seasonal sea ice is ephemeral, but nonetheless is likely to be important in that it provides a concentrated food source for a period of time in an otherwise oligotrophic environment. In first year ice, the epontic community is by necessity simple, since development of autochthonous invertebrate species requires the continuity of multi-year ice (LØNNE and GULLIKSEN, 1991b). CAREY (1985) pointed out that the sympagic fauna in multi-year ice tend to be pelagic forms such as *Gammarus wilkitzkii*, whereas the shorefast ice community is dominated by benthic forms. While hopefully more information will be gathered about the more complex multi-year ice communities, at present most of the information available for the Arctic relates to first year or seasonal sea ice.

2. Marginal Ice Zone Regimes

In seasonal sea ice zones, there is no event as dramatic or which has greater impact on the areas affected by sea ice than its annual advance and retreat. The environmental effects are many; they include effects on light penetration, wind mixing, heat and moisture exchange, access to the water and sediment surface, and more. The effect of ice on primary productivity is clear. There are four major influences of ice on the primary production. First, melting ice provides the physical mechanism for initiating biological spring. The presence of ice advances the spring bloom on the order of weeks (NIEBAUER et al., 1990). Second, the ice provides the medium for ice algae growth which later, as the ice breaks up, seeds the spring bloom at the ice edge. Third, ice limits light penetration into the water and can reduce annual primary production in areas where nutrients are abundant and where, in the absence of ice, a longer production season might be possible.

Table 1 summarizes primary production in marginal ice zones. The Bering Sea, Barents Sea, coastal Antarctic, and Ross Sea study areas overlay continental shelves, whereas the Greenland Sea (near the Polar Front) and Weddell Sea areas are >1500 m deep. All these regions, except at times the Greenland Sea, undergo substantial retreat of the ice margin during spring and summer, resulting in conditions conducive to ice-edge blooms. The Greenland Sea is unusual in that the ice edge is constrained by the East Greenland Polar Front, a boundary between water masses derived from North Atlantic and Arctic Ocean surface water. The position of the marginal ice zone is relatively fixed, and melting can occur at any time of year if winds move the ice cover over the warmer North Atlantic water (SMITH, 1987). All these marginal ice zones also show similarities. In each case, meltwater stabilizes the water column, leading to a phytoplankton bloom (SMITH, 1987). The spatial scale of the density anomalies generated is similar, but the horizontal extent of the ice-melt influence was smaller in the Greenland Sea, probably because the ice was not retreating.

The Bering Sea has the highest chlorophyll concentrations and primary productiv-

ity of any ice-edge system studied to date. Several factors contribute to this. First, the high primary productivity is in part a function of the large biomass of phytoplankton. At the depth of the chlorophyll maximum, the chlorophyll-specific primary productivity, in units of mgC mgChl. $a^{-1} d^{-1}$, is 5 in the southeast Bering Sea, 6 to 11 in the Greenland Sea, 7 to 8 in the Barents Sea, 3 in the Ross Sea, 16 in the coastal Antarctic (12 to 13° E), 18 in the Weddell-Scotia Sea (45 to 50°W longitude) in spring, 1986, but only 0.7 in the Weddell-Scotia Sea (36 to 41°W) in spring 1983 and 1 in fall.

The southeastern Bering Sea is quite shallow; our studies have concentrated on an area which is 50 to 100 m deep. Storm-caused mixing events delay blooms for a short period by increasing mixing, but cells may be able to adjust buoyancy and return to the euphotic zone after winds decrease. Periodic storm mixing probably increases total production by adding nutrients to the euphotic zone. In the 50 to 100 m-deep area of the shelf, nutrient-rich water always underlays the surface nutrient-depleted zone.

The physical regime in the Greenland Sea is quite different from the Bering Sea, and the bloom phytoplankton communities also differ, with diatoms predominating in the Bering Sea (SCHANDELMEIER and ALEXANDER, 1981) and small flagellates in the Greenland Sea (SMITH et al., 1987). However, similar factors limit primary production, nutrient depletion and self-shading by phytoplankton cells (SMITH, 1987). The depth and intensity of stratification of the meltwater-induced layer is similar, as is the productivity: chlorophyll ratio. Maximum chlorophyll concentrations are lower by a factor of three in the Greenland Sea; this may be due to the lower initial amounts of nitrate, 12 μM vs. >20 μM over much of the Bering Sea middle shelf. Another factor is the very limited grazing of the Bering Sea bloom, at least by copepods and euphausiids, which consume <2% of ice-edge primary production (COYLE and COONEY, 1988). In contrast, SMITH (1987) estimated that the amount of carbon necessary to maintain the growth of the dominant herbivores (copepods) was greater than the primary production near the ice edge in the Greenland Sea in summer.

The Barents Sea overlies a continental shelf, and the ice edge there recedes over 400 km in summer; thus the physical regime is more like that of the southeast Bering Sea than is the Greenland Sea. Summer productivity values are low due to nutrient limitation. The spring primary productivity of 120 mmoles C $m^{-2} d^{-1}$ is similar to the Greenland Sea productivity, but lower than that of the Bering Sea. Lower initial nitrate (10 μM) is likely a factor limiting the accumulation of chlorophyll in the Barents Sea, also. Grazing also limits accumulation of biomass. EILERTSEN et al. (1989a, b) estimated that 16 to 18% of primary production in early spring and 65 to 90% in summer is grazed by copepods.

Mixing limits the productivity of the Weddell Sea (SMITH, 1987); here stratification is weak in spring and mixing is relatively extensive, leading to a greater depth distribution of chlorophyll and a rather low productivity: chlorophyll ratio. The Weddell Sea is the least productive and has the lowest chlorophyll concentration in late summer (SMITH, 1987). Nutrients were abundant and the stratification was actually stronger than in spring, although the ice was not melting at the time of the study. NELSON et al. (1989) suggested that the low biomass was due to light limitation, micronutrient (e.g. iron) limitation, or protozoans. Grazing by larger zooplankton was thought to have a minor impact on phytoplankton biomass.

Table 1. *Comparison of the Bering Sea with other ice-influenced systems. Sp=spring, Su=summer and F=fall*

Location	Mixed layer depth (m)		Δ sigma-t[c]	Nitrate[a] (μM)		Chlorophyll maximum[a]			Primary prod. (mmole C m^{-2}d^{-1})		Zooplankton Biomass[b] (g C m^{-2})	References
						Concentrations		Extent				
	Init.	Max.[b]		Init.	Min.	mg m^{-3}	mg m^{-2}	m×km	Init.	Max.		
SE Bering Sea Middle Shelf (Sp)	20–50	10–30	0.3–0.5	12–26	0	30–40	900–1300	75×150	50–100	200–500	0.05–0.5	d
SE Bering Sea Middle Shelf (Su)	30–70	5–15	0.2	18	0	>30	1100–1400	-	20–50	200–500	2	e
N Bering Sea (Su)	-	10	-	-	5–10	100	>600	-	-	130–145	-	f
Greenland Sea (Su)	10	10	0.6	12	0	4.0–10	300	50×50	15	140	0.5–5	g
Greenland Sea (F)	40	20	0.8–1.7	0.2–0.3	<0.1	2	40	30×>70	20	37	-	h
Barents Sea (Sp)	50	40	0.3	10	0	6	200	60×>200	-	130	-	i
Barents Sea (Su)	-	10	1.0–1.7	0	0	2–8	20–90	70×>200	-	20–40	4–5	j
Ross Sea (Sp)	20	20	0.8	15–20	5–10	6	300	30×250	51	80	-	k
Weddell-Scotia Sea (early Sp)	35	35	0.6	28	22	2	170	90×>200	-	-	-	l
Weddell-Scotia Sea (Sp)	20	10	0.6	28	>20	-	80	-	-	120	-	m
Weddell-Scotia Sea (Sp)	50–60	60	0.1	28	21	7	550	100×250	17	31	-	n
Weddell-Scotia Sea (late Su)	25	30	0.7–0.9	28	25	0.6	50	120×250	7	4	0.6	o
Antarctic Coast, 12–13°E (Su)	-	10–20	0.4	23	7	4	75–120	-	-	80–190	-	p

[a] Nitrate concentrations are those in the euphotic zone. Chlorophyll concentrations at the peak of the bloom, per unit area and per unit volume. Also, the depth and horizontal distance (perpendicular to the ice) over which elevated chlorophyll concentrations were observed is shown.

[b] Init.=at the initiation of the bloom; Max.=at the peak chlorophyll concentration produced by the bloom. The initiation of the bloom is defined as the time when chlorophyll concentrations first exceed 2 × "background" concentrations in the unstratified water column.

[c] The change in sigma-t over the upper 60 m of the water column, at the site where the ice-edge stratification is strongest.

[d] NIEBAUER and ALEXANDER (1985), COYLE and COONEY (1988), NIEBAUER *et al.* (1990), this work.

[e] SAMBROTTO *et al.* (1986), VIDAL and SMITH (1986). Primary productivity was estimated from nitrate uptake rates assuming a C : N ratio of 6.6 and an f-ratio (OLSON, 1980)of 0.5. Zooplankton biomass is integrated from the surface to the bottom, *i.e.,* 50 to 100 m depth. Data are for 1979 to 1981, when the study area over the SE Bering Sea Shelf was not ice-covered.

[f] HANSELL *et al.* (1989). Data are for summer when no ice is present. Values for the West "bloom" which occurs in a small area influenced by nutrient-rich Anadyr Water, located near 65.2°N, 170°W. Primary productivity is the average range estimated for the summer months. The peak rate measured was 1300 mmol C $m^{-2}d^{-1}$.

[g] SMITH *et al.* (1987), SPIES *et al.* (1988), SMITH (1988). Zooplankton biomass was integrated to 50 m, ± 40 km from ice edge.

[h] HEIMDAL (1983).

[i] REY and LOENG (1985).

[j] REY and LOENG (1985), EILERTSEN *et al.* (1989). Zooplankton biomass integrated to 80 m.

[k] NELSON and SMITH (1986), WILSON *et al.* (1986).

[l] BIANCHI *et al.* (1992), VETH *et al.* (1992).

[m] CADEE (1992), MATHOT *et al.* (1992).

[n] SMITH (1987).

[o] NELSON *et al.* (1987), HOPKINS and TORRES (1988), NELSON *et al.* (1989), SMITH and NELSON (1990). Zooplankton biomass was integrated to 1000 m. Units of g dry weight were converted to g C by multiplying the value by 0.5.

[p] VERLENCAR *et al.* (1990).

The spring Weddell-Scotia Sea marginal ice zone was quite different between 1989 and 1983; the relative contribution of spatial and temporal variability to the difference is unclear. The water-column stratification was much stronger in 1989, with a shallower mixed layer. Between the two years, the 1989 bloom was more productive but resulted in less accumulation of chlorophyll; the chlorophyll-specific productivity was much greater in 1989. Low biomass accumulation in 1989 may have been due to the early stage of the bloom. Also, protozoan grazing was estimated to consume about 30% of the net primary production (MATHOT et al., 1992).

The Ross Sea also exhibits greater primary productivity but less chlorophyll than the 1983 Weddell Sea spring bloom. This is largely due to an unusually high carbon: chlorophyll ratio of 120 in phytoplankton, assumed to be an adaptation to low temperatures (SMITH and NELSON, 1985). However, even though water temperatures at the Bering Sea ice edge were even lower, the carbon: chlorophyll ratios were normal at ~38 (NIEBAUER et al., 1995). Carbon: chlorophyll was not unusually high in the Weddell Sea in spring, although high ratios were found in fall, perhaps due to detrital particulate carbon (NELSON et al., 1989).

Thus, the high productivity of the Bering Sea ice-edge area in spring is apparently due to a fortuitous combination of high initial nutrient concentrations, strong meltwater-induced stratification, a shallow water column, and limited grazing. Furthermore, this is the lowest latitude ice-edge system among those described, and therefore the solar angle at the time of melting is higher, allowing more penetration of light. None of the other ice-edge systems which have been described share all of these characteristics.

3. The Bering Sea Shelf

The map of the Bering Sea (Fig. 1) provides a framework for the following discussion. The Bering Sea shelf, among the most complex and productive regions among the arctic adjacent seas, is impacted seasonally by sea-ice. A number of physical (including topographic, climatic and geographic) features appear to contribute to its productivity. The continental shelf of the Bering Sea is the largest in the world, with the exception of the huge Siberian shelf in the Arctic Ocean. The Bering Sea shelf is shallow, generally less than 60 m deep. Yukon River water enters on the east side, adding significant amounts of fresh water. The deep basin to the southwest is connected to the shelf by a series of canyons. There is a trend for northward flow of water from the basin over the shelf, which ultimately passes through the Bering Strait as the only inflow to the Arctic Ocean from the Pacific Ocean.

Ice cover varies dramatically from year to year. Ice extends all the way to the shelf break in cold years, but its advance may stop several hundred kilometers to the north in warm years (NIEBAUER, 1988). This variability in ice is extremely dramatic. The 1960s and 1970s were high ice years, with a trend towards reduced ice cover in the 1980s. Because of the role of ice in the annual primary production cycle, especially the spring bloom, this could be an important control on interannual productivity variations.

The northward flow over much of the shelf is slow, at about 1–3 cm s^{-1}, although to the west the rate is higher due to the influence of the Bering Slope current ($\sim$10 cm s^{-1}). This flow traverses along the shelf edge from the southeast to northwest, before it
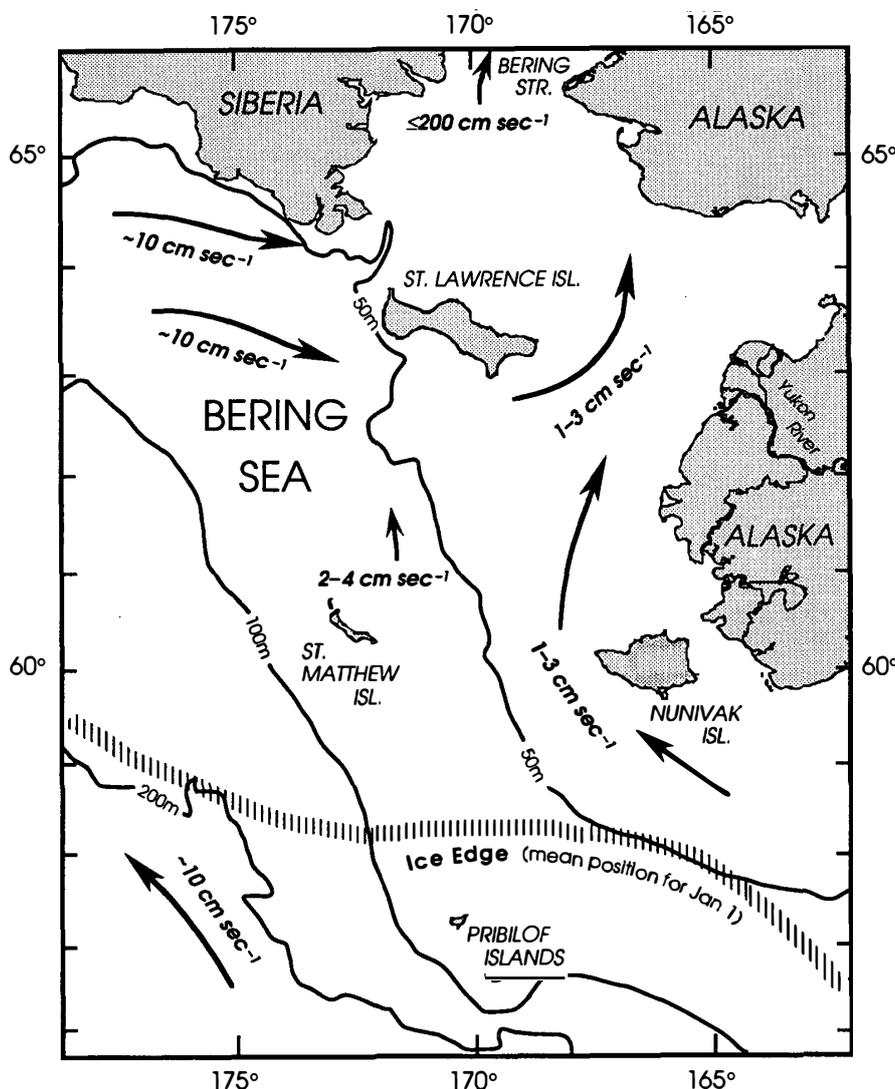
Fig. 1.   Chart of the eastern Bering-Sea continental shelf region, showing major currents.

diverges at Cape Navarin. One branch moves north into the Gulf of Anadyr. Before passing north toward Bering Strait, a small portion moves east, to the south of St. Lawrence Island. This nutrient-rich water originates in the deeper Bering Sea and supports persistent primary production in the northern Bering Sea throughout the summer months. The resulting particulate carbon, a large proportion probably living, is carried northward with the flow. There are areas of deposition north of St. Lawrence Island and in the Chukchi Sea. The nutrients are not exhausted as the water enters the Arctic Ocean. Since this water moves through the Gulf of Anadyr at about 15 cm s^{-1}, the transport contributes significantly to the total nutrient load moving through the Bering Strait (WALSH et al., 1989). Nothing is known about the ice-related production in this more nutrient-rich area. It is likely that ice-related production accounts for less than 10% of the annual primary production in the nutrient-rich portions of the northern Bering Sea. However, in the sea-ice impacted parts of the southeast Bering Sea shelf, it can account for as much as half or more of the annual primary production.

4. Features of Ice-related Primary Production

4.1. The ice algae

In seasonally ice-covered seas, the first growth of algae occurs on the underside of the ice. It is not clear how persistent this growth is. In the vicinity of Barrow, it is a rather short-lived pulse, lasting on the order of weeks, and the total carbon fixation is low (Clasby et al., 1976). In the adjacent arctic seas, with seasonal sea ice cover, the growth of ice algae is constrained in time. Ice algae were first reported for the Bering Sea by McRoy and Goering (1974), who suggested that the contribution of ice algae could be significant, since in the more southerly regions of the Bering Sea shelf the plants could start growing as early as February and persist until ice melt. No algae were present before February. These conclusions were based on three late winter or early spring ice breaker cruises.

We performed a survey of ice algal distribution in the sea ice of the Bering Sea in April, following the extremely cold winter of 1977, using a helicopter based from Nome (Alexander and Chapman, 1981). We found extreme patchiness in the abundance of ice algae, which were present throughout the entire region. Local small-scale patchiness was as great as the overall patchiness. In other words, there was less of a regional trend than simply extremely high variability in the distribution of biomass. On another occasion, we were fortunate to participate in a cruise of the U.S. Coast Guard icebreaker POLAR SEA, and made a southward transect from St. Lawrence Island past St. Matthew Island. Once again, sampling was done for chlorophyll; however, the sample collection had to be done in the open water track created by the vessel, and inevitably there was disturbance of the ice cover; 77 stations were occupied. A summary of the results are shown in Table 2.

Table 2. Results from the U.S. Coast Guard Polar Sea Transect, April 1985 (from north to south).

Station group	Chlorophyll a concentration (mg m^{-3})*
1	1.47
2	1.25
3	1.02
4	0.54
5	0.47

There were also three clusters of stations.

		Mean	Range
Cluster A	4/7/85	4.0	1.7–6.9
Cluster B	4/11/85	1.5	0.8–3.0
Cluster C	4/12/85	2.0	1.6–2.3

* Ice/water slurry from surface.

4.2. The spring bloom

We have published a number of papers describing the spring bloom which takes place at the ice edge in the Bering Sea. The southeast Bering Sea shelf ice-edge bloom

begins in the last few days of April or early May. This bloom starts very suddenly as active melting begins, and within a few days develops extremely high chlorophyll concentrations (ALEXANDER and NIEBAUER, 1981; NIEBAUER and ALEXANDER, 1985; NIEBAUER et al., 1990, 1995). During a brief period, on the order of ten days to two weeks or less, as much as 50 g C m^{-2} can be fixed. While some euphausiid grazing occurs, our hypothesis is that the majority of this material sinks to the shallow shelf bottom, where it may play an important role in sustaining the benthos and demersal fishes. If this is the case, then the dramatic shift in ice extent which occurred in the late 1970s and the inter-annual variability which continues to occur could affect the biological regime. For example, Tanner crab spawning in this region occurs in April, and if the early spring bloom does not occur because the ice has not extended over the region, then food supply could be a problem for the larvae. This is, at this stage, only speculation, but it does provide an attractive concept, in the absence of other viable hypotheses for the decline of crab populations following the warming trend in the late 1970s.

It is interesting to note that much of the primary production is new production, probably based on nitrogen imported onto the shelf during the winter. The "f" factor is more than 0.5 during the spring bloom (MÜLLER-KARGER and ALEXANDER, 1987).

4.3.   Post-ice system

The fate of the carbon following the spring bloom is an important question. It is clear that a lot of the material does sink from the surface water column, reaching the bottom quite rapidly. The shelf here is shallow, and the material reaching the bottom could be resuspended. Having lain over the bottom, where nutrients are available even after they have been depleted in the water column, the material could be resuspended by wind-driven or tidal currents, and if photosynthetically capable, continue to grow.

5.   Submarine Sampling of the Benthic Layer

We undertook two experiments using submersibles to examine the phytoplankton immediately above the sediment surface following the ice retreat, to determine the viability of the algae which had sunk to the bottom. The first experiment was done on June 14–18, 1987 using the submersible MERMAID II, tended by the mother ship ALOHA. During this study, we accomplished 10 dives in the central and northern Bering Sea. On each dive, we collected 5 liters of bottom water and made CTD and in vivo fluorescence measurements using hull-mounted instruments and sampling equipment. There has always been a problem with sampling the bottom layer from the surface, and there were also problems with the submersible causing some resuspension of sediments. However, there was a near-bottom current which restored conditions to normal fairly quickly.

A description of the station locations and characteristics are shown in Table 3, and Table 4 presents the results of primary productivity measurements using ^{14}C. Table 5 shows results obtained in late July 1989, on another cruise using a submarine. On this latter occasion, only chlorophyll data were obtained. The results from this work are preliminary, since there were a number of problems encountered with our first attempted use of submarines for primary production work. However, it is clear from the results shown in Table 4 that the algal cells adjacent to the bottom were viable, and capable of

Table 3.   Station Descriptions—Submersible Cruise, Bering Sea, June 1987, R/V Aloha, Mermaid II Submersible.

Drive #	Latitude	Longitude	Depth	Bottom type
1	60°05.11′ N	169°54.68′ W	44 m	Sandy mud
2	60°59.66′ N	169°53.52′ W	41 m	Mud over sand
3	62°00.03′ N	168°00.67′ W	21 m	Mud over sand
4	63°00.09′ N	168°00.67′ W	18 m	Sand
5	64°00.18′ N	167°59.25′ W	28 m	Low visibility
6	64°56.59′ N	168°04.33′ W	24 m	(no information)
7	65°44.11′ N	168°52.28′ W	42 m	Rock
8	65°44.11′ N	169°31.99′ W	37 m	Mud over sand
9	63°59.53′ N	167°59.53′ W	29 m	Mud
10	63°30.80′ N	166°25.70′ W	21 m	Mud with sand

Table 4.   Primary production and chlorophyll a from submersible-collected samples, June 1987, R/V Aloha, Mermaid II Submersible.

Dive number	Primary production ($mg\ C\ m^{-3}\ hr^{-1}$)		Chlorophyll a ($mg\ m^{-3}$)	
	Incubation at 1%	Incubation at 100%	Surface	Bottom
1	0.1	12.87	3.0	12.9
2	0	3.5	0.8	5.3
3	0.3	3.6	-	-
4	0.1	5.5	0.3	1.2
6	0.8	74.6; 8.7(s)*	1.1	4.2
7	0	60.3; 80.3(s)	4.2	2.0
8	-	238.0	7.9	6.5
9	0	421.7; 296.3(s)	8.4	0.8
10	3.6	151; 150.8(s)	8.4	8.7

* Denotes a sample collected ∼18 cm below the surface, incubated at 100% light.

Table 5.   Submersible Cruise, Bering Sea, July 22–29, 1989, R/V McGaw, Delta Submersible.

Station #	Latitude	Longitude	Depth	Date	Chlorophyll a ($mg\ m^{-3}$) Bottom	Chlorophyll a ($mg\ m^{-3}$) Surface
2	57°30′ N	164°00′ W	49 m	7/26/89	0.4	1.7(5 m)
3	57°25′ N	163°39′ W	49 m	7/24/89	3.1	0.2
5	58°00′ N	164°00′ W	40 m	7/26/89	1.5	3.8(5 m)
6	57°55′ N	163°30′ W	42 m	7/25/89	11.5	0.2
8	57°00′ N	164°00′ W	65 m	7/27/89	4.3	0.2(20 m)
9	56°55′ N	163°30′ W	65 m	7/23/89	4.0	0.2

photosynthesis when exposed to full surface light. The chlorophyll data presented in Table 5 were collected further to the south, where chlorophyll concentrations were rather high during the sampling period.

6.   Discussion

The original results presented here are preliminary, and are intended to show that cells remaining over the bottom of the shallow shelf following the retreat of ice and the

associated spring bloom are viable one or two months later. GREBMEIER and COOPER (1995) also found large amounts of chlorophyll at some stations over the bottom in June immediately to the south of St. Lawrence Island, and we found a similar distribution one month later (COYLE and ALEXANDER, unpublished data from the 1990 cruise of the Hokkaido University Training Vessel OSHORO MARU; Data Rec. Oceanogr. Obs. Expl. Fish. Hokkaido Univ. No. 34, 1991). Since this area is influenced by Anadyr water, is transected by a number of boundaries between water masses, and lies within the area embraced by the polynya which forms in the area during the winter, it is difficult to unequivocally connect the deep chlorophyll with ice-related primary production. Further to the east, in the Alaska coastal water, the ice-related bloom is the major primary production event during the early summer and it is reasonable to assume that this is the source of the benthic chlorophyll layer.

It is interesting to note that the algae comprising the ice edge bloom do not behave as though they are shade adapted. Even in the early stages of the spring ice edge bloom, they are able to photosynthesize effectively at full surface light (ALEXANDER and CHAPMAN, 1981). Our results presented here also show that deep algae sampled by submersible and brought to the surface are able to photosynthesize at full light, although we did not obtain light: photosynthesis curves. Photosynthesis at the low light levels extant at depth was minimal. COTA et al. (1986) have found that the photosynthetic efficiencies of ice algae from the high arctic regions are unusually high, so that photosynthesis can occur down to 0.01% of surface light, and that the cells exhibit extreme shade adaptation. The cells in the ice edge bloom of the Bering Sea, on the other hand, appear to have adapted rapidly to surface light levels, and yet survive at depths for one or two months following the ice retreat.

Acknowledgments

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