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Biological observations in the marginal ice zone of the East Greenland Sea

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ABSTRACT

The distribution of nutrients, phytoplankton and zooplankton was investigated during summer, 1983 in the marginal ice zone of the East Greenland Sea. Nutrient levels, especially inorganic nitrogen, were extremely low, and probably limited the growth of phytoplankton during this period. An ammonium maximum at the base of the euphotic zone, generally around 50 m, was found repeatedly and appeared to be controlled by active nitrogen regeneration and decreased ammonium uptake at low light levels. Chlorophyll *a* levels were elevated at the ice-edge, but were even higher in an area influenced by an eddy. Species of zooplankton were accurate indicators of the origin of the two major water masses in this area, and zooplanktonic biomass was similar to other polar regions. Calculations of their impact on phytoplankton distributions indicated that grazing losses resulting from ingestion by large copepods may have been small. The dynamics associated with mesoscale eddies appear to be important in introducing new nitrogen into the euphotic zone and structuring the distribution of plant biomass at the ice-edge of the East Greenland Sea.

1. Introduction

Marginal ice zones, where pack ice meets the open ocean, are influenced in their spatial configuration by prevailing winds and currents (Johannessen *et al.*, 1983c; Martin and Kaufman, 1983), wave action (Martin and Kaufman, 1983; Wadhams, 1983), and the temperature of the surrounding water (McPhee, 1983). In the portion of the Greenland Sea between Spitsbergen and Greenland, the position of the ice-edge is relatively invariant. This is because there is a system of opposing currents in which the cold E. Greenland Current, carrying ice out of the Arctic Ocean, meets the warm W. Spitsbergen Current that flows into the Arctic Basin. Therefore, the marginal ice zone in this portion of the Greenland Sea exhibits melting much of the year, whenever it is forced over the warm W. Spitsbergen Current, but relatively little geographic movement. In contrast, some marginal ice zones such as those in Baffin Bay, the

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Southern Ocean and the Bering Sea retreat about 10° poleward during the warm season (Defant, 1961; Zwally *et al.*, 1979; Hibler and Ackley, 1983; Niebauer, 1983), a distance sufficient in the Bering Sea to eliminate the marginal ice zone during summer.

Important mesoscale processes occur within marginal ice zones. For example, observations in the Greenland Sea's marginal ice zone have shown dramatic wind effects. Along ice-edge winds, with the edge to the right when looking down-wind, or on-ice winds resulted in a straightening of the ice-edge, as well as an ice-edge jet in which the outermost 15 km of ice were moving faster than either the adjacent open water or ice, and on-ice transport in the upper mixed layer (Johannessen *et al.*, 1983c). During off-ice winds, divergence occurred. The ice-edge became irregular and dispersed (Johannssen *et al.*, 1983c), a configuration that should accelerate melting. Calm conditions resulted in an ice-edge similar to the case when off-ice winds prevailed. In the ice-edge region, relatively vigorous upwelling and downwelling circulations may also occur as a consequence of winds interacting with the ice-edge (Buckley *et al.*, 1979; Johannessen *et al.*, 1983c; Røed and O'Brien, 1983), and a divergence zone should arise because an equatorward current (E. Greenland Current) is positioned to the west of a poleward current (W. Spitsbergen Current) in the northern hemisphere.

A prominent mesoscale feature found in our study region is a permanent, or quasi-permanent, cyclonic eddy located near 79° 30'N and 2E. This feature has been discussed by a number of authors (Wadhams, 1985; Wadhams and Squire, 1983; Smith *et al.*, 1984). In addition, the presence of the opposing East Greenland and West Spitsbergen currents and the resulting frontal conditions from the juxtaposition of warm and cold waters make the occurrence of transient eddies likely (Johannessen *et al.*, 1983c; Wadhams and Squire, 1983; Smith *et al.*, 1984; Wadhams, 1985).

Marginal ice zones are known to be areas of intense biological activity and enhanced standing stocks. Large accumulations of herbivores and higher trophic level organisms (fishes, marine mammals, birds) are often observed within a marginal ice zone, and many organisms have life strategies that exploit the high biomass present (Bradstreet and Cross, 1982). Increased standing stocks of higher trophic levels ultimately may depend on increased primary productivity at the ice-edge (Alexander and Niebauer, 1981), and a number of hypotheses have been provided to explain this enhancement in the marginal ice zone. Prominent among these is the idea that ice-melt produces a highly stable surface layer that provides an improved light regime for growth of phytoplankton early in the season (Marshall, 1957; McRoy and Goering, 1974). A separate hypothesis is that local wind conditions result in ice-edge upwelling, thereby increasing surface nutrient concentrations which stimulate phytoplankton growth (Alexander and Niebauer, 1981; Niebauer, 1982). As noted above, eddies and the divergence produced by the opposing E. Greenland and W. Spitsbergen Currents could be additional contributors to upwelling in the Greenland Sea's marginal ice zone. A third potential mechanism that has been suggested is the release of epontic algae

during ice-melt (Ackley *et al.*, 1979; Schandelmeier and Alexander, 1981). Although high concentrations of algae may be present in the ice (Hameedi, 1978; Apollonio, 1980) and the residence times of cells released from the ice are unknown, they may sink rapidly out of the surface layer (Horner and Shrader, 1982).

Among possible factors that limit the growth of phytoplankton in the marginal ice zone of the East Greenland Sea is the relatively low ambient concentration of nutrients. In the Greenland Sea and adjacent Arctic Ocean, pre-bloom nutrient concentrations are low. For example, data taken in the permanent ice-pack to the north of Spitsbergen during April 1981 suggest maximum nitrate, reactive phosphorus and dissolved silicon concentrations in the upper 50 m of ~ 5 , 0.5 and 6 μM , respectively (Garfield *et al.*, 1982). These observations were in cold Arctic Ocean surface water with salinities less than 34‰. Pre-bloom nitrate concentrations in the surface layers of the warm, high-salinity waters carried northward in the W. Spitsbergen Current may be somewhat higher, but they probably do not exceed the values found in the subsurface "Atlantic Water" mass that they form upon entering the Arctic Ocean and sinking beneath the surface layer (Treshnikov, 1977). North of Spitsbergen, nitrate, reactive phosphorus and dissolved silicon concentrations in the "core" (depth >200 m) of this water mass are about 12, 0.75 and 6 μM , respectively (Garfield *et al.*, 1982). In contrast, pre-bloom nitrate, reactive phosphorus and dissolved silicon concentrations in the surface layers around Antarctica and in the Bering Sea are commonly >15 (sometimes above 20), 1 and 30 μM (Alexander and Niebauer, 1981; El-Sayed and Taguchi, 1981; Glibert *et al.*, 1982; Niebauer *et al.*, 1983a, b). Based on these values, one would expect relatively low standing stocks of phytoplankton in the Greenland Sea's marginal ice zone.

Another potential factor that could control the ice-edge bloom of phytoplankton is grazing by the large copepods such as *Calanus finmarchicus*, *Calanus hyperboreus*, and *Calanus glacialis* that are known to be abundant in the area (Wiborg, 1955). These copepods feed without showing saturation over a wide range of food concentrations (Conover, 1966; Huntley, 1981), grow efficiently (Conover, 1962; Conover, 1964), and provide food for higher trophic levels that congregate in the marginal ice zone (Bradstreet and Cross, 1982).

As suggested by the above comments, the ecosystem associated with the ice-edge of the Greenland Sea could differ substantially from the relatively well documented ice-edges of the Bering Sea and Antarctica. In this study we shall examine conditions in the Greenland Sea's ice-edge during late July 1983 and attempt to correlate physical variables (e.g., melting, advection, and upwelling), nutrients, and potential grazing pressure with the observed phytoplankton populations.

2. Methods

This investigation was part of the MIZEX-83 project (Johannessen *et al.*, 1983b; Muench, 1983) conducted in the Greenland Sea during July 15–29, 1983. Four

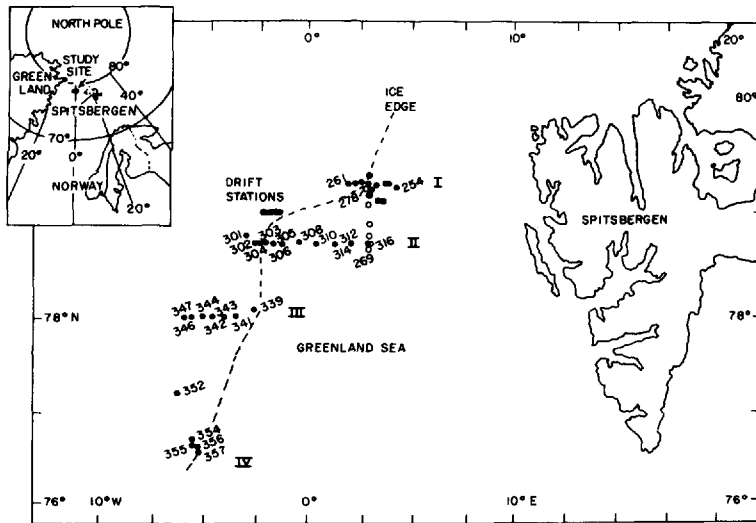


Figure 1. Locations of biological stations and the ice-edge in the east Greenland Sea (Fram Strait) in July 1983. The four east-west sections are noted as I–IV.

sections normal to the ice-edge were sampled with each taking 12 h or less to complete (Fig. 1). A north-south section (stations 269–278) was also taken in the northern portion of the survey area. This section crossed an anticyclonic eddy that may be associated with the quasi-permanent cyclonic feature mentioned above.

Temperature and salinity profiles were collected at each station using a Neil Brown C.T.D. calibrated with Nansen bottle casts. Results of the C.T.D. program are contained in Johannessen *et al.* (1983a). Occasionally the sections contained more C.T.D. stations than biological stations. We have included the additional C.T.D. data to give the most complete sections of temperature and salinity, but the sections of biological variables therefore do not necessarily match the C.T.D. sections exactly. Water samples were collected using 5-liter Niskin bottles. Samples for nutrient analyses were collected in 60-ml linear polyethylene bottles that had been seasoned by exposure to low nutrient surface water from the Sargasso Sea. Some nutrient samples were frozen at approximately -15°C while another set had three drops of saturated HgCl_2 added to stop biological activity. Nutrient analyses were carried out with a Technicon AutoAnalyzer using procedures based on the manual method of Murphy and Riley (1962) for reactive phosphorus and the methods of Armstrong *et al.* (1967) for dissolved silicon, nitrate, and nitrite. Ammonium was measured by the phenol-hypochlorite method of Koroleff (1969), adapted to the AutoAnalyzer by Slawyk and MacIsaac (1972). The automated methods and their precision have been described by Friederich and Whitley (1972). Comparison of frozen samples with those treated with HgCl_2 suggests that there were problems with the latter preservation technique. However, the nitrate values from the samples preserved with HgCl_2 appeared usable

with precisions about half as good as normal, and such values have been used in Figures 8 and 9 since there were no frozen samples taken for these sections.

Chlorophyll *a* was determined fluorometrically by filtering 50 to 500 ml of seawater through Gelman A/E glass fiber filters under low pressure and extracting with 90% acetone (Holm-Hansen *et al.*, 1965). Fluorescence was measured before and after acidification with a fluorometer calibrated with a chlorophyll *a* standard (Sigma) dissolved in 90% acetone. Light attenuation coefficients for the water column were determined from the depth at which a secchi disk disappeared (Parsons *et al.*, 1984). Whole water samples for phytoplankton taxonomy were preserved in 2% glutaraldehyde.

Zooplankton were collected in vertical hauls (maximum depth ~120 m) in the ice or oblique hauls (maximum depth ~35 m) out of the ice of 60 cm diameter Bongo frames fitted with 333 μm mesh nets and General Oceanics flowmeters. Subsequent sampling with a multiple opening-closing net in 1984 showed that most of the biomass of zooplankton in this area was in the upper 25 m (Lane, pers. comm.). Although we have used the two types of hauls in this study as if they were equivalent estimators of abundance in the upper 35 m, the vertical hauls in the ice may underestimate true abundance in this upper layer. The samples were split and counted for selected taxa with at least fifty individuals of all dominant taxa counted. Dry weights of specimens preserved in a 5% formalin-seawater solution were measured using a Cahn model 26 electrobalance. Several individuals of single species and particular stage of development were sorted from preserved samples, rinsed with distilled water, transferred to preweighed aluminum boats, and dried in a drying oven at 40 to 50°C for at least 24 h before the dry weight determinations. A mean loss of 40% of dry weight because of preservation in formalin has been assumed (Vidal and Smith, 1985).

3. Results

a. General remarks. The effects of the cold, low salinity, surface waters of the E. Greenland Current and the melting of ice are evident near the ice-edge where the stability in the upper 25 m is strong, with surface salinities frequently falling below 33‰ (e.g., Figs. 2, 3, 7, and 9). The influence of the warm, high salinity waters being transported northward from the North Atlantic is also evident. The cold, polar waters seemed to be more dominant in the southwestern sections (Figs. 7 and 9) presumably because these sections penetrated into the E. Greenland Current.

Data from the three sections (Figs. 2, 4, and 11) for which the entire suite of nutrient data were available (ammonium, nitrate, nitrite, reactive phosphorus, and dissolved silicon) suggest that inorganic nitrogen tended to be the major plant nutrient in shortest supply. Average values in the upper ten meters were 0.7, 0.2, and 3.5 μM for combined nitrogen (ammonium + nitrate + nitrite), reactive phosphorus and dissolved silicon, respectively. The normal uptake ratio of N:P (by atoms) is ~16:1, while silicon is not required by all phytoplankton (e.g., Redfield, 1958).

A prominent feature in the nutrient distributions was a well developed ammonium maximum that occurred at most stations (Figs. 2, 4, and 11). Maximum ammonium concentrations were frequently above $1.5 \mu\text{M}$, and they occurred at a depth of approximately 50 m. Nitrite concentrations (not displayed in this report) were usually less than $0.5 \mu\text{M}$. Maximum nitrite concentrations tended to occur below the ammonium maximum, possibly as a result of light inhibition of nitrification as suggested by Olson (1981). Chlorophyll *a* concentrations ranged from 0.9 to 15.6 mg m^{-3} , with the concentrations in the upper 20 m averaging $3.8 \pm 1.9 \text{ mg m}^{-3}$ (Figs. 2, 4, 8, 9 and 11). Particularly high concentrations of chlorophyll *a* were found in the northern part of our study area (Figs. 2, 11 and 13).

The community of herbivorous zooplankton was dominated both numerically and in terms of biomass by three relatively large, herbivorous copepods, *Calanus hyperboreus*, *Calanus finmarchicus*, and *Calanus glacialis*. Abundances of all copepodid stages of the three copepods combined ranged from 3 to 200 m^{-3} , with biomass ranging from 5 to $30 \text{ mg dry weight m}^{-3}$ (Figs. 5 and 6). All copepodid stages of each species of copepod were captured at one station or another during the study.

b. Sections normal to the ice-edge. Salinity and temperature distributions in the most northerly section (stations 254–261) indicate a high degree of stratification in the upper ~ 25 m that increased in intensity toward the ice-edge (Fig. 2). These data and the geostrophic calculations of Johannessen *et al.* (1983a) also suggest the presence of a gyre with a cold, low-salinity, low-density core centered at station 260. With such a density distribution, anticyclonic flow with a convergence zone in the center of the section (stations 257 and 258) would be expected, and this appears to be the case since the nutrient isopleths “dip” at the centrally located stations. While the depression in nitrate isopleths could be related to the higher salinity water masses at the periphery (see above), this is not a likely explanation for the ammonium distributions, since ammonium is generated by local biological processes, or for dissolved silicon which tends to be relatively high in the low salinity waters associated with the polar outflow (e.g., Codispoti and Lowman, 1973).

The stability configuration is very similar to that of the upper layer in the Bering Sea during melting and retreat of ice in spring (Niebauer and Alexander, 1985) and to results of a model incorporating melting and winds at an ice-edge (Niebauer, 1982). For two days prior to sampling this section, winds were from the west at speeds of $\sim 2\text{--}6 \text{ m s}^{-1}$, a condition of off-ice winds that would favor dispersion of the ice-edge. In the upper layers, nutrient concentrations were low everywhere, but there was a relative increase under the ice-edge, particularly at station 261 where there was $\frac{1}{10}$ ice coverage. A subsurface ammonium maximum was ubiquitous and centered at a depth of ~ 50 m. Concentrations of chlorophyll *a* in the surface layers were high everywhere, but the highest values occurred at stations farthest from the ice-edge (Fig. 2).

The relatively low chlorophyll *a* and high surface layer nutrient values at station 261

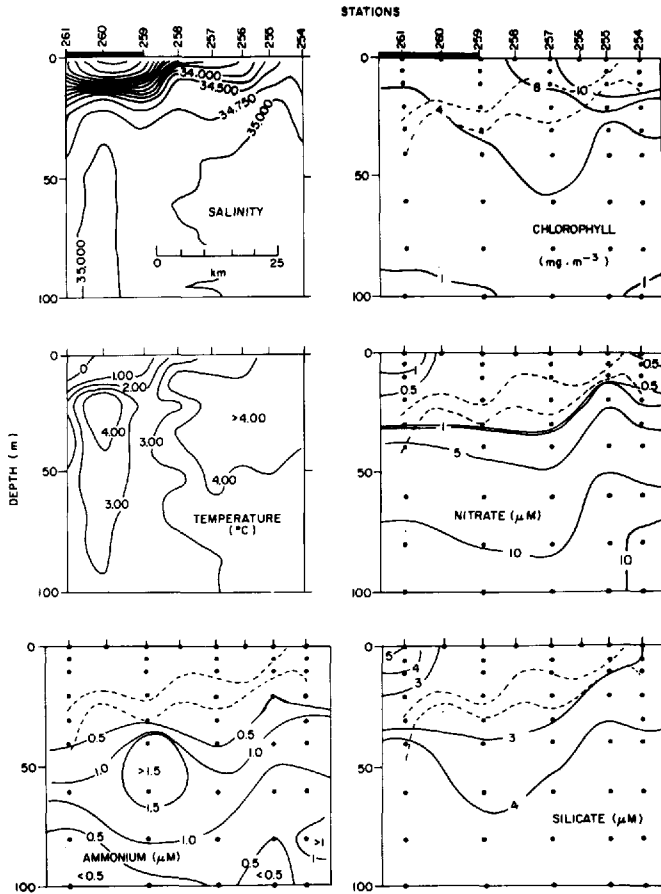


Figure 2. Nutrients, chlorophyll *a*, salinity and temperature from the most northerly section (I), stations 254–261. Solid bar indicates extent of ice-cover. Ice at station 260 was 4/10, at 257 and 258, 0/10. Section is 50 km long. Dashed lines correspond to 34.5 and 34.75‰ isohalines. Density in this section closely paralleled salinity with the 34.0‰ isohaline approximately equivalent to the 27.0 isopycnal.

suggest an inhibitory effect of the ice-cover on phytoplankton growth presumably due to reduced light penetration. As we shall discuss below, however, the elevated off-ice chlorophyll values may be related to the eddy found in this region. Outside the ice-edge, at the station with the highest surface chlorophyll *a* concentration (station 254), the euphotic zone was 16 m deep while in open water at the innermost station, the 1% light depth was 35 m. No zooplankton data are available from this section.

The phytoplankton community on the northern transect was dominated numerically by flagellated chrysophytes, and diatoms were in general quite scarce in the whole water samples of the transect. However, thick mats of the benthic diatom *Melosira*

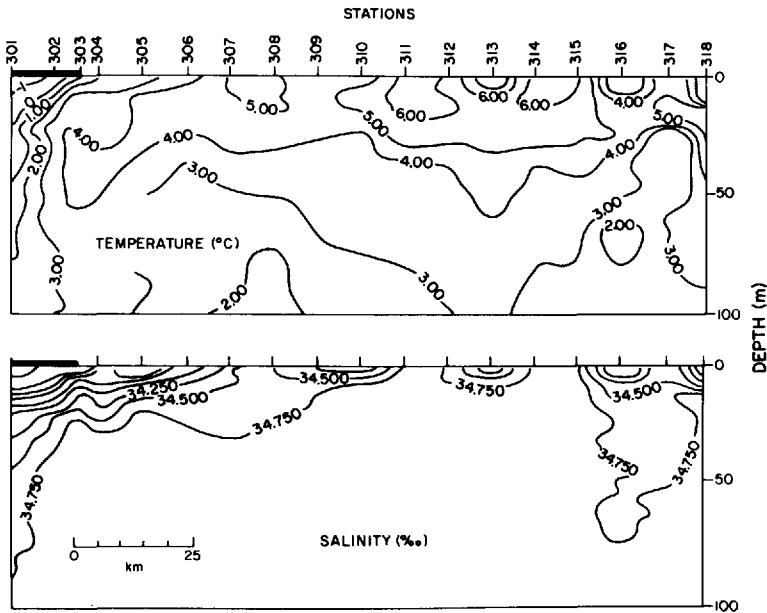


Figure 3. Temperature and salinity from section II, stations 301–318. Solid bar indicates extent of ice-cover. Station 301 had 4/10 ice and station 302 had 5/10. All others were ice-free, with 303 just into open water. Section is 136 km long.

artica were released into the water as the floes melted and fractured; these mats floated on the surface for short periods (less than 24 h) and then disappeared. *M. arctica* was rarely observed as a component of the water column plankton. Diatoms contributed a larger portion of the phytoplankton biomass in other transects, but in general flagellated nanoplankton were the dominant members of the community during this period.

The longest section perpendicular to the ice (stations 301–316 in Figs. 1, 3, and 4) was occupied primarily by warm (maximum temperatures $>6^{\circ}\text{C}$) and saline (maximum salinities $>34.75\text{‰}$) waters. Thus, this section was heavily influenced by the northward flow of the W. Spitsbergen Current which has temperatures and salinities in its “core” of $>6^{\circ}\text{C}$ and near 35.0‰ , respectively (Coachman and Aagaard, 1974). The influence of the melting ice in contact with warm water appears as a thin layer (20 m) of cool, low-salinity water under the ice and extending approximately 25 km off the ice (Fig. 3). In contrast with the previous section, chlorophyll *a* concentrations were highest in a subsurface maximum under the ice where a small nitrate maximum also occurred (station 301, Fig. 4). Another zone of relatively high chlorophyll *a* concentration occurred between stations 312–316, and it is worth noting that nitrate concentrations in the upper 10 m at stations 312 and 316 were slightly higher than at most of the other stations (Fig. 4). As in the previous section, a ubiquitous ammonium maximum

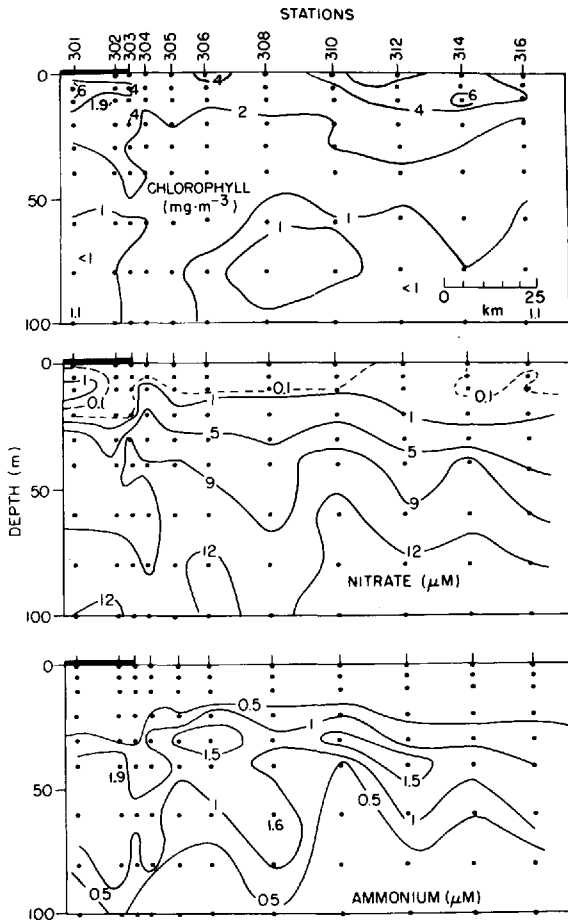


Figure 4. Nutrients and chlorophyll *a* from section II, stations 301–316. Solid bar indicates extent of ice-cover described in caption of Figure 3. Section is 127 km long.

centered at about 50 m was observed. The distributions in this section suggest the possibility of more than one eddy with associated cross circulations that cause nutrient isopleths to rise in some locations (e.g., stations 304 and 312). The near surface waters under the ice also appear to be a nutrient source.

The zooplankton of this section were dominated numerically and in terms of biomass by the copepod typical of the North Atlantic, *Calanus finmarchicus* (Figs. 5 and 6). The larger arctic copepod, *Calanus hyperboreus*, was not numerous in the section, but by virtue of its size comprised approximately half the biomass (Fig. 6).

The third section perpendicular to the ice-edge (stations 339–348) was entirely ice-covered. Temperatures were less than 1°C from the surface to 400 m over half the section (Fig. 7), indicating water originating in the Arctic Ocean. Lowered salinity in

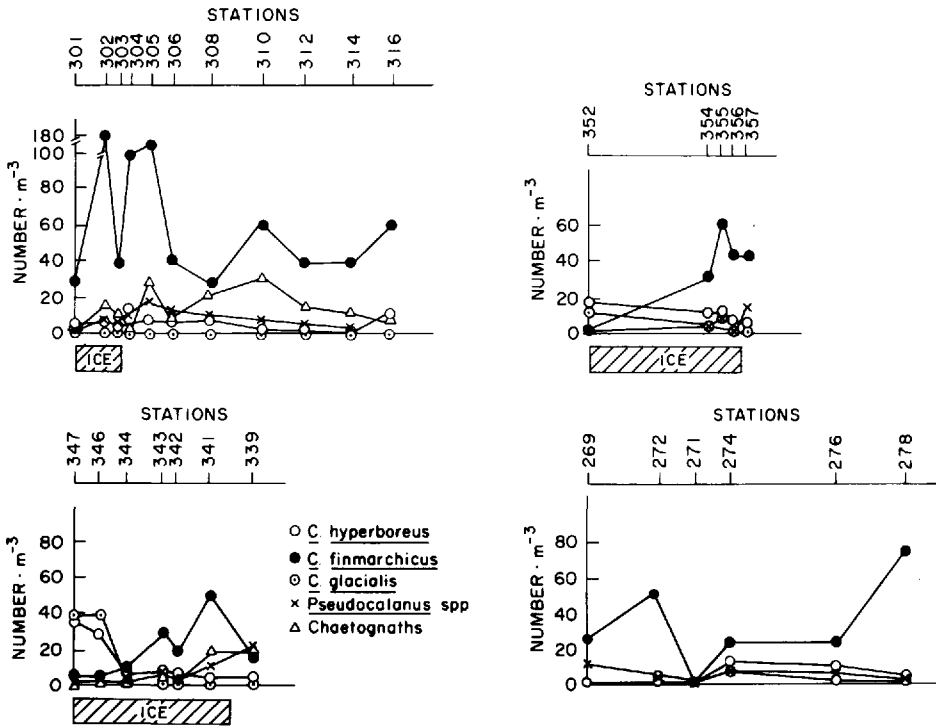


Figure 5. Abundance of various taxa of zooplankton in four sections in the marginal ice zone. Extent of ice-cover indicated at the bottom. Vertical net hauls (0–120 m) were used at stations 269, 301, 302, 303, 341, 342, 343, 344, and 354. All other stations were sampled by oblique hauls covering the upper 35 m approximately.

the upper layer, varying in thickness from 0 to 120 m, can be attributed to melting ice and the Arctic Ocean origin of the water at stations 344–348 (Fig. 7). Winds for two days prior to the section were from the southwest at 1 to 7 m s⁻¹, conditions favoring divergence of the ice-edge. Nitrate concentrations in the upper 10 m were <0.25 μM except for values of ~3 and 0.7 μM at stations 343 and 342, respectively (Fig. 8). Chlorophyll *a* concentrations exceeded 2 mg m⁻³ in the upper 20 m at most stations and were quite variable (Fig. 8). Nitrate concentrations at depth were also variable, and station 343, where the two water masses may have been interleaving, was particularly unusual. Subsurface nitrate concentrations tend to rise toward the east where the influence of the high salinity Atlantic waters is greater. Concentrations of chlorophyll *a* under the ice are similar to those observed under the ice in the most northerly section (Fig. 2). The depth of the euphotic zone (1% light penetration) in this section was on average 32 m (±10.0; *N* = 6), similar to the 35 m euphotic zone measured in the ice of the northerly section. The euphotic zones at stations in water of

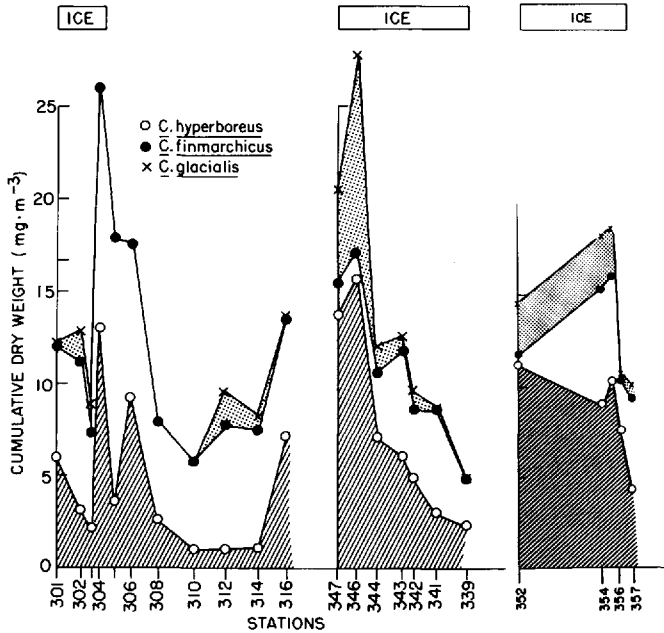


Figure 6. Biomass ($\text{mg dry weight m}^{-3}$) of the three largest herbivorous copepods collected in three sections at the ice-edge. Extent of ice-cover indicated at the top.

Arctic Ocean origin (stations 346 and 347) were shallower (24 and 16 m, respectively) than the euphotic zones of stations 339–342 in water of North Atlantic origin (35, 34, and 41 m, respectively).

The distributions of herbivores in the section were unambiguously associated with the Arctic Ocean or North Atlantic origin of the water masses. The portion of the section with the largest volume of cold, low salinity water originating from the Arctic Ocean, stations 346 and 347 (Fig. 7), had zooplankton dominated both numerically and in terms of biomass by *Calanus glacialis* and *C. hyperboreus* (Figs. 5 and 6). All copepodid stages of *C. glacialis* and *C. hyperboreus* (except CI) were collected in the area where they were most abundant (stations 346 and 347), and their age-structures indicated active reproduction. For example, *Calanus hyperboreus* in these samples from late July were primarily stages CII (38%) and CIII (36%), suggesting a development time identical to that described for *C. hyperboreus* in the fjords of East Greenland where an annual life cycle was observed (Ussing, 1938). *Calanus glacialis* at these two stations was on average 20% copepodid stage I, 27% copepodid stage II and 24% copepodid stage III, also suggesting an annual life cycle. The *C. hyperboreus* collected in the area of the ice-edge bloom of phytoplankton at 78N, although clearly associated with water of Arctic Ocean origin, seems to have a life cycle that is

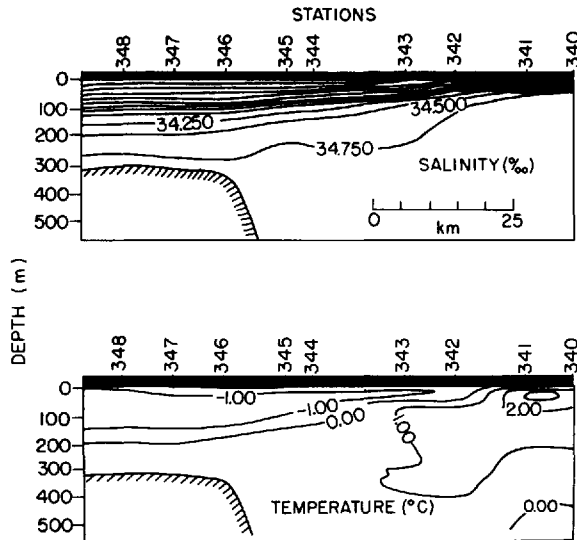


Figure 7. Temperature and salinity from section III entirely within the ice-cover (stations 340–348) and 80 km long. Stations 344, 346 and 347 had 4/10 ice-cover, station 343, 3/10, and station 341, 1/10.

accelerated relative to that described in the central Arctic Ocean (Dawson, 1978). Outside of the water of Arctic Ocean origin, *Calanus glacialis* was not abundant and was represented only by copepodid stage V, indicating that this portion of the population, removed from its normal arctic environment, had ceased reproduction and growth and probably had entered diapause.

Conversely, *Calanus finmarchicus* was most abundant in relatively warm (2°C) water of North Atlantic origin (station 341; Figs. 5 and 6). At that station, *C. finmarchicus* comprised 63% of the biomass accounted for by the three dominant herbivorous copepods (Fig. 6), and had an age-structure indicating active reproduction and growth (CI = 16%; CII = 40%; CIII = 8%; CIV = 10%; CV = 18%; adult females = 8%). In water of Arctic Ocean origin, however, *C. finmarchicus* was not particularly abundant (Fig. 5) and was primarily present as copepodid stage V (70%) and adult females (24%), again indicating diapause in a relatively unfavorable environment.

The most southerly section, stations 352–357, was 75 km long and included water of Arctic Ocean origin (stations 352–354) and North Atlantic origin (stations 355–357), with stations 352–356 ice-covered (Fig. 9). For two days prior to this section winds were from the southeast at 4 to 10 m s⁻¹, conditions which cause convergence of the ice-edge. The salinity and temperature distributions in this section suggest a cyclonic eddy with a high salinity and high density center near stations 359 and 360. One would expect nutrient concentrations to rise toward the core of this eddy because of the rising

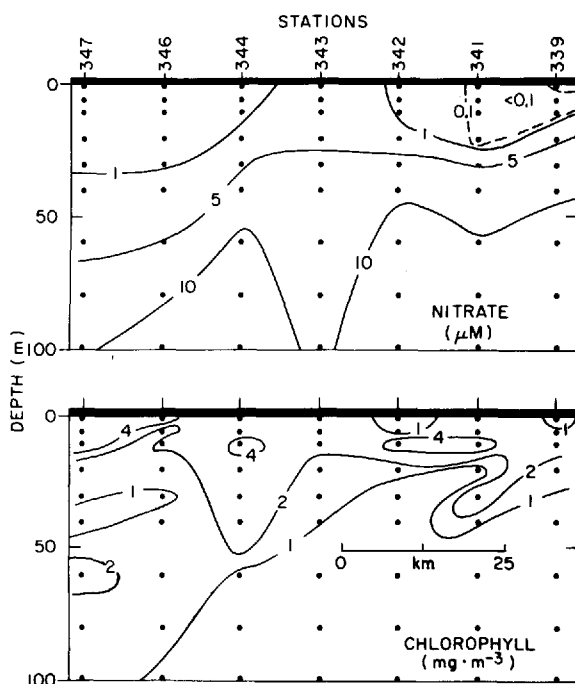


Figure 8. Chlorophyll *a* and nitrate from section III, stations 339–347. Ice-cover indicated by solid bar, and described in caption of Figure 7.

motions to be expected and the greater influence of water from the North Atlantic. This appears to be the case as nitrate concentrations did rise as the center was approached, but the nutrient data stop at station 357. Chlorophyll *a* concentrations greater than 4 mg m^{-3} were at the surface under the ice (station 352) and at subsurface depths near the ice-edge (Fig. 9). Chlorophyll *a* concentrations greater than 1 mg m^{-3} extended nearly to 100 m at station 352 well into the ice, and to depths greater than 40 m at most stations of this section (Fig. 9). The abundance of *Calanus finmarchicus* increased from near zero in waters from the Arctic Ocean to between 40 and 60 m^{-3} in waters from the North Atlantic (Fig. 5). *Calanus glacialis* showed the opposite trend, which is expected for an Arctic Ocean organism (Fig. 5). In the waters from the Arctic Ocean, *Calanus finmarchicus* was primarily (80%) copepodid stages IV and V and adult females (stations 352–354) while in North Atlantic waters copepodid stages II through IV comprised 84% of the population, indicating active growth and reproduction. In terms of biomass, *Calanus hyperboreus* and *Calanus finmarchicus* were dominant (Fig. 6), with *C. hyperboreus* accounting for 77% of the biomass in water of Arctic Ocean origin. In waters of North Atlantic origin, *C. hyperboreus* comprised 57% of the biomass and *C. finmarchicus* accounted for 35% (Fig. 6).

On 21 July 1983 the ship was allowed to drift with the ice in the vicinity of $78^{\circ} 55' \text{N}$,

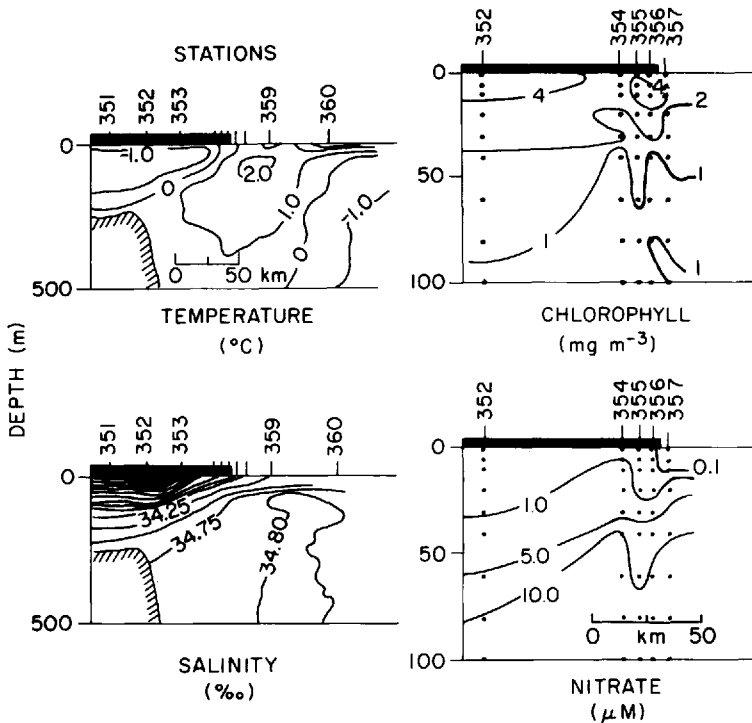


Figure 9. Temperature, salinity, chlorophyll *a* and nitrate from section IV, stations 352–357. Extent of ice-cover shown as a solid bar. Station 354 had 9/10 ice-cover and stations 355 and 356 had 1/10.

2W (Fig. 1) and measurements of abundance of zooplankton were made each 2–4 hours from 0100 h through 2000 h (Fig. 10a). In general the abundance of the dominant herbivores remained constant (Fig. 10a) indicating that diel vertical migration into and out of the upper 120 m did not occur and that grazing and excretion by herbivores occurred continuously in this layer. The variance in abundance (log-transformed) of the three species of *Calanus* over the 20-hour period was small, 1–4% of the mean. Biomass of the dominant herbivores was relatively constant, ranging from 20 to 31 mg dry weight m⁻³ (Fig. 10b). *Calanus hyperboreus* on average comprised 48% of the biomass, while *C. finmarchicus* accounted for 38%, and *C. glacialis* 14% (Fig. 10b). The age-structure of *C. hyperboreus* and *C. finmarchicus* did not change dramatically during the study indicating no advective event or drift into water of Arctic Ocean origin (Fig. 10b), and sigma-*t* over the upper 150 m also showed no evidence of change in the water mass during the study (J. Johannessen, pers. comm.). Therefore, the relative abundances of the dominant calanoid copepods gives quite an accurate indication of the water masses present in this area. The copepods do not exchange rapidly between the water masses, so our sections give community structure

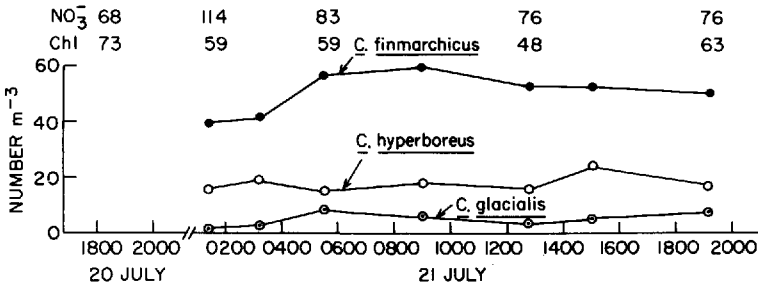


Figure 10a. Abundance of three herbivorous copepods collected during a drift station in the ice at 78°55'N, 2W. Concentrations of nitrate and chlorophyll *a* integrated through the upper 30 m are indicated at the top.

that is temporally stable and faithful to the origin of the water mass. There was a small increase in the frequency of copepodid stage I of *C. finmarchicus* toward the end of the time-series (Fig. 10b) which may indicate active recruitment in this species.

c. *Section across an eddy.* This north-south section (Fig. 11) crossed a well-developed eddy. Water of North Atlantic origin predominated, but stations 274–276, near the center of the section, had somewhat reduced temperatures and salinities. Geostrophic velocities (Johannessen et al., 1983a) showed the eddy to be anticyclonic. At the

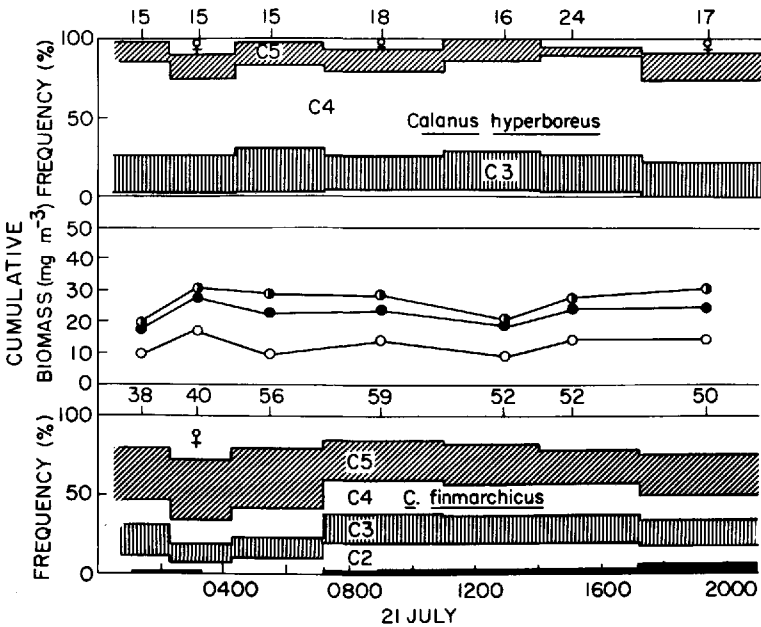


Figure 10b. Biomass (cumulative dry weight) of three herbivorous copepods collected during a time-series in the ice at 78°55'N, 2W and the age-structure of two of the copepods.

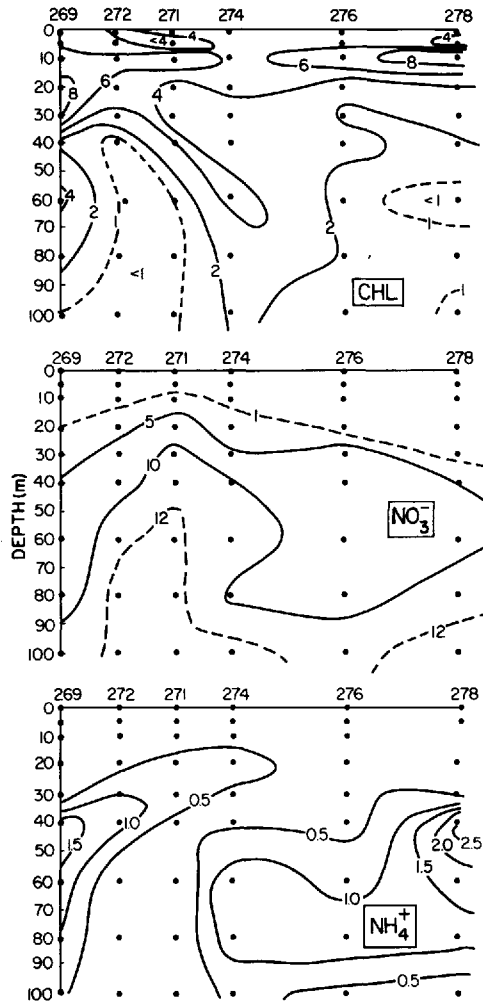


Figure 11. Nitrate, ammonium and chlorophyll *a* from a north-south section (stations 269–278) crossing an eddy near 79N. The section was ice free. Units are μM for nitrate and ammonium and $\text{mg} \cdot \text{m}^{-3}$ for chlorophyll *a*.

southern end of the section the nitrate isopleths form a dome with a center at station 271 where concentrations of more than $1 \mu\text{M}$ reach 10 m and concentrations $>10 \mu\text{M}$ reach 30 m (Fig. 11). An ammonium maximum was also present in this section, and the distributions of nitrate, ammonium, and chlorophyll *a* suggest a well developed cross-circulation with sinking at stations 274–276 and a zone of rising motions in the vicinity of stations 271–272. The distribution of geostrophic velocities (Johannessen *et al.*, 1983a) also suggests a zone of sinking centered at station 276. Concentrations of chlorophyll *a* in deep waters of high nitrate concentration were low, but subsurface

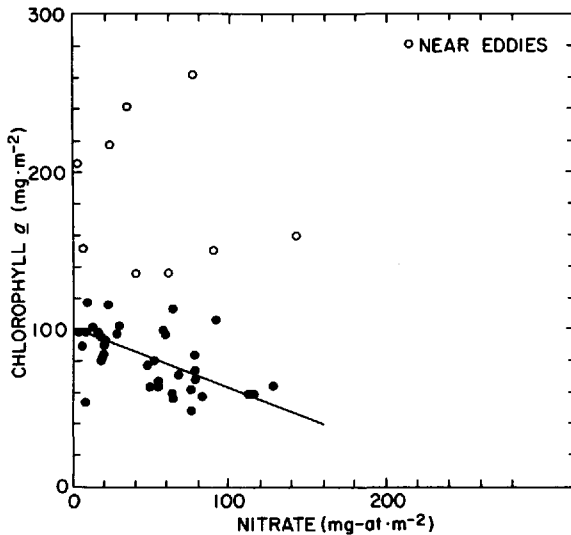


Figure 12. Nitrate and chlorophyll *a* in the upper 30 m from all stations sampled showing the effect of eddies near the ice-edge.

concentrations of chlorophyll *a* in excess of 8 mg m^{-3} were observed at the northern and southern ends of this section (Fig. 11). Chlorophyll *a* concentrations in the upper 10 m were generally $>4 \text{ mg m}^{-3}$ (Fig. 11). The copepod that was numerically dominant, *Calanus finmarchicus* (Fig. 5), is characteristic of the North Atlantic and was most abundant at stations having high subsurface concentrations of chlorophyll *a* (stations 272 and 278; Fig. 11). *Calanus hyperboreus* and *Calanus glacialis* were most abundant in the center of the section (stations 274 and 276; Fig. 5), which suggests that the lower temperature and salinity in the center of the eddy are the result of water of Arctic Ocean origin becoming trapped. As noted above, nitrate concentrations also tend to be lower in Arctic waters, so the nitrate dome could be augmented by the juxtaposition of different water masses.

d. Integrated chlorophyll a distribution. When nitrate and chlorophyll *a* concentrations from all stations in this study are integrated over the upper 30 m and correlated with one another, the relationship is reasonably linear with the exception of six samples collected from the section through the eddy and three from the offshore portion of the most northerly section perpendicular to the ice which may have sampled the eddy also (stations 254–257; Fig. 12). The anomalous points in the region of the eddy where chlorophyll *a* concentrations are high and nitrate is not depleted suggest advective effects associated with the eddy have a great influence on the distribution of plant biomass in the East Greenland Sea. A plan diagram of integrated chlorophyll *a* in the upper 100 m shows the dominant effect of the eddy very clearly (Fig. 13); highest biomass of plants was confined to the area of the eddy (Fig. 13).

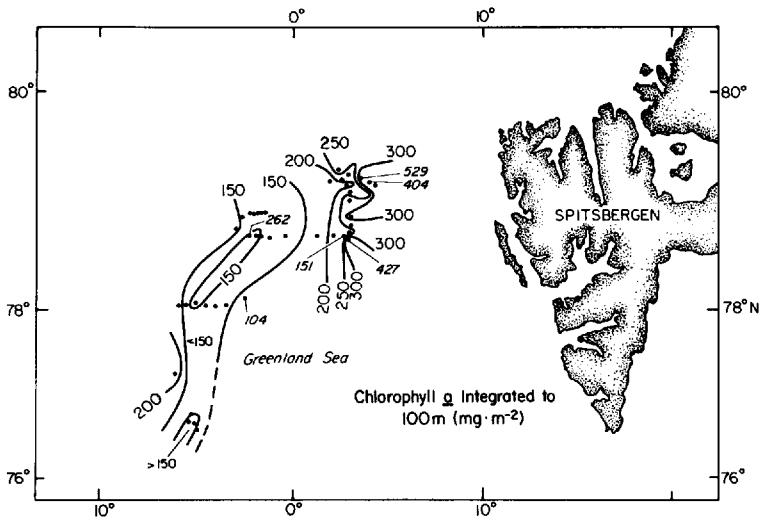


Figure 13. Plan view of chlorophyll *a* integrated over the upper 100 m showing its relationship with the ice-edge and the eddy near 79N.

4. Discussion

Our observations are sufficient to evaluate some of the biological factors in the marginal ice zone of the Greenland Sea with respect to adjacent regions and to the biological regimes of other ice edges. Nutrient levels in the upper layers, exemplified by nitrate, were low during our study, usually less than $1 \mu\text{M}$. Nitrate at 100 m, which can be used as an approximation to pre-bloom concentrations, was $12 \mu\text{M}$ in our study region and $10 \mu\text{M}$ in the open Greenland Sea during the YMER expedition (Anderson and Dyrssen, 1981). In view of the variability encountered, this difference is not statistically significant, but it is in line with the notion that a large scale divergence should be set up by the presence of the opposing E. Greenland and W. Spitsbergen Currents. It is also apparent that nutrient levels in the Greenland Sea's marginal ice zone are very different from those in the Bering Sea or in Antarctica where pre-bloom nitrate concentrations are often greater than $20\text{--}25 \mu\text{M}$ (Table 1).

When the concentrations of chlorophyll *a* at the ice edge in our study are compared to those of other marginal ice zones, it can be seen that maximum levels of chlorophyll *a* tend to be much lower than those of the Bering Sea (Alexander and Niebauer, 1981), which is probably a result of the lower nutrient concentrations initially present (Table 1). However, chlorophyll *a* concentrations in the Weddell and Ross Seas are similar to those noted in our study even though the former areas have much higher pre-bloom nitrate concentrations. This is probably due to greater mixing in the Weddell Sea which results in reduced growth rates and a more even distribution of phytoplankton biomass within the water column. These factors may also contribute to the low values in the Ross Sea, but during the Ross Sea bloom, elemental ratios were anomalous and

Table 1. Comparison of means of various parameters observed during bloom conditions in four different geographic conditions. Weddell Sea data from El-Sayed and Taguchi (1981), Ross Sea data from Smith and Nelson (1985), Bering Sea data from Alexander and Niebauer (1981), and East Greenland Sea data from this study.

	Weddell Sea	Ross Sea	Bering Sea	East Greenland Sea
Depth of mixed layer (m)	15	8	0-15	2
N^2 (cycles ² sec ⁻²)*	$.88 \times 10^{-4}$	1.39×10^{-4}	$.49 \times 10^{-4}\ddagger$	1.84×10^{-4}
Nitrate at 0 m (μ M)	12.0	8.6	<1	0.3
Nitrate at 100 m (μ M)	26.0	29.4	>25	11.8
Chlorophyll <i>a</i> at 0 m (mg m ⁻³)	1.63	2.70	21.8	3.83
Chlorophyll <i>a</i> , 0-30 m** (mg m ⁻²)	—‡	69	455	84
1% Light Depth (m)	20.3	18.8	—‡	23.0
Zooplankton Biomass (mg dry wt m ⁻³)	13.0***	—‡	—‡	14.7

* N^2 , the Brunt-Väisälä frequency, was approximated by $N^2 = -g(\delta\sigma_t/\delta Z)10^{-3}$ and was calculated for the entire 0-100 surface layer.

†Calculated from the bottom (70 m) density.

**Stations 254-257, where an eddy influenced chlorophyll *a*-nitrogen relationships, were omitted.

‡No data reported.

***Calculated using the conversion equation, dry wt. = 0.13 wet wt. (Mullin, 1969).

chlorophyll *a* was an inaccurate measure of phytoplankton biomass (Smith and Nelson, 1985). The strength of stability (quantified by the Brunt-Väisälä frequency) in the East Greenland Sea was much stronger than in other systems, and the mean depth of the mixed layer was less. Therefore, it appears that in the Greenland Sea stability induced by meltwater is great enough to allow for rapid phytoplankton growth in early spring, but that growth is rapidly limited by the supply of nitrogen. In contrast, Antarctic water rarely if ever becomes nutrient limited, but because of a lack of stability, the growth and accumulation of phytoplankton is slower.

Post-bloom surface nutrient levels were similar to those in the Bering Sea but much lower than those in the Southern Ocean. The bloom of phytoplankton at the ice-edge in the East Greenland Sea undoubtedly occurs earlier than the spring bloom in the open ocean of the region because, as Niebauer and Alexander (1985) point out, stratification due to meltwater influence would precede thermal stratification. The ice-edge bloom in the East Greenland Sea (79N) also probably occurs significantly later than that in the Bering Sea (58N) simply due to the large difference in latitude. Nonetheless, the conditions we encountered during our study were clearly not conditions representative of the period of maximal growth but rather those of low growth and maximal biomass (e.g., nitrate below 1 μ M, high chlorophyll *a* concentrations). The appearance of a receding ice-edge in a polar sea will have the effect of

lengthening the growing season; if other hydrological events such as upwelling at the ice-edge were to occur, then the annual productivity would also be markedly increased.

Zooplankton standing stocks in the study area were substantial and similar to those reported for the Weddell Sea (Table 1). To estimate the impact that grazing of the zooplankton populations might have on the phytoplankton, we calculated potential ingestion of carbon by three major species in the area. Assuming that the three major herbivorous copepods ingest 100% of their body weight per day (Paffenhöfer, 1971; Falkowski *et al.*, 1983), ingestion at the ice-edge is, on average, $\sim 13 \text{ mg C m}^{-3} \text{ day}^{-1}$. If one further assumes a carbon:chlorophyll ratio of 50 (Parsons *et al.*, 1984), approximately $0.3 \text{ mg chlorophyll } a \text{ m}^{-3} \text{ day}^{-1}$ would be ingested by the large copepods. Biomass of the other species we collected in the tows was so small that it would not significantly alter this calculation. The relationship between grazing rates and plant stocks, a turnover time of ~ 13 days if no plant growth was taking place, is considerably longer than that observed during the spring bloom over the slope of the Bering Sea where large herbivorous copepods also dominate the zooplankton (Smith and Vidal, 1984; Vidal and Smith, 1985). Over the slope of the Bering Sea during May, the period of the spring bloom in 1980, ingestion by the large copepods (using the same assumptions as above) was $65 \text{ mg C m}^{-3} \text{ day}^{-1}$ in 1980 and $36 \text{ mg C m}^{-3} \text{ day}^{-1}$ in 1981. Standing stocks of plants were $\sim 5 \text{ mg chlorophyll } a \text{ m}^{-3}$ in 1980 and $\sim 2 \text{ mg m}^{-3}$ in 1981, corresponding to turnover times of 4 and 3 days.

An ammonium maximum was observed in all of the sections for which we have ammonium observations. The maximum occurred at approximately 50 m and peak concentrations usually were $1.0\text{--}2.0 \mu\text{M}$. Such a subsurface peak is not unusual in colder waters (Saino *et al.*, 1983), but has never been reported for the East Greenland Sea. Although we do not have any rate data to demonstrate the causes of the feature, we believe that it arose from the combined effects of reduced phytoplankton uptake, which is weakly light dependent (McCarthy, 1981) and active nutrient regeneration by bacteria, microzooplankton and zooplankton. If the *Calanus* species which we observed were evenly distributed over the water column and if their rates of ammonium release were similar to those of *Neocalanus plumchrus* and *N. cristatus* in the Bering Sea (Vidal and Whitlege, 1982), the average daily rate of ammonium excretion would have been $4.81 \mu\text{g-at m}^{-3}$. This rate is similar to that reported for populations dominated by large, herbivorous copepods in the Bering Sea in spring ($4.49 \mu\text{g-at m}^{-3}$; Dagg *et al.*, 1982) and for the large copepods in the Ross Sea in the austral summer ($3.84 \mu\text{g-at m}^{-3}$; Biggs, 1982). However, preliminary results from stratified samples collected in 1984 have shown that zooplankton were concentrated in the upper 25 m (Lane, pers. comm.). If this were the case, ammonium excretion in this upper layer would have been $\sim 23 \mu\text{g-at m}^{-3}$.

To estimate the importance of this nutrient input to phytoplankton, the potential nutrient demand was calculated as follows. For each mg of chlorophyll *a*, carbon

uptake is approximately $1 \text{ mg C m}^{-3} \text{ hr}^{-1}$ (Platt *et al.*, 1982; Smith, unpubl. data). If the average carbon:nitrogen ratio were 5.0, then this carbon uptake represents $0.2 \text{ mg N m}^{-3} \text{ hr}^{-1}$, or $340 \text{ } \mu\text{g-at m}^{-3} \text{ day}^{-1}$. If the average biomass of phytoplankton in the upper 30 m (Table 1) is representative, then nitrogen uptake is $952 \text{ } \mu\text{g-at m}^{-3} \text{ day}^{-1}$. Thus, excretion by larger zooplankton may have been only 2% of daily nitrogenous uptake by phytoplankton. Therefore it is possible that in the marginal ice zone of the Greenland Sea, under conditions of nitrogen limitation for phytoplankton growth, that a large portion of the nitrogen is not being recycled by larger zooplankton but rather via an active microbial food loop consisting of microzooplankton and bacteria. Although we did not assess the role that these organisms play in the region's nitrogen dynamics, we have noticed significant numbers of microzooplankton in the preserved samples (Wilson, unpubl. data). Our data are by no means conclusive, but do point to the need to accurately assess the role that small heterotrophic organisms play in nitrogen dynamics of polar seas.

Throughout our description of the data we pointed out the presence of features associated with eddies that appear to be present throughout our study area. The most prominent effects of vortex motion were associated with our two northernmost sections (Figs. 2, 11, 12 and 13). These two sections may have crossed the same anticyclonic feature, and it is clear that chlorophyll *a* concentrations in the vicinity of the eddies in these sections were unusually high. Historical data on the Greenland Sea suggest the presence of large-scale meanders and gyres (Codispoti, 1968), and the anticyclonic feature that we observed may lie just to the south of a semipermanent cyclonic gyre found over a topographic depression (Wadhams and Squire, 1983; Smith *et al.*, 1984). Theoretical considerations (Smith *et al.*, 1984) suggest the likelihood of the development of anticyclonic features as water advects southward from the region of the quasi-permanent gyre. It is unfortunate that we have no observations from the quasi-permanent cyclonic gyre since high chlorophyll *a* concentrations are to be expected around its center, which is a zone of divergence. It is nevertheless clear to us that the high chlorophyll *a* concentrations associated with our two northernmost sections (Figs. 2 and 11) are in part the result of vertical motions associated with eddies which bring new nitrogen into the euphotic zone. To a lesser extent, such motions also appear to be important in our other sections. We conclude, therefore, that the eddies associated with the boundary between the E. Greenland and W. Spitsbergen Currents may play a dominant role in maintaining biological productivity after the initial bloom period.

During the initial period, factors associated with the melting of ice may be more important, and even during our observations there were indications that the waters under the ice were relatively high in nutrients and also contributed to the relatively high levels of chlorophyll *a* that were observed. In this respect it is important to remember that a fundamental difference between the ice-edge of the East Greenland Sea and those of the Bering Sea and the Southern Ocean is that the Greenland Sea's

ice-edge and ice-edge processes persist throughout much of the year. Ice is exported from the Arctic Basin by the East Greenland Current continually, and it melts where it comes in contact with the warm waters of North Atlantic origin. Much of the ice tends to be multiyear, and the ice-edge position is relatively invariant (Vinje, 1977). The Bering Sea, however, has an ice-edge which has a large (2000 km) extent, retreats extremely rapidly (e.g., 200 km in eleven days; Alexander and Niebauer, 1981), and completely disappears by early summer. The ice-edges of the Southern Ocean also tend to consist of newly formed pack ice that retreat over extremely large areas. Therefore, the ice dynamics of the East Greenland Sea are unique, and in conjunction with the unusual conditions created by the eddies that we have described, result in the distinctive biological conditions we observed.

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