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Seasonal inorganic nitrogen distributions and dynamics in the southeastern Bering Sea

TERRY E. WHITLEDGE,* WILLIAM S. REEBURGH† and JOHN J. WALSH‡

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Abstract—The annual cycle of the distribution of nitrate and ammonium concentrations in the PROBES area of the southeastern Bering Sea was highly interactive with the physical and biological processes. Nitrate concentrations were replenished over the shelf during the autumn and winter at a very uniform rate until the spring bloom commenced. In the middle shelf after nitrate concentrations were depleted in the upper mixed layer during the spring bloom, large quantities of ammonium were produced in the bottom layer. Cross-shelf diffusion, vertical diffusion, vertical mixing by storms, benthic release, and possibly nitrification interacted to supply nitrogen utilized by primary production. Nitrogen uptake by photosynthetic processes as estimated by nitrate depletion and nitrogen isotope measurements agreed with primary production estimates made by radiocarbon uptake rate measurements and ΣCO_2 budgets.

INTRODUCTION

THE availability of nutrients and incident radiation have long been known to be necessary for phytoplankton growth in the sea but despite many measurements of nutrient concentrations in the coastal and open ocean there still remain many questions about nutrient availability for primary production, especially over relatively long periods of time. The major factors associated with the basic nutrient–phytoplankton–zooplankton–fish interactions with the natural ecosystem were studied in the Processes and Resources of the Bering Sea shelf (PROBES) project in order to better understand their temporal behavior and variability.

The area studied by PROBES (described in detail in McROY *et al.*, 1986) was located between the Pribilof and Aleutian Islands and from the 40 m isobath to outside the shelf break at about 1500 m (Fig. 1). This shelf region, particularly on the southeastern side near the Alaska Peninsula, has sustained large catches of both shellfish and finfish (HOOD, 1983). Previous to PROBES studies only sporadic nutrient analyses (McROY *et al.*, 1972; McROY and GOERING, 1974) had been described for this area and except near ice edges only a few indications of the magnitude of the phytoplankton bloom had been described. A series of cruises predominately in the spring and summer over a 5-year period produced nearly 50 transects across the shelf at standard locations for a total of about 1000 stations (Fig. 1), several 48-h time series stations, and a few sections along the shelf. This large set of data collected with the same methods allows for a range of interpretation of nutrient supply and variability on time scales of hours to years.

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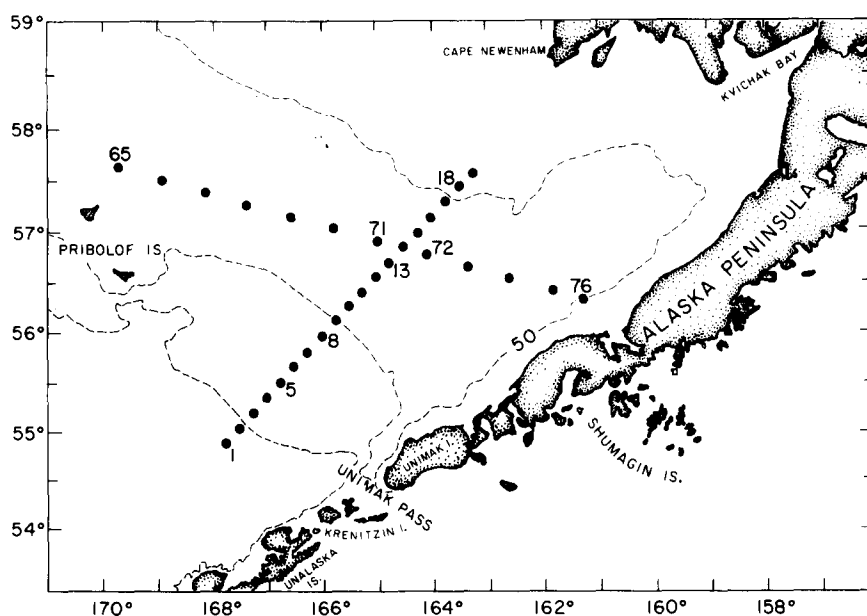


Fig. 1. PROBES across-shelf main line and 70 m along-isobath transects.

METHODS

Cruises were taken in each of the years from 1977 to 1981 and minor field program in 1982. The cruises usually commenced in early to mid-April and finished in late June or July. Additional samples were analyzed from ships of opportunity to complete the seasonal cycle for two of the years. Most of the analyses were run aboard ship immediately to maintain high quality data and to have the values available in real time. Only samples from ships of opportunity were frozen for later analysis in the laboratory. Comparison analysis for nitrate and ammonium showed that the difference between fresh and frozen samples was <10%. The water samples were normally collected in association with temperature and salinity measurements by a CTD/rosette system. Within a short time (~1 h) the chemical analyses were completed on a Technicon AutoAnalyzer II system with manifolds of our design (Whitledge *et al.*, 1981). The basic analytical methods were described by Armstrong *et al.* (1967) for nitrate. Ammonium was measured by the phenolphthorite method of Koroleff (1970) as adapted to the AutoAnalyzer by Slawyk and MacIsaac (1972) and modified by Patton and Crouch (1977). The data analysis system was computer-controlled using a Hewlett-Packard model 9845 which provided an enhanced sample analysis rate that could continue daily for 3 to 4 months thereby providing means for obtaining large amounts of reliable data on long cruises. Chlorophyll concentrations were measured *in vitro* with a Turner Designs model 10-005 R fluorometer using the method of Yentsch and Menzel (1963).

Samples for benthic nutrient studies were either collected with a four-barrel corer (Pamatmat, 1971) or box corer. The nutrient release studies were performed by storing the cores in a refrigerator at 4°C and drawing samples for analysis from the water above the cores at 4-h intervals for 3 to 4 days.

RESULTS

The annual cycle of nitrogen concentrations across the shelf

Like other continental shelf areas (WALSH *et al.*, 1985) there is a significant annual variation in the inorganic nitrogen concentrations in the southeastern Bering Sea. During times of low phytoplankton uptake of nutrients in the winter when incident radiation is small and the water column is mixed homogeneously, the inorganic nitrogen concentrations are a maximum (15 to 30 $\mu\text{g-at. l}^{-1}$). The spring phytoplankton bloom decreases these values to minimum levels during late spring and early summer.

A series of eight across-shelf transects on the PROBES main line (Fig. 1) made from summer 1979 to summer 1980 illustrates the transition of an inorganic nitrogen impoverished upper mixed layer for the outer 400 km of the shelf in late summer, a winter enrichment, and a decline during the spring bloom (Fig. 2). Each of the 5 years had the same general pattern of increase and decrease throughout the months; however, there were some interesting interannual differences attributable to wind that are discussed in a later section. To better understand the enrichment and depletion processes occurring along this standard across-shelf transect, three station locations at 50, 75, and 130 m depths (Stas 18, 13, and 5, respectively) were chosen to represent the three basic shelf domains crossed by this section, coastal ($H < 50$ m), central ($50 < H < 100$ m) and outer ($100 < H < \text{shelf break}$) (COACHMAN, 1982; KINDER and SCHUMACHER, 1981; IVERSON *et al.*, 1979a, b). The low nitrate concentrations in August extended down to 25 m where it was separated from the deeper source water by the pycnocline. The nitrate was undetectable in the upper 20 m at many of the stations (Fig. 2) and integrated concentrations of $< 20 \text{ mg-at. m}^{-2}$ in the upper 40 m were common. These concentrations represented the low values after spring productivity had utilized nearly all the nitrate from the water column before replenishment had occurred. The nitrate concentrations began to increase during the autumn at a slow and nearly linear rate (Fig. 3). By the end of October, the nitrate had increased at all locations by 5 to 30 $\mu\text{g-at. l}^{-1}$ (Fig. 2) with the largest changes occurring at the offshore end of the transect.

At the end of the winter season in February and March, the outer domain nitrate concentrations remained constant but the mid-shelf values continued to increase. The maximum winter values in the upper 40 m of water column varied from about 900 to 700 $\text{mg-at. NO}_3\text{-N m}^{-2}$. These yearly differences were not clearly associated with warm or cold year variations. For example, the maximum nitrate concentrations for the cold year 1980 were the same as the warmer year 1979 at Stas 5 and 13 (Fig. 3).

As spring approached in mid-April nitrate losses were observed in the upper water column, especially in the inner and central domain regions. The trend continued in late April and by late May the nitrate was depleted in the euphotic zone of the inner and middle shelf areas. The rapid decline of nitrate concentration during the spring bloom occurred in the month of May for the shelf stations. Very little difference was noted for the time of the start of the spring bloom at the 50 and 75 m stations (Fig. 3). When the integrated nitrate concentrations were compared for the years 1977 to 1981, only the shelf-break station at 130 m and those farther offshore appeared to have a lag of 1 to 3 weeks for the initiation of the bloom. These middle shelf observations are quantitatively similar to seasonal variations of nitrate concentrations in the Middle Atlantic Bight off Long Island where the shelf was not as wide and the winter concentrations were about 5 rather than 15 to 20 $\mu\text{g-at. l}^{-1}$ (WALSH *et al.*, 1985). The first large depression of $p\text{CO}_2$ values were noted on 11 April in 1980 and 22 April in 1981 (CODISPOTI

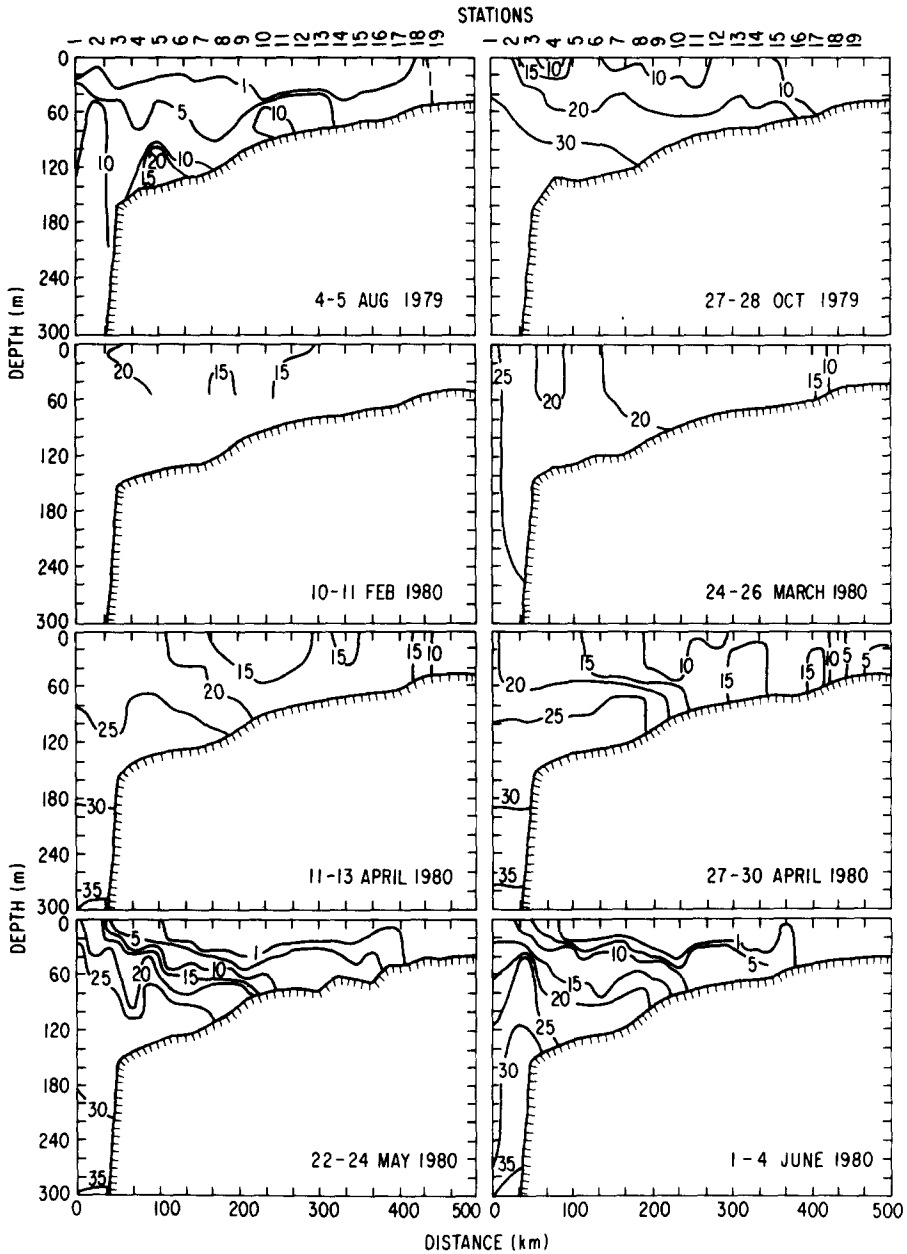


Fig. 2. Across-shelf distribution of nitrate ($\mu\text{g-at. l}^{-1}$) collected on the PROBES main line (Stas 1 to 24) over a 1-year period.

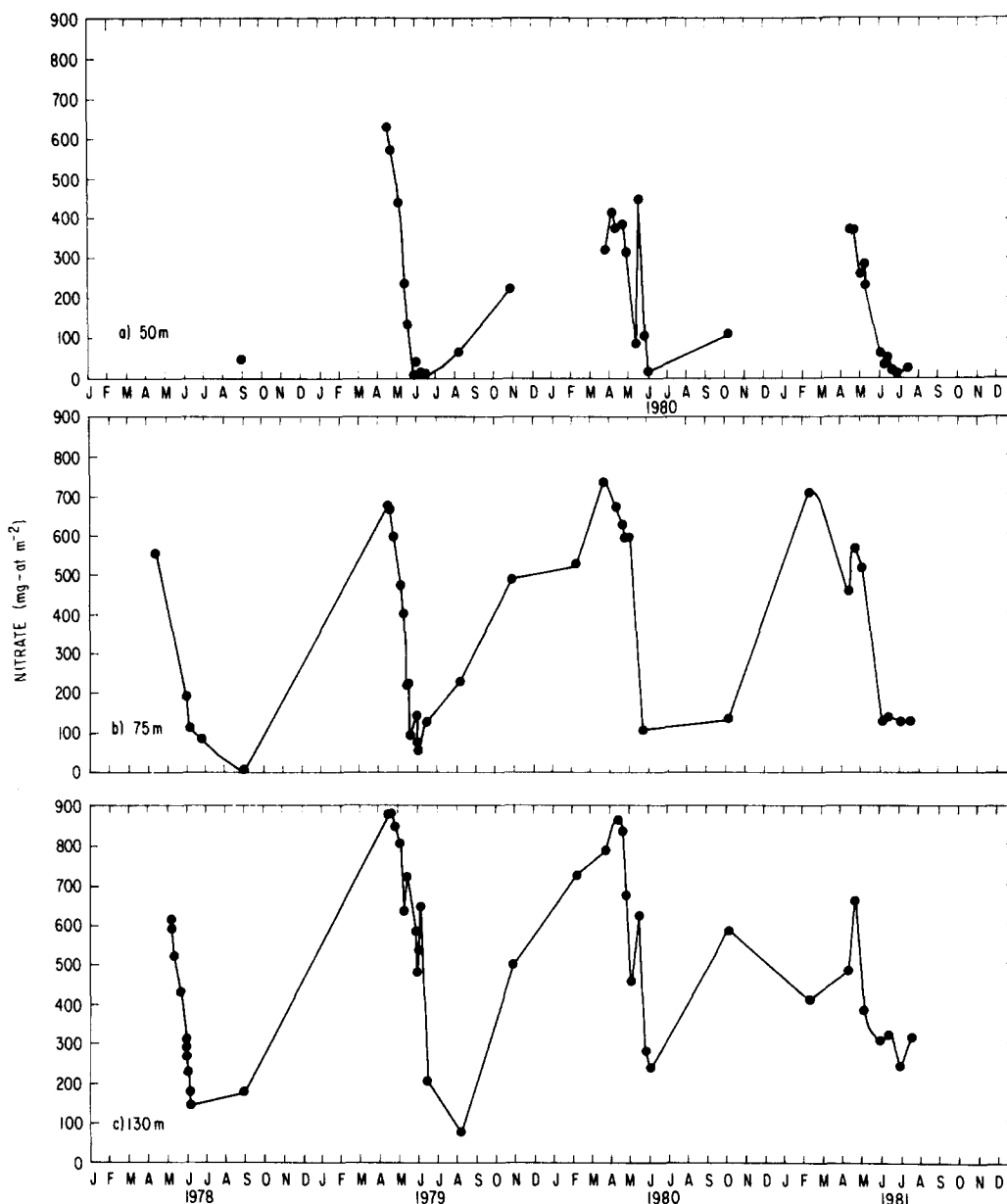


Fig. 3. Nitrate concentrations (mg-at. m⁻²) over the upper 40 m of the water for Stas 5 (130 m), 13 (15 m), and 18 (50 m) on the PROBES main line.

et al., 1986) which corresponds to the initial decline of nitrate concentrations; however, the maximal rates of nitrate loss were not observed until May.

The early summer conditions were established in June with a further offshore movement of depleted nitrate in the upper water column to the shelf break; however, 10 to 15 $\mu\text{g-at. l}^{-1}$ was still present at Sta. 1 on the offshore end of the transect. The nitrate in the offshore area was subsequently utilized during June and July.

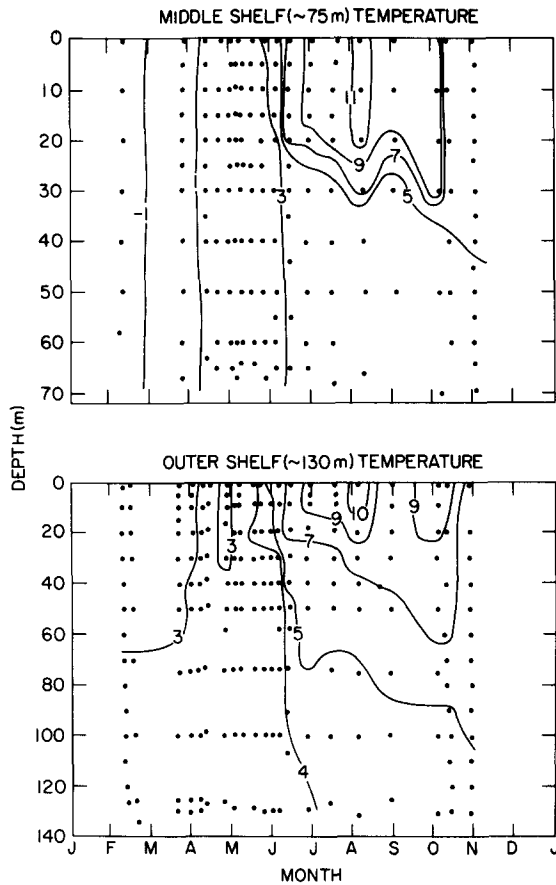


Fig. 4. Seasonal distribution of temperature ($^{\circ}\text{C}$) for PROBES main line Sta. 13 in the middle shelf domain (18 stations) and Sta. 5 in the outer shelf domain (26 stations) for the years 1979 to 1981.

The annual cycle was examined further by combining temperature, nitrate, chlorophyll, and ammonium data from the years 1978 to 1981 into vertical time series (Figs 4 to 7). The temperature of the middle shelf at PROBES main line Sta. 13 on the 75 m isobath in January was colder than -1°C and the entire 75 m water column was isothermal (Fig. 4). As the water column warmed in the months of February and March the nitrate concentrations (Fig. 5) continued to increase until the spring bloom commenced as shown by the rapidly increasing chlorophyll concentrations in May (Fig. 6). When the pycnocline was established at the beginning of June the nitrate concentrations had been depleted to $<1 \mu\text{g-at. l}^{-1}$ and the chlorophyll concentrations declined to $<1 \mu\text{g l}^{-1}$. The strong pycnocline effectively isolated the euphotic zone from the abundant nitrate concentrations below the pycnocline depth. At the beginning of June, the ammonium concentrations in the lower layer increased markedly probably as a result of degradation of the phytoplankton from the large spring bloom (Fig. 7). As the summer progressed, ammonium concentrations remained very high until the autumn cooling and mixing events occurred. The nitrate concentrations started to increase in the water column and finally reached maximum levels in the following winter (Fig. 5).

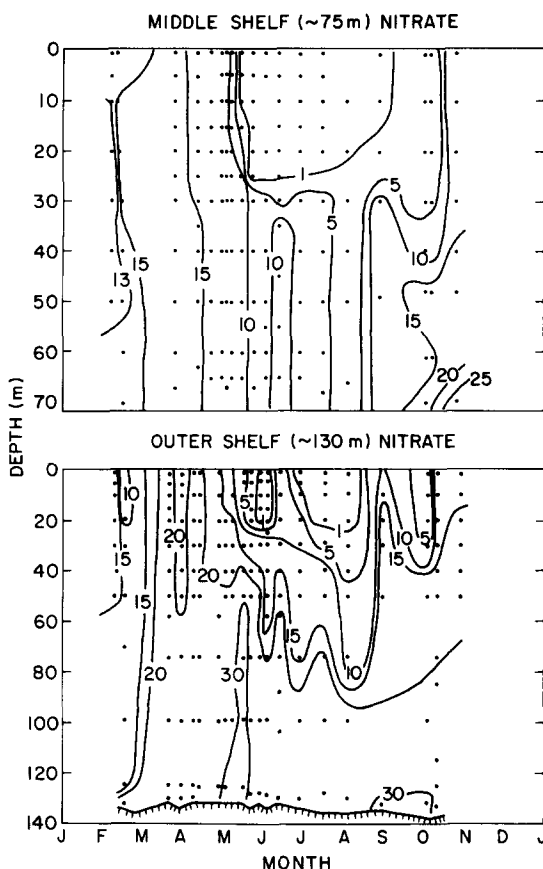


Fig. 5. Seasonal distribution of nitrate concentrations ($\mu\text{g-at. l}^{-1}$) for PROBES main line Sta. 13 in the middle shelf domain (19 stations) and Sta. 5 in the outer shelf domain (26 stations) for the years 1979 to 1981.

Station 5 on the PROBES main line in the outer domain at the 130 m isobath proceeded through a similar cycle as the middle shelf station with some interesting differences. The temperature in late winter was 4°C warmer in the upper layer and 5°C warmer below 75 m (Fig. 4). The spring warming commenced at about the same time but the pycnocline was not as strong since the 4°C temperature gradient was spread vertically over 50 m rather than 10 m. This allowed the nitrate concentrations to decrease in the upper layer more slowly because of the extra vertical flux associated with a weaker pycnocline (Fig. 5). The chlorophyll concentrations were only 50% as large as the middle shelf as a result of the weak stability (Fig. 6). The upper surface layer of the outer domain in the summer was depleted of nitrate for only 6 weeks compared to the 16 weeks in the middle domain. As the nitrate concentrations increased in September and October, chlorophyll also increased in response. The ammonium observed on the outer shelf at mid-depth reached concentrations as high as $5 \mu\text{g-at. l}^{-1}$ (Fig. 7) for about a month during May and June. Profiling current meter data show some offshore flow at mid-depth from the middle shelf (COACHMAN, personal communication), which suggests the observed ammonium had a source in the middle domain. In any event, the

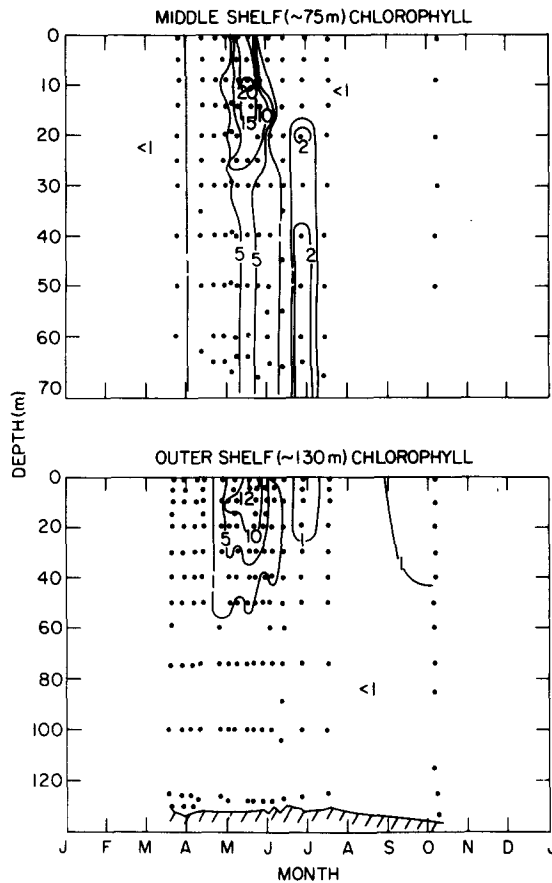


Fig. 6. Seasonal distribution of chlorophyll ($\mu\text{g l}^{-1}$) for PROBES main line Sta. 13 in the middle shelf domain (13 stations) and Sta. 5 in the outer shelf domain (20 stations) for the years 1979 to 1981.

zooplankton excretion in the outer domain was found to be capable of producing only 20% of the quantity of ammonium observed (DAGG *et al.*, 1982). The lack of ammonium production near the bottom on the outer shelf was initially perplexing; however, later budgets indicated that phytoplankton were eventually advected from the outer shelf to deeper regions on the upper slope (WALSH and McROY, 1986) so there is a smaller quantity of phytoplankton material available for remineralization than on the middle shelf.

Station 1 at the offshore end of the PROBES main transect in 1500 m of water produced no spring bloom in April or May but chlorophyll concentrations increased for a brief period in late June and July. The relatively low salinity water (32.37‰) suggests that shelf water [see COACHMAN (1986) for details of salinity distribution] was moved offshore in the surface layer. No chlorophyll concentrations larger than $2.5 \mu\text{g l}^{-1}$ were observed in water with salinities of 33.0‰ or higher. The nitrate concentration became $<5 \mu\text{g-at. l}^{-1}$ at the end of June and continued low until the salinity increased in late August. Thus, it appears that the deep-water outer stations of the PROBES transect had characteristics of the shelf break for periods of time when shelf water moved offshore. However, the majority of time chlorophyll concentrations

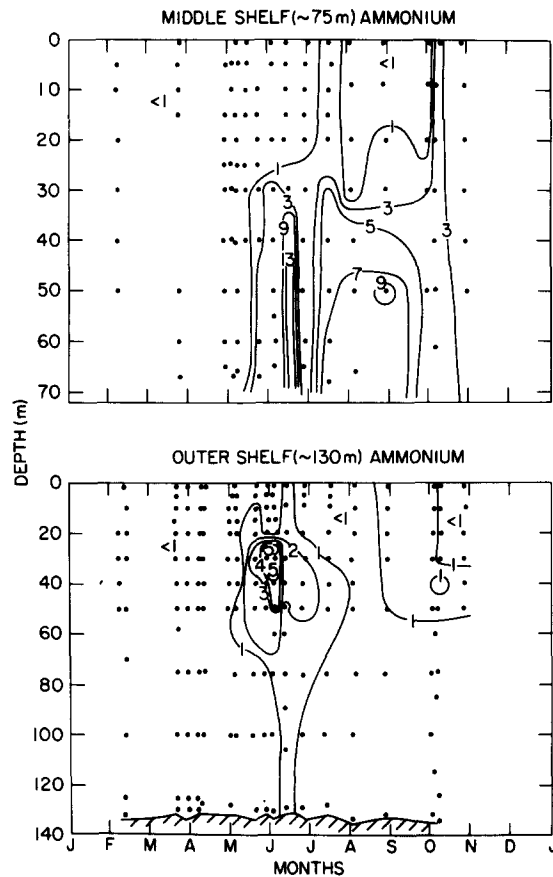


Fig. 7. Seasonal distribution of ammonium concentrations ($\mu\text{g-at. l}^{-1}$) for PROBES main line Sta. 13 in the middle shelf domain (18 stations) and Sta. 5 in the outer shelf domain (26 stations) for the years 1979 to 1981.

were $<2 \mu\text{g l}^{-1}$ and the nitrate about $10 \mu\text{g-at. l}^{-1}$. The oceanic character of the outer station was very much like observations at Sta. P in the North Pacific. The lack of a bloom in waters with salinities above 33‰ was probably related to the lack of a strong pycnocline and/or the presence of plentiful grazers. There were adequate nutrients and light for primary production to occur and the lack of it must have been due to other causes.

The seasonal difference in properties at specific stations on the PROBES main transect for the year 1981 are shown in Fig. 8. The spring–summer nutrient and chlorophyll content at each of six stations across the shelf show relatively high nutrient concentrations in the upper 40 m especially at the offshore location (Sta. 1) where nitrate concentrations were nearly double those of the central (Stas 10 and 16) and inner domain (Sta. 19). The chlorophyll content offshore was not as high as inshore, probably as a result of higher zooplankton grazing rates (DAGG *et al.*, 1982). The timing of the chlorophyll increase which started in mid-April was nearly simultaneous in the outer half of the transect. The inshore portion had a chlorophyll peak in early May and the concentrations were as high as 400 mg m^{-2} in the upper 40 m of the water column. Analysis of (1) surface temperatures, (2) the absolute

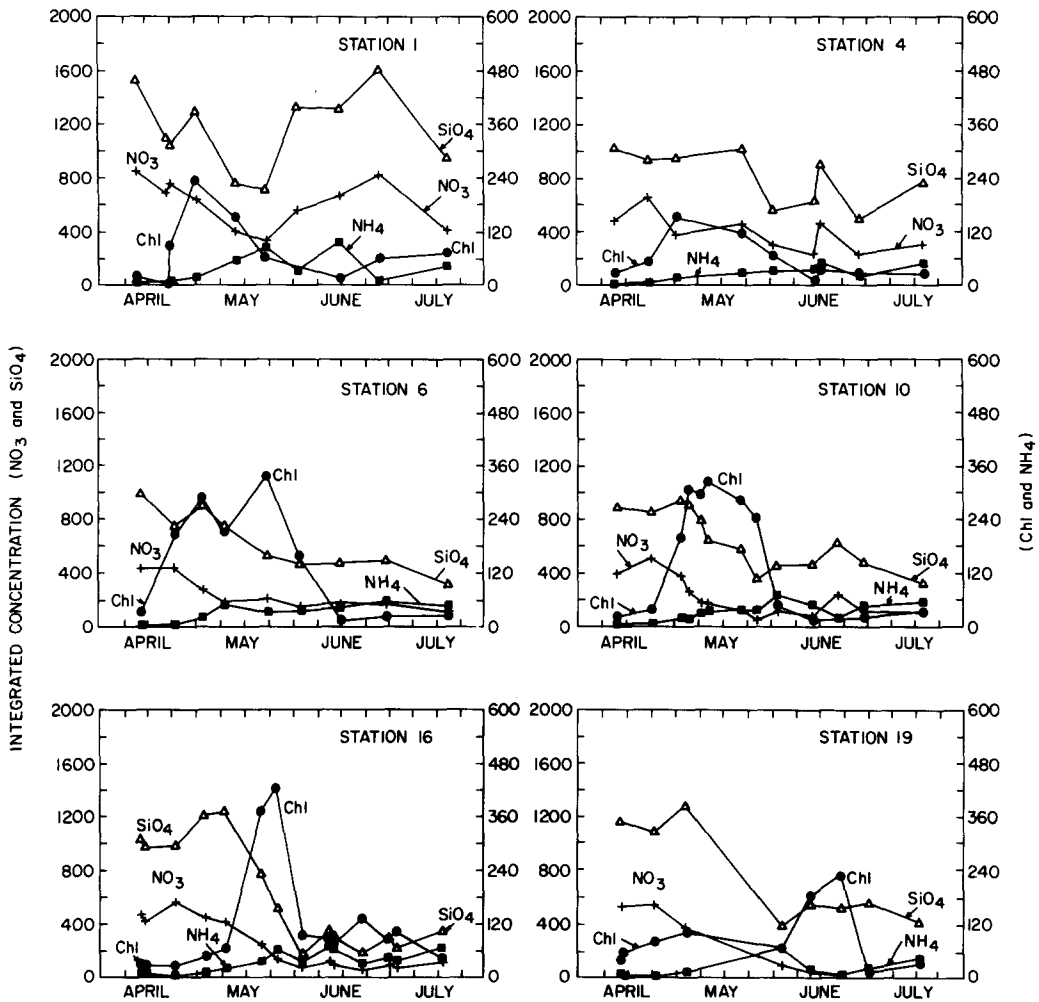


Fig. 8. Seasonal concentrations of nitrate, ammonium, silicate (mg-at. m^{-2}) and chlorophyll (mg m^{-2}) over the upper 40 m for six stations with water depths of 1500 (Sta. 1), 138 (Sta. 4), 126 (Sta. 6), 90 (Sta. 10), 65 (Sta. 16) and 45 m (Sta. 19), respectively, on the PROBES main line in 1981.

difference in σ_t at the surface and 40 m, and (3) the thermocline depth indicated that all three parameters could be used to identify a change in the water density properties that would allow a bloom to occur (Fig. 9). The difference in σ_t between the surface and 40 m was the most informative of the three parameters as evidenced by a striking change in this property just before chlorophyll concentrations increased. The bloom was most likely triggered by heating of the water column forming a stable upper mixed layer since salinity changes were probably not large enough to influence σ_t .

The silicate concentrations in the water column generally followed the trend of nitrate but the amount of silicate was double the nitrate concentrations in almost all observations at the six station locations (Fig. 8) indicating there was probably sufficient silicate to adequately support diatom growth. The silicate concentrations at Sta. 1 were highest and displayed the

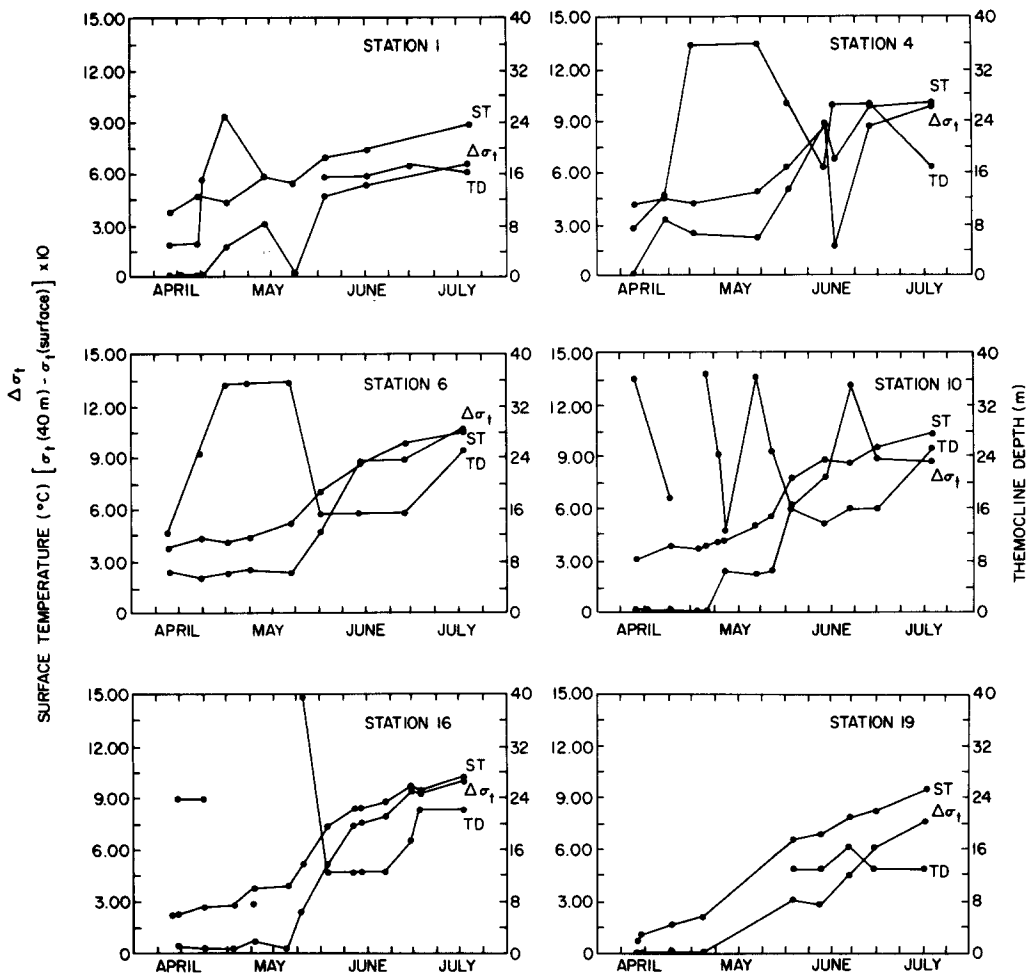


Fig. 9. Surface temperature (ST), thermocline depth (TD) and the change of σ_t between the surface and 40 m for six stations on the PROBES main line in 1981.

largest variation during the 4-month observation period. The chlorophyll concentration rapidly increased during the bloom period but later decreased during replenishment of nitrate and silicate in mid-May following a wind event. Stations 6 and 10 had a relatively uniform decline in silicate concentrations during the period of observation. Station 16 in the central domain had a rapid loss of silicate in the upper 40 m that coincided with a large increase in chlorophyll concentration probably resulting from diatom growth.

Ammonium concentrations in the across-shelf transects reached as high as $150 \text{ mg-at. m}^{-2}$ in the upper 40 m; however, the highest concentration most years was observed near the bottom (Fig. 10). The ammonium concentrations were very small when the spring phytoplankton bloom was initiated in April; however, the observed concentrations were large during June. In each of 4 years the across-shelf transect in the middle shelf region between Stas 11 and 17 contained more than $5 \mu\text{g-at. l}^{-1}$ of ammonium in a bottom layer that was often vertically dispersed over the entire layer below the pycnocline. The relative distribution

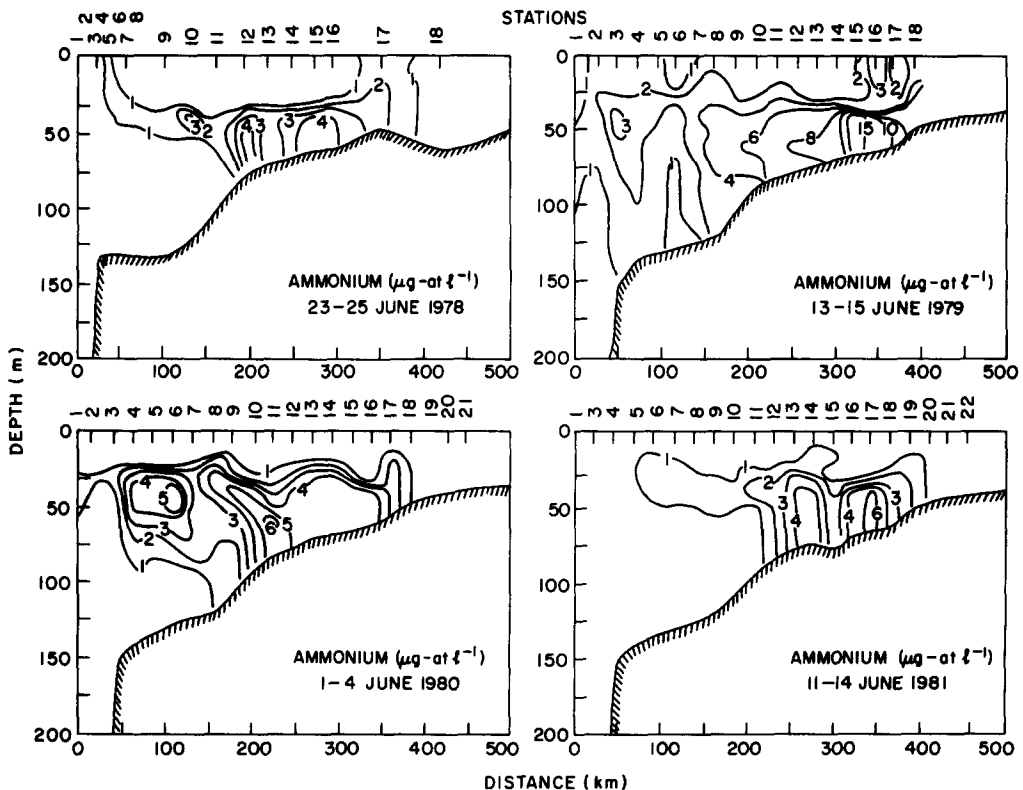


Fig. 10. Ammonium concentrations ($\mu\text{g-at. l}^{-1}$) observed on the PROBES main line in June of four successive years.

of urea measured in 1981 coincided with ammonium. Elevated values of urea-N ($>0.5 \mu\text{g-at. l}^{-1}$) were found at Stas 15 to 19. This would support the suggestion of HATTORI and GOERING (1981) and SAINO *et al.* (1983) that shellfish populations in the middle shelf domain are contributing to the ammonium produced in the bottom layer. A maximum ammonium concentration of $>15 \mu\text{g-at. l}^{-1}$ was observed in mid-June 1979 at Stas 14 to 16 which followed an especially intense phytoplankton bloom that was triggered by vigorous wind mixing in late April. A subsequent period of weak winds in the following 2 weeks (Fig. 11) established a stable upper layer in which the phytoplankton bloomed and sank.

The ammonium observed in the outer shelf domain at mid-depth had no apparent source in the near-bottom layer. Attempts to attribute this offshore ammonium maximum to zooplankton regeneration processes (VIDAL and WHITLEDGE, 1982) were unsuccessful because their biomass was so small (DAGG *et al.*, 1982). Later observations of 'tongue-like' distributions of ammonium in the mid-depths of the outer domain showed that they were associated with the finestructure ubiquitous to the outer shelf (COACHMAN, personal communication). The resulting layers or parcels of water contain significant admixtures of neutral shelf bottom layer water with high ammonium. The finestructure layers are formed in the middle front and slowly work their way seaward across the outer domain (COACHMAN and CHARNELL, 1979).

The ammonium production rate in the bottom layer was estimated in each of 3 years 1979 to 1981 at the center of maximum concentrations on the middle shelf. The concentrations at

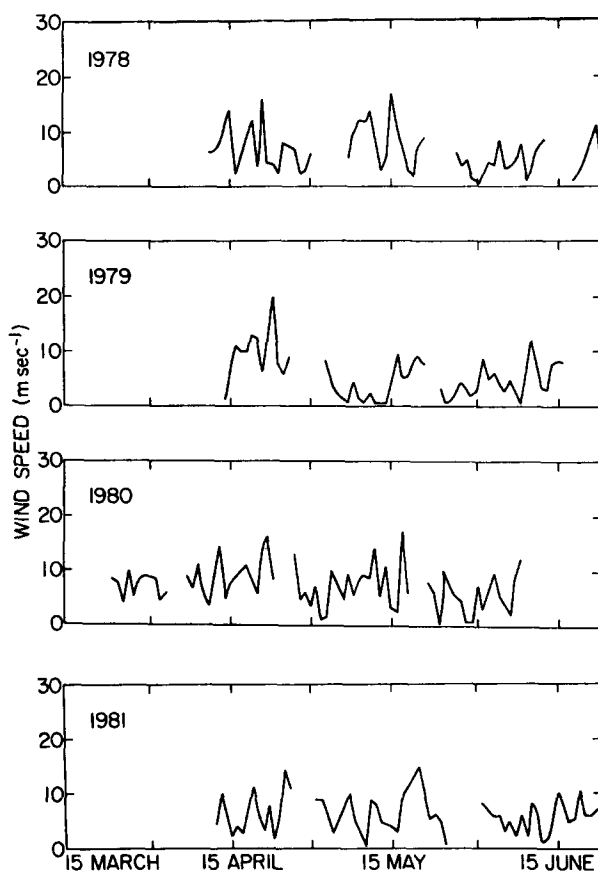


Fig. 11. Shipboard winds collected during PROBES cruises during sampling in the spring of 4 years.

the sampling depths from the pycnocline to the bottom were integrated over the time period when the apparent maximum ammonium production occurred. The years 1980 and 1981 had ammonium produced at 2.0 to 9.3 $\text{mg-at. m}^{-2} \text{d}^{-1}$ over nearly a 2-week period at the three stations with mean values of 4.7 and 8.4 $\text{mg-at. m}^{-2} \text{d}^{-1}$ (Table 1). The year 1979 had a similar ammonium evolution rate of 7.2 to 9.4 and a mean of 8.5 $\text{mg-at. m}^{-2} \text{d}^{-1}$ but it occurred over 30 days or more, nearly three times longer than 1980 and twice as long as 1981. The daily amount of nitrogen produced as ammonium was the same in 1979 and 1981 but the year 1979 produced 3.57 g nitrogen m^{-2} over the 30-day period while only 1.53 g nitrogen m^{-2} was produced in the 13-day period in 1981. The nitrogen recycled in 1980 was the lowest value, 0.72 g m^{-2} , over the 11-day period. The observed concentrations (Fig. 10) were nearly the same in 1980 and 1981 indicating that the whole production period may not have been adequately sampled. There was an increase of 25 ppm of surface $p\text{CO}_2$ concentrations during the 11-day period in 1980 (CODISPOTI *et al.*, 1982). In addition, organic carbon consumption rates in the water column estimated from the inorganic carbon system measurements after the maximum bloom period ranged from 2.4 gC $\text{m}^{-2} \text{d}^{-1}$ in 1980 to 1.2 gC $\text{m}^{-2} \text{d}^{-1}$ in 1981 (CODISPOTI *et al.*, 1985). The authors believed that the low rate in 1981 was the result of

Table 1. Ammonium production below upper mixed layer* middle shelf

Sta.	Ammonium evolved (mg-at. m ⁻² d ⁻¹)				Nitrogen		Carbon*†	
	13	14	15	\bar{X}	(gN m ⁻² d ⁻¹)	(gN m ⁻²)	(gC m ⁻² d ⁻¹)	(gC m ⁻²)
1979 (30 days) 14 May–14 June	8.9	7.2	9.4	8.5	0.12	3.57	0.51	15.3
1980 (11 days) 23 May–3 June	8.3	2.0	3.9	4.7	0.07	0.72	0.30	3.1
1981 (13 days) 21 May–2 June	8.8	9.3	7.1	8.4	0.12	1.53	0.51	6.56
Mean	8.7	6.2	6.8	7.2	0.10	1.94	0.44	8.32

*Mixed layer depth was designated as the depth at which σ_t was 0.02 > surface σ_t .

† Conversions from nitrogen to carbon were made on the basis of a C : N of 5 (by atoms) (BANSE, 1974; WALSH and McROY, 1986).

incomplete degradation or export of the organic carbon by the date the last sample was collected.

If a value of 5 is used for the C:N ratio (by atoms) for phytoplankton material (WALSH and McROY, 1986) the carbon that was released or incorporated into new tissue (e.g. bacteria) was 15.3, 3.1, and 6.6 gC m⁻², respectively for 1979 to 1981. The actual C:N (by atoms) had a mean value of about 7.5 for the years 1980 and 1981 (R. IVERSON, personal communication), however the detrital component is probably significant. This is supported by phytoplankton experiments run by STRICKLAND *et al.* (1969) where a C:N (by atoms) of 5.25 was measured. Further analysis of several sets of C:N data by BANSE (1974) concluded that it is difficult to estimate the C:N ratio for natural phytoplankton samples even if the analytical results are rigorously evaluated. So the more typical C:N of 5 was used for the phytoplankton decomposition and uptake calculations.

An additional concern about the large quantities of ammonium (Fig. 6) on the middle shelf is the possibility of nitrification being important in producing some of the nitrate that appeared near the bottom (Fig. 4) as ammonium decreased. No direct measurements of nitrification were made; however, an estimate of nitrate appearance over a 60-day period on the PROBES line was about 0.12 µg-at. l⁻¹ d⁻¹ at the 75 m middle shelf station where ammonium decreased at 0.10 µg-at. l⁻¹ d⁻¹. While these are only estimates from the water column concentrations, they are only about twice as large as oceanic waters of the western North Pacific (MIYAZAKI *et al.*, 1975) where the ambient ammonium concentrations are much smaller.

Cross-shelf transport

The outer shelf of the Bering Sea has been characterized as a region which receives nutrient enrichment by cross-shelf diffusion driven by the tides (COACHMAN and WALSH, 1981) and a model was constructed for the fluxes during the spring bloom. The observations based on a salt balance were found to apply to nitrate enrichments as confirmed by uptake rates of nitrogen by the biota. The strong vertical stratification of the pycnocline hindered the vertical flux of nutrients into the euphotic zone (Fig. 4) and the frontal areas in the Bering Sea

provided a horizontal hindrance to the advection of nutrients from offshore (Fig. 2). The seasonal observations of nitrate indicated that the concentrations increased slowly from autumn until early spring in a nearly linear fashion for both the middle and outer domains (Fig. 3). The most vivid example was observed from March 1979 until June 1980 which showed a general offshore gradient of nutrient concentrations throughout the entire year and the winter replenishment rate at the 50 m isobath appeared to lag those on the outer shelf. If advective processes were responsible for the over-winter enrichment of the shelf by net onshore transport, the observations would likely be more episodic and keyed to wind events. It is apparent that a rapid flushing of shelf water did not occur as a single event. An alternate mechanism for the shelf nutrient replenishment in the upper layer could result from a steady erosion of the bottom layer by vertical wind mixing, resulting in the mixed surface layer increasing in nutrient concentration. Vertical stratification remained, however, until the middle of October when nitrate concentrations reached nearly 50% of their winter maximum.

The rate of nitrate increase, calculated for PROBES main line Stas 5, 8, 13, and 18 using the integrated values in Fig. 3 for the period of August 1979 to March 1980, respectively, was 0.08, 0.06, 0.07, and 0.03 $\mu\text{g-at. l}^{-1} \text{d}^{-1}$. The values for the central and outer domains were similar but the inner domain was <50% of the others. The values calculated by COACHMAN and WALSH (1981) over a smaller lateral distance (50 km) in April and May ranged from 0.05 to 0.69 $\mu\text{g-at. l}^{-1} \text{d}^{-1}$ for the upper layer of 30 m. The calculated values for winter enrichment were smaller because the concentration gradient was relatively small and the distance large. The biological uptake rates calculated by COACHMAN and WALSH (1981) ranged from 0.42 to 0.81 $\mu\text{g-at. l}^{-1} \text{d}^{-1}$. When the spring bloom commenced in May the uptake rates could overtake the resupply by diffusion in about 24 days since the uptake rates were as high as 10 times the resupply rate and was clearly demonstrated in the changes in the ambient nitrate concentrations in the upper water column (Fig. 3).

Flux calculations made for October 1979, February 1980, and March 1980 in the middle domain (Fig. 2) using the observed gradients across the shelf and an estimated horizontal eddy diffusion coefficient of $10^7 \text{ cm}^2 \text{ s}^{-1}$ gave results of 53, 24, and 33 $\mu\text{g-at. cm}^{-1} \text{ s}^{-1}$ with a mean value of 37 $\mu\text{g-at. cm}^{-1} \text{ s}^{-1}$. The values of Coachman and Walsh ranged from 16 to 72 $\mu\text{g-at. cm}^{-1} \text{ s}^{-1}$ in the different months (April to June) and had a mean value of 34 $\mu\text{g-at. NO}_3^- \text{ cm}^{-1} \text{ s}^{-1}$. The flux rates calculated here would result in an actual accumulation rate over the middle shelf of 0.076 $\mu\text{g-at. l}^{-1} \text{d}^{-1}$ or 18.2 $\mu\text{g-at. l}^{-1}$ over an 8-month period of August to March. The horizontal eddy diffusion coefficient of $10^7 \text{ cm}^2 \text{ d}^{-1}$ which COACHMAN and WALSH (1981) used in the analysis of spring data in the outer domain represented a long-term mean which combined the effect of both advection and diffusion having an equivalent velocity of 10 cm s^{-1} . This combined coefficient representing steady diffusion and sporadic advection produced concentrations that approximated the actual accumulation rate (COACHMAN and WALSH, 1981). Sub-tidal flows have been measured to be $<1 \text{ cm s}^{-1}$ in the central shelf and $<5 \text{ cm s}^{-1}$ on the outer shelf (KINDER and SCHUMACHER, 1981; COACHMAN, 1982; SCHUMACHER and KINDER, 1985). Other studies, especially those across Fladen Ground in the North Sea, used an eddy coefficient as high as $2 \times 10^7 \text{ cm}^2 \text{ s}^{-1}$ (STEELE, 1956) and nutrient flux calculations of Riley (1967) were as high as $3 \times 10^6 \text{ cm}^2 \text{ s}^{-1}$ across the northeast United States shelf break off Long Island. The horizontal eddy diffusion coefficient used in these calculations may best match the apparent flux of nutrients across the shelf during the winter when the fronts are weak.

The mean value of the observed nitrate flux rate over the upper 40 m of the water column for the period August 1979 to March 1980 (Fig. 3) was 0.07 $\mu\text{g-at. l}^{-1} \text{d}^{-1}$ and was compar-

able to the calculated accumulation rate of $0.076 \mu\text{g-at. l}^{-1} \text{d}^{-1}$ from diffusion for the same 8-month duration. Both of these estimates were similar to $0.08 \mu\text{g-at. l}^{-1} \text{d}^{-1}$ that had been previously estimated (HATTORI and WADA, 1974) for the same region in the summer for the whole shelf and were smaller than the May 1976 to 1979 value of $0.41 \mu\text{g-at. l}^{-1} \text{d}^{-1}$ of COACHMAN and WALSH (1981) on the outer shelf probably as a result of the weaker winter gradients.

Comparable estimates of the diffusive flux over the New York shelf were $3 \mu\text{g-at. cm}^{-1} \text{s}^{-1}$ over the winter season. This rate would accumulate nitrate over the shelf at $0.017 \mu\text{g-at. l}^{-1} \text{d}^{-1}$ or $3 \mu\text{g-at. l}^{-1}$ over the 6-month enrichment period. The observed enrichment rates from autumn mixing until the spring bloom are about 3 to $4 \mu\text{g-at. l}^{-1}$ of nitrate and are equivalent to the rates calculated by MALONE *et al.* (1983).

Microstructure and vertical diffusion

The outer shelf region of the southeastern Bering Sea has been characterized as a region having vertical finestructure in the temperature and salinity fields (COACHMAN and CHARNELL, 1977, 1979). It was subsequently proposed that the relatively greater large-scale vertical eddy coefficients ($5 \text{ cm}^{-2} \text{ s}^{-1}$) in the outer domain are probably due to finestructure shearing of the property fields (COACHMAN and WALSH, 1981). The finestructure in nutrient profiles was apparent during the summer season when closely spaced samples were analyzed for nutrient content, especially ammonium (Fig. 12). The nitrogen with an offshore source (nitrate) had finestructure properties that could be matched with temperature variations in the interleaving water masses. The most apparent example of nutrient finestructure occurred with ammonium which had a primary source from decomposition processes inshore and displayed vertical gradients of about $2 \mu\text{g-at. ammonium-N l}^{-1}$ difference over a 1 to 2 m thick layer.

An estimate of the possible nitrogen contribution to the mixed layer euphotic zone was made using a vertical eddy coefficient for finestructure scale of $10^{-2} \text{ cm}^2 \text{ s}^{-1}$ which has been proposed in previous salt balance and oxygen depletion studies (COACHMAN and CHARNELL, 1979; COACHMAN and WALSH, 1981; FALKOWSKI *et al.*, 1980). With a difference of $2 \mu\text{g-at. l}^{-1}$ of ammonia over a 1 m thick layer, the flux was calculated to be $2 \times 10^{-6} \mu\text{g-at. cm}^{-1} \text{ s}^{-1}$ which would lead to an accumulation rate of $0.17 \mu\text{g-at. l}^{-1} \text{d}^{-1}$. So with the variation in gradients and thickness of the layers an accumulation of 0.08 to $0.34 \mu\text{g-at. l}^{-1} \text{d}^{-1}$ would be reasonable for a possible contribution of ammonium during the summer. The nitrate would be similar since gradients were from 1 to $2 \mu\text{g-at. l}^{-1}$ over the thickness of the layers. The areal extent of the interleaving layers is on the order of 100 to 150 km wide (COACHMAN and CHARNELL, 1979) and seaward of the middle front. Recent unpublished results indicated that the interleaving layers detached with the oscillating tides and produced lenses that were on the order of 20 km diameter (COACHMAN, personal communication). These areas of microstructure probably represent no more than 5 to 10% of the shelf area but they could effectively increase the vertical nitrogen flux in the outer shelf domain from 0.2 to $0.6 \mu\text{g-at. l}^{-1} \text{d}^{-1}$ during the critical summer months.

Along domain variations

To complement the numerous across-shelf transects and to determine the lateral extent of the middle shelf properties, i.e. (1) depleted nitrate in the surface layer, (2) large subsurface and near-bottom chlorophyll concentrations and (3) high ammonium concentrations in the bottom mixed layer, 500 km isobathic transects (Stas 65 to 76) at 70 m (Fig. 1) were taken in 1980 and 1981. In 1980 the nitrate was depleted in the surface layer and the Aleutian end of

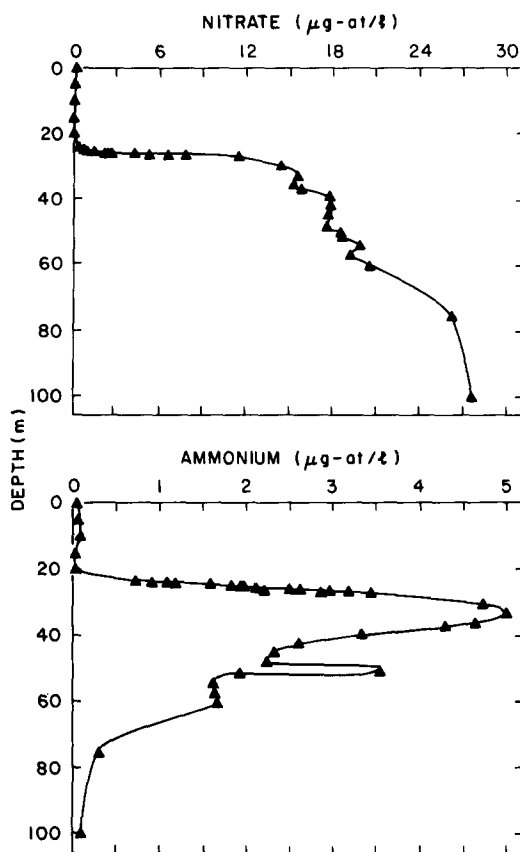


Fig. 12. The finescale vertical distribution of nitrate and ammonium ($\mu\text{g-at. l}^{-1}$) observed with 36 samples on Sta. 5 of the PROBES main line in the outer shelf domain.

the transect was typical of middle domain water which was vertically homogeneous and contained reduced nitrate concentrations (Fig. 13). The chlorophyll concentrations were distributed heterogeneously with concentration maxima in the surface, mid-depth and at the bottom at differing locations along the transect. Likewise the ammonium produced by decomposition processes in the bottom layer was distributed inversely to nitrate and ranged from 0.4 to 5.1 $\mu\text{g-at. l}^{-1}$ going from west to east on the transect.

In the following year, 1981, the general trends along the transect were similar to 1980 but the gradients of properties were not as strong, a possible effect of sampling in July rather than May. In addition, the 10 $\mu\text{g-at. l}^{-1}$ isopleths of nitrate, the ammonium maximum, and both chlorophyll maxima were displaced to the northwest in 1981 compared to 1980. The currents on the shelf in this region are reported to be $<1 \text{ cm s}^{-1}$ (SCHUMACHER and KINDER, 1985) and it has been noted in the period of April to June that the bottom water temperature interface shifts northward (TAKENOUTI and OHTANI, 1974). Apparent temperature differences along the 70 m isobath are complicated by the colder bottom water formation of 1980 ($\sim 2^\circ\text{C}$) than in 1981 ($\sim 4^\circ\text{C}$). The most important aspect of these alongshore variations may be to alert those making budget calculations on the PROBES across-shelf transect, especially regeneration-related processes like ammonium or carbon dioxide evolution. Since the PROBES main line

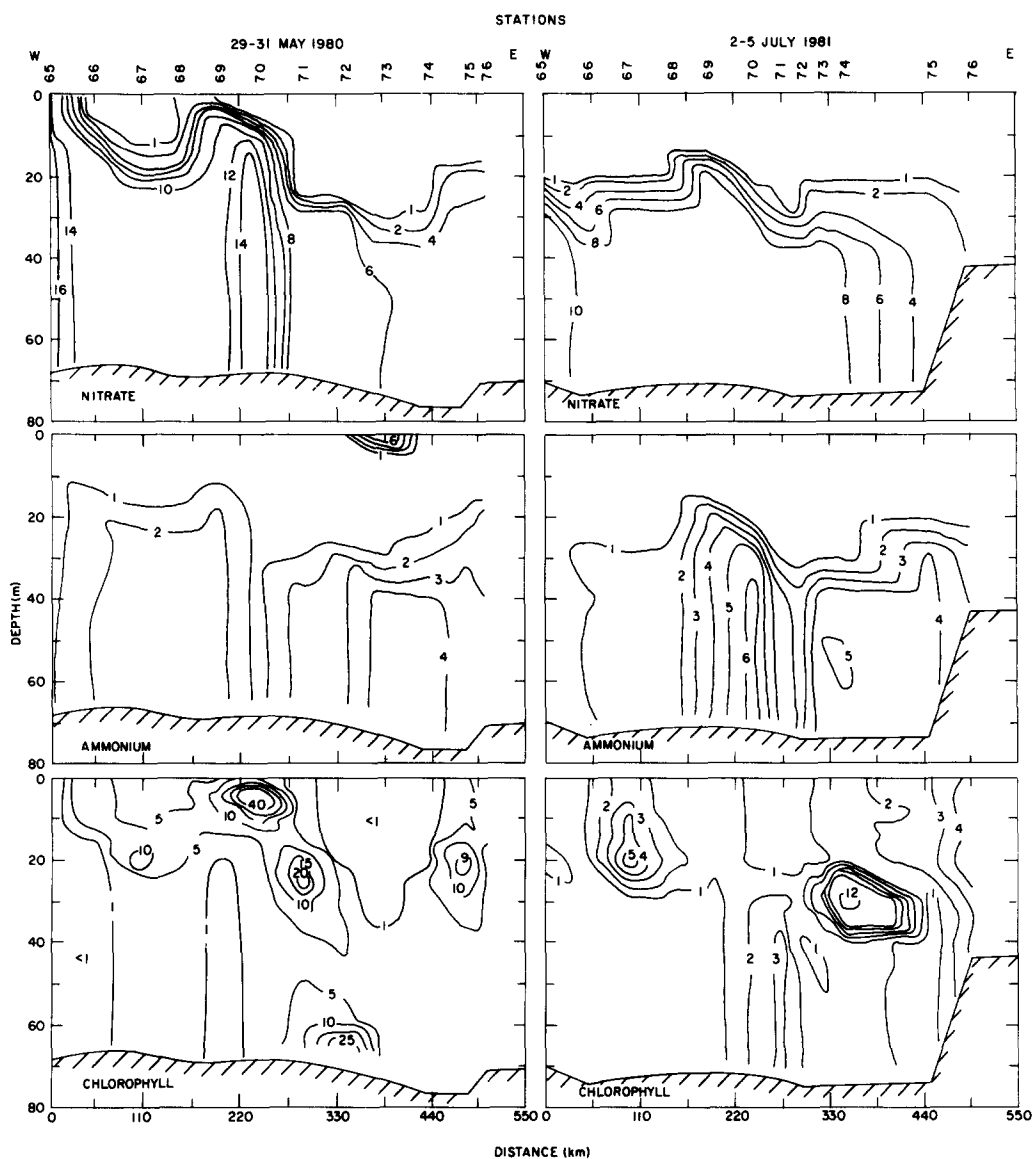


Fig. 13. The distributions of nitrate, ammonium ($\mu\text{-at. l}^{-1}$), and chlorophyll ($\mu\text{g l}^{-1}$) observed in a transect along the 70 m isobath in 1980 and 1981.

transect crosses the 70 m isobathic transects near the center (Sta. 71) where the horizontal gradients are large, temporal changes used in calculations may be contaminated by spatial variations. For this reason the production attributed to ammonium values estimated in Table 3 were calculated for late May and early June.

The storm response

The long-term variations of nutrient concentrations observed in the seasonal changes of the annual cycle (Fig. 3) are modified by relatively short-term wind events that enrich the upper

layer. Each of the short-term increases of integrated nitrate concentration in the central and outer domains was coincident with an increase in the shipboard winds. Shipboard observations of wind velocity for 4 years indicated that increased wind speeds occurred as frequently as every 5 to 6 days (Fig. 11). During the spring bloom period of March to June 1980, there were at least 13 separate periods when the shipboard wind speeds were $>10 \text{ m s}^{-1}$ therefore a wind event was produced every 6.9 days. In May 1979 an extended period of low wind speeds followed a wind event and created the most notable primary production response during the PROBES sampling period.

A short-term response following strong winds ($\sim 20 \text{ m s}^{-1}$) was observed in nutrient profiles before and during the maximum spring bloom period. The change in the vertical profiles of nutrient concentrations shows in detail how the upper ocean responded to these strong and rapid wind perturbations. Before the storm the nutrient content of the upper 40 m layer was homogenous. After the storm passed the mixed layer had deepened to about 50 m and the net result was an increase of nutrients in the newly deepened upper mixed layer and a decrease of nutrient concentrations in the upper portion of the bottom layer. The net increase in nitrate concentration was about $1.25 \mu\text{g-at. l}^{-1}$ (50 mg-at. m^{-2}) if the ambient nitrate concentrations were between 10 and $15 \mu\text{g-at. l}^{-1}$. A month later when the upper ocean was nitrate impoverished (Fig. 14), a storm again led to an increase of about $1.5 \mu\text{g-at. l}^{-1}$ (30 mg-at. m^{-2}). As a result of this nitrate enrichment high phytoplankton biomass with chlorophyll reaching $>40 \mu\text{g l}^{-1}$ occurred. A mean increase in phytoplankton of $14.7 \mu\text{g l}^{-1}$ over the 20 m euphotic zone resulted. With storms arriving at 7-day intervals, the vertical mixing could introduce as much as $900 \text{ mg-at. m}^{-2}$ into the euphotic zone, an amount that is equivalent to the nitrate present in the upper layer in late winter before the phytoplankton bloom. It is estimated that $0.21 \mu\text{g-at. l}^{-1} \text{ d}^{-1}$ is introduced from storm events during the spring and summer bloom period.

Benthic release

The benthic inputs were examined on several occasions with both near-bottom gradients, pore-water analyses, and release rates from undisturbed cores. In general, the ammonium fluxes were low and variable (1 to $10 \mu\text{g-at. N cm}^{-2} \text{ y}^{-1}$) in the middle shelf area in mid-summer, a range which would produce up to $0.27 \text{ mg-at. NH}_4^+ + \text{-N m}^{-2} \text{ d}^{-1}$. Additional

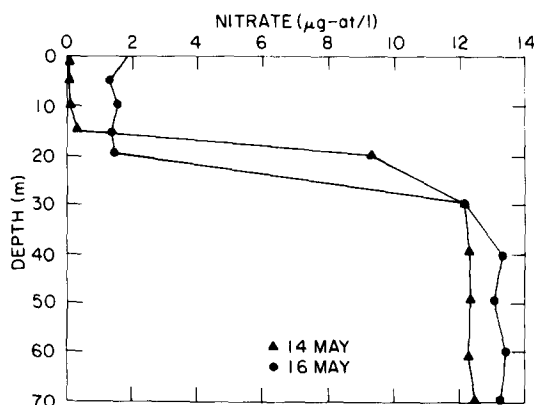


Fig. 14. The vertical distribution of nitrate ($\mu\text{g-at. l}^{-1}$) at Sta. 12 in the middle shelf domain before and after a wind event during 1979.

benthic release experiments (7 stations, 21 samples) produced a similar inorganic nitrogen flux from the sediments of $0.25 \text{ mg-at. N m}^{-2} \text{ d}^{-1}$ (W. PHOEL, personal communication). With the exception of the two inshore stations nitrate was released while ammonium was consumed, thereby providing additional evidence that nitrification was occurring.

Radon distributions in the bottom layer were usually homogeneous below the pycnocline (D. GLOVER and W. REEBURGH, personal communication) indicating that mixing in the lower layer was intense and that accumulations near the bottom were not possible. Interstitial water concentrations of ammonium were high but the gradients in the sediments were small and uniform so diffusive input from the sediments does not appear to be a major recycling process. The best estimate of benthic release rates is thus about $0.26 \text{ mg-at. m}^{-2} \text{ d}^{-1}$ for the summer season which is about 10% of the nitrogen uptake by phytoplankton.

Nitrogen uptake

The decline of ambient nitrogen concentrations (nitrate) during the spring bloom over a 4-week period in April and May of the years 1979 to 1981 was very rapid and indicated that the rate of phytoplankton utilization of nitrogen in the euphotic zone was much faster than achieved by renewal processes. The loss of nitrate from the upper mixed layer (mean depth of 27.2 m, $N = 330$) of the water column for 31-day periods in 1979 to 1981 was 938, 677, and 359 mg-at. m^{-2} , respectively, for the outer shelf and 964, 931, and 777 mg-at. m^{-2} for the central domain (Table 2). These losses represented a nitrate uptake rate of 11.6 to 30.3 $\text{mg-at. m}^{-2} \text{ d}^{-1}$ for the outer domain and 25.1 to 31.1 $\text{mg-at. m}^{-2} \text{ d}^{-1}$ for the middle domain. The carbon fixed in photosynthesis with an estimated C:N (by atoms) of 5 (BANSE, 1974; WALSH and McROY, 1986) ranged from 0.69 to 1.82 $\text{gC m}^{-2} \text{ d}^{-1}$ for the outer domain and 1.50 to 1.87 $\text{gC m}^{-2} \text{ d}^{-1}$ for the middle domain.

The 31-day bloom period, as indicated by nitrate depletion, was compared directly to ^{14}C estimates of productivity during that time period. The carbon production rates calculated from nitrate loss had a mean of 31 gC m^{-2} for the outer shelf and 51 gC m^{-2} on the middle shelf for the years 1980 and 1981 (Table 3). The direct measurements of primary productivity with ^{14}C were 98 and 109 gC m^{-2} for the same time period on the outer and middle shelf. So nitrate loss from the euphotic zone during the spring bloom represented only 30% of ^{14}C uptake on the outer shelf and 49% of ^{14}C uptake on the middle shelf. A large portion of the

Table 2. Mixed layer nitrate uptake during the spring bloom, 1979 to 1981*

Dates	Days	Outer shelf (Stas 3 to 9)			Middle shelf (Stas 12 to 17)		
		ΔNO_3 (mg-at. m^{-2})	ΔN ($\text{mg-at. m}^{-2} \text{ d}^{-1}$)	ΔC^\dagger ($\text{gC m}^{-2} \text{ d}^{-1}$)	ΔNO_3 (mg-at. m^{-2})	ΔN ($\text{mg-at. m}^{-2} \text{ d}^{-1}$)	ΔC^\dagger ($\text{gC m}^{-2} \text{ d}^{-1}$)
1979 26 April– 27 May	31	938	30.3	1.82	964	31.1	1.87
1980 23 April– 24 May	31	677	21.8	1.31	931	30.0	1.80
1981 13 April– 14 May	31	359	11.6	0.69	777	25.1	1.50
Mean		658	21.2	1.27	891	28.7	1.71

* Mixed layer depth was designated as the depth at which σ_t was $0.02 >$ surface σ_t .

† Conversions from nitrogen to carbon were made on the basis of a C:N of 5 (by atoms) (BANSE, 1974; WALSH and McROY, 1986).

Table 3. Nitrate-carbon production comparison during the spring bloom for 31 days, 1980 to 1981

	Outer shelf (Stas 3 to 9) (gC m ⁻²)			Middle shelf (Stas 12 to 17) (gC m ⁻²)		
	C _{NO₃}	¹⁴ C _{prod}	$\frac{C_{NO_3}}{^{14}C}$	C _{NO₃}	¹⁴ C _{prod}	$\frac{C_{NO_3}}{^{14}C}$
1980	40.6	116	35	55.8	142	39
1981	21.4	81	26	46.5	77	60
Mean	31.0	98	30	51.1	109	49

remaining 60 to 70% of carbon uptake must utilize ammonium as the required nitrogen source which is comparable to the range of values that were determined in ¹⁵NH₄ uptake rate experiments (SAMBROTTO *et al.*, 1986). However, the mean daily carbon uptake calculated for the combined middle and outer shelf data from nitrate loss of the water column (Table 2) was 1.50 gC m⁻² d⁻¹ which represented about 73% of the annual mean Bering Sea shelf ¹⁴C uptake rate of 2.05 gC m⁻² d⁻¹ (R. IVERSON, personal communication). Finally, assuming the diffusive resupply flux of 0.29 μg-at. NO₃-l⁻¹ d⁻¹ that COACHMAN and WALSH (1981) calculated for the spring bloom period in a 30-m water column, the calculated mean primary production based on nitrate utilization data would be 2.01 gC m⁻² d⁻¹ for the 31-day periods in 1979 to 1981. Additionally, estimates of community production from ΣCO₂ data were 2.32 and 1.72 gC m⁻² d⁻¹ with a mean value of 2.02 gC m⁻² d⁻¹ for the years 1980 to 1981 (CODISPOTI *et al.*, 1986). Their estimate of ~100 gC m⁻² of primary production during the spring bloom period reaffirms the ¹⁴C estimates in Table 3 and further shows the need for diffusive nitrate input.

Further direct comparison of ¹⁵NO₃ uptake rates after converting to equivalent carbon with a C:N ratio of 5 (BANSE, 1974; WALSH and MCROY, 1986) produced a mean primary production rate of 0.91 gC m⁻² d⁻¹ over the outer and middle shelf domains. This value should be compared to the nitrate loss in the euphotic zone (19 m) which was calculated to be equivalent to 1.06 gC m⁻² d⁻¹.

CONCLUSIONS

The dynamics of nitrogen distribution and cycling on the southeastern Bering Sea shelf are complex as demonstrated by the variability of the processes and our lack of understanding of the magnitude of the driving forces. It is instructive however to combine the estimates discussed here into a simple budget. Unfortunately most of our sampling occurred during the spring and early summer not allowing discussion of other seasons.

For the spring season COACHMAN and WALSH (1981) calculated a horizontal diffusive flux of nitrate of 0.41 μg-at. l⁻¹ d⁻¹ for the outer domain; addition of 0.04 μg-at. l⁻¹ d⁻¹ for vertical diffusion; 0.21 μg-at. l⁻¹ d⁻¹ for vertical storm mixing; 0.01 μg-at. l⁻¹ d⁻¹ for benthic release from sediments; and 0.10 μg-at. l⁻¹ d⁻¹ for nitrification yields a total of 0.77 μg-at. l⁻¹ d⁻¹. This value is virtually equal to the estimated nitrate uptake rate by phytoplankton of 0.8 μg-at. l⁻¹ d⁻¹. The middle domain would probably have smaller values for horizontal and vertical diffusive fluxes.

Later during the summer and autumn the horizontal diffusion flux estimate for both the central and outer domains decreases to $0.08 \mu\text{g-at. l}^{-1} \text{d}^{-1}$ providing about $0.30 \mu\text{g-at. nitrate l}^{-1} \text{d}^{-1}$ to the euphotic zone. The importance of ammonium has increased in the summer so possibly another $0.3 \mu\text{g-at. l}^{-1} \text{d}^{-1}$ could be added by vertical diffusion and storm mixing for a total of $0.6 \mu\text{g-at. l}^{-1} \text{d}^{-1}$ introduced into the euphotic zone. The winter season would have horizontal diffusive flux primarily but little biological uptake.

The other main points can be summarized by the following:

1. The annual cycle of nitrate concentrations over the southeastern Bering Sea shelf is remarkably the same from year to year with some differences in nutrient content in relatively cold or warm years.

2. Replenishment of nitrate to the shelf begins in the bottom layer in the middle and outer domains in late summer, continues through autumn overturn causing a vertically homogenous water column sometime between October and February and finally reaches maximum concentrations in April when the spring phytoplankton bloom is initiated.

3. The spring phytoplankton bloom occurs earliest in the inner domain although in general all shelf stations at 100 m or less show rapid nitrate loss in the euphotic zone during May. The stations in water depth >100 m generally lag the shelf stations by 3 to 4 weeks in nitrate depletion which is probably the result of greater mixing in the surface layer.

4. After the spring phytoplankton bloom large quantities of ammonium are produced in the bottom layer of the middle domain to a maximum of $15 \mu\text{g-at. l}^{-1}$ probably as a result of phytoplankton decomposition and/or benthic processes as evidenced by simultaneous increases of urea-N.

5. Cross-shelf diffusion driven by the tides could be enriching the outer and middle domains with nitrate at the mean rate of $0.07 \mu\text{g-at. l}^{-1} \text{d}^{-1}$ during the winter when the fronts are not well developed.

6. Vertical diffusion of nitrate resulting from interleaving water masses on the outer shelf may flux 0.08 to $0.34 \mu\text{g-at. nitrate-N l}^{-1} \text{d}^{-1}$ into the upper layer over about 10% of the outer shelf during summer months.

7. Enhanced vertical mixing by storms on the average of every 7 days during the spring and summer in the central and outer domains is calculated to bring a mean of $0.21 \mu\text{g-at. nitrate l}^{-1} \text{d}^{-1}$ into the upper mixed layer.

8. Benthic release of inorganic nitrogen was found to be predominately ammonium which could support nitrification processes.

9. Nitrate uptake by phytoplankton during the spring bloom agrees well with production estimates measured by $^{15}\text{NO}_3$ and ^{14}C and community production values from ΣCO_2 .

10. Alongshore differences in nitrate, ammonium, and chlorophyll concentrations at the 70 m isobath could be significant because of the apparent gradients of all measured properties.

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