Stable C and N isotopic composition of sinking particles and zooplankton over the southeastern Bering Sea shelf

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Abstract

Stable carbon and nitrogen isotopic composition of zooplankton, suspended particulate organic matter (SPOM), and sinking particles collected using sediment traps were measured for samples obtained from the southeastern Bering Sea middle and outer shelf during 1997–1999. The quantity of material collected by the middle shelf sediment trap was greater in both spring and late summer and fall than in early and mid-summer. The $\delta^{15}N$ of SPOM, sinking material and zooplankton showed greater inter-annual variability at the middle shelf site (M2) than at the outer shelf site (M3). Zooplankton and sinking organic matter collected by M2 sediment traps became more depleted in ^{15}N from 1997 through 1999, associated with a change from unusually warm to unusually cold conditions. Suspended and sinking organic matter and zooplankton collected from M3 decreased only slightly in $\delta^{15}N$ from 1998 to 1999. SPOM, zooplankton, and sediment trap samples collected at M2 were usually enriched in $\delta^{15}N$ and $\delta^{13}C$ over those from M3. However, in 1999 sediment trap samples from the middle shelf were enriched in ^{13}C over M3 material, but the $\delta^{15}N$ of samples from the two sites was similar. The geographic pattern could be explained greater productivity over the middle shelf, associated with either isotopically heavy nitrogen being regenerated from sediments, or with utilization of a greater fraction of the available inorganic nitrogen pool during most years.
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1. Introduction

The Bering Sea ecosystem supports some of the world's richest fisheries and large populations of marine mammals and seabirds, but shows marked inter-annual and inter-decadal variability in productivity at high trophic levels (National Research Council, 1996; Hunt et al., 2002). Limited sampling in space and time has hampered characterization and especially understanding of the reasons for this variability. Most field research has been conducted in spring and early summer (e.g., Sambrotto et al., 1986; Whitledge et al., 1986; Niebauer et al., 1995), and there have been large temporal gaps in collection of many important types of data. To achieve significant improvements in understanding of the ecosystem, cost-efficient approaches that yield continuous information over long periods of time are needed. Moored sediment traps offer a means to examine temporal variability, on time scales of weeks to years, in the composition and quantity of sinking particles.

Stable nitrogen and carbon isotopic data have been previously used to investigate euphotic zone

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processes such as photosynthesis, nutrient uptake, particle regeneration via bacteria and zooplankton, particle removal from the euphotic zone by zooplankton repackaging, and higher trophic level dynamics. For example, Mingawa and Wada (1984) and Fry (1988) showed stepwise enrichment of $\delta^{15}N$ from primary producers to primary and secondary consumers. Altabet and Francois (1994) related nitrogen isotopic ratios of deep-sea surface sediments to nitrate utilization in overlying surface waters. Wu et al. (1997, 1998) found a seasonal signal in the $\delta^{15}N$ and $\delta^{13}C$ values of sinking particulate matter in the northeastern Pacific Ocean, related to nutrient uptake and regeneration. Rau et al. (1989) found a strong inverse correlation between $\delta^{13}C$ enrichment of plankton and $[CO_2]_{aq}$ in the South Atlantic and Weddell Sea. On the other hand, Villinski et al. (2000) observed seasonal patterns of $\delta^{13}C$ in SPOM from the Ross Sea that were mainly related to aspects of phytoplankton dynamics, such as growth rate or species-specific fractionation. Laboratory research has demonstrated that $\delta^{13}C$ of phytoplankton is largely controlled by growth rates and cell size, rather than being a direct, simple function of $[CO_2]_{aq}$ (Laws et al., 1995; Popp et al., 1998).

This study aimed to elucidate inter-annual variations in the timing of primary production, nutrient availability, and zooplankton grazing. A time series of stable isotopic data from suspended particulate organic matter (SPOM), sinking material collected by sediment traps, and zooplankton provided indicators of these processes on a seasonal and inter-annual basis. This research is a component of SEBSCC (Southeast Bering Sea Carrying Capacity), a research program whose goals include increased understanding of the Southeast Bering Sea ecosystem and its carrying capacity for walleye pollock. The sediment traps used in this research were deployed at two sites on the Bering Sea shelf in conjunction with biophysical moorings, which collected current, fluorescence, temperature and salinity data (Stabeno et al., 2001, 2002). Collaborators measured carbon and nitrogen uptake rates and nutrient concentrations (Rho, 2000).

2. Materials and methods

Two indented rotating sphere sediment traps, equipped with an 11-sample carousel, collected a time series of sinking particles (Peterson et al., 1993). A unique feature of this trap design is the indented rotating sphere that excludes swimmers from sample tubes. The traps were deployed at two sites on the Bering Sea shelf. The first site, referred to as M2, is located on the middle shelf (56°53′N, 164°02′W), where the water depth is 73 m. The trap was deployed at 35 m depth. The second trap, at site M3 (56°04′N, 166°20′W), was located over the outer shelf where the depth is 123 m. The trap was deployed at 70 m depth. The M2 trap has been deployed year-round since February 1997. The M3 trap was deployed from February through September in 1997 and 1998 and year-round in 1999. The traps were recovered and redeployed twice a year, in February and September.

Prior to trap deployment, 5 g NaCl and 50 mg $HgCl_2$ were placed in the sample-collection tubes (Lee et al., 1992). The duration of each sample collection interval was 1–3 weeks, depending upon projected flux to the traps. On retrieval samples were immediately stored in pre-combusted glass jars that had been baked at 460°C for 8 h. Each jar lid was lined with acid-cleaned Teflon®. The samples were frozen until split for isotopic, microscopic and lipid analysis.

Sediment trap samples used for isotopic analysis were filtered using baked Whatman GF/F filters, then oven dried at 60°C and acid fumed. Once the samples were dry, the filters were cut in halves or quarters. Stable isotope analysis of sediment trap samples was performed using one of two instruments, the Europa Scientific Roboprep C/N Biological Sample Converter/20-20 Stable Isotope Analyzer, or the Carlo Erbo Autoanalyser Con Flo II Model NC 2500 with the Finnegan Mat Delta Plus Mass Spectrometer. Instrument precision was $\pm 0.26‰$ for nitrogen and $\pm 0.1‰$ for carbon. A working standard (peptone) was run every 10 samples. The isotope ratios for nitrogen and carbon, relative to the standards air and PDB (PeeDee Belemnite), are reported as follows:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 10^3,$$

where $X = {}^{15}N$ or ${}^{13}C$, and $R = {}^{15}N/{}^{14}N$ or ${}^{13}C/{}^{12}C$.

Microscopic analysis was performed on each sediment trap sample using the inverted microscope method. A sub-sample of each sediment trap sample was dispersed into a combined plate-settling chamber; this consisted of a tall cylinder (approximately a 60 ml capacity) and a bottom-plate chamber (1.5 ml capacity). The chamber was filled with 25 ml of water and each sub-sample was allowed to settle into the bottom-plate chamber for 24 h. After sedimentation, the cylinder was removed. The bottom plate chamber was fitted with a cover slip and placed into the mechanical stage of the Zeiss Telaval 31 inverted microscope. Phytoplankton cells were counted and identified until a total of 300 was reached; other particle types seen in each field viewed, such as fecal pellets, also were enumerated.

Plankton were collected by oblique tow in February 1997–1998, April 1997–1999, May 1999, and September 1999 aboard the NOAA Ship Miller Freeman R-223 using a 53-μm CalVET, and 153- and 333-μm bongo nets. Plankton samples also were collected aboard the R/V Wecoma in June 1997 and May 1998 and aboard the R/V Thomas G. Thompson in February 1999, using 153- and 333-μm bongo nets. Plankton were collected at each mooring site and at four surrounding stations. Plankton also were collected at a second, northern, middle shelf site, M4, when it was ice-free. Upon collection, copepods, euphausiids, Scyphozoan medusae, and chaetognaths were sorted to genus or species by picking individual organisms under a dissecting microscope, placed in glass vials, and frozen immediately at $-20°C$. Plankton samples used for isotopic analysis were oven dried at $60°C$ for 24 h and acid fumed. Between 1 and 1.5 mg of each sample was weighed using a Cahn 26 Automatic Electrobalance and submitted for isotopic analysis as described for the sediment trap samples. Reported means are the average of all zooplankton samples analyzed for the specified location and year. A t-test ($p = 0.05$) was used to test the means for significant differences.

Bering Sea sediments were collected using a modified Soutar box corer during the May 1998 cruise aboard the R/V Wecoma. The top 2 cm of each core were frozen and stored for isotopic analysis. Sediments were acid treated with concentrated HCl, dried at $60°C$ for 24 h, and then homogenized and weighed for isotopic analysis.

Water samples for SPOM analysis were collected in 5- or 10-l Niskin bottles. The entire bottle was emptied into a polycarbonate carboy through 333-μm net to remove larger zooplankton. An aliquot of about 1 l was filtered through a 25-mm Whatman GF/F precombusted glass fiber filter, and the filters were stored frozen until analyzed. After thawing and drying at $60°C$, the filters were fumed with HCl vapors in a vacuum desiccator, dried, cut in sections, and analyzed as described earlier for stable isotopic analyses of sediment trap samples.

Nutrients were analyzed using standard methods modified for small volumes (Whitledge et al., 1981, 1986) using an ALPKEM RFA model 300 automated nutrient analyzer. February samples were stored frozen and returned to Fairbanks for analysis. For other sampling times analyses were completed on board ship.

3. Results

3.1. Zooplankton

Zooplankton collected over the middle shelf (M2, M4) were consistently enriched in ^{15}N relative to those collected near the outer shelf station M3, for all 3 years and for all taxonomic groups examined (Table 1). For example, in 1997, middle shelf copepods (Calanus marshallae) were more than 4‰ heavier than outer shelf copepods (Neocalanus cristatus and N. plumchrus), This difference continued in 1998 and 1999, but was smaller. Middle shelf euphausiids (Thysanoessa raschi) were almost 3‰ heavier than outer shelf euphausiids (T. inermis) in 1997, and, as for the copepods, the difference was less in 1998 and 1999. Chaetognaths (Sagitta spp.) and Scyphozoan medusae were also enriched in ^{15}N at M2 relative to M3. In addition, zooplankton collected at M2 and M4 were usually enriched in ^{13}C relative to those collected near M3 (Table 1). Calanus (M2) was enriched in ^{13}C over Neocalanus spp. (M3) throughout the study. T. raschi (M2) was enriched

Table 1
Stable isotopic composition of zooplankton over the southeastern Bering Sea shelf, 1997–1999

Year collected	Zooplankton type	Station	Mean 1[a] $\delta^{15}N$ (‰)	s.d.	Mean 1[a] $\delta^{13}C$ (‰)	s.d.	Mean 2[a] $\delta^{15}N$ (‰)	Mean 2[a] $\delta^{13}C$ (‰)	n
1997	Copepod	M2	13.2	1.5	−22.8	1.8	13.6	−22.4	7
1997	Copepod	M3	9.0	1.2	−24.8	3.8			5
1998	Copepod	M2	9.8	1.0	−23.2	0.7	9.9	−22.8	15
1998	Copepod	M3	7.5	1.5	−25.1	1.9			14
1999	Copepod	M2	10.7	1.0	−20.4	0.9	10.8	−20.6	9
1999	Copepod	M3	7.9	1.1	−25.1	1.5			21
1997	Euphausiid	M2	12.3	1.7	−20.0	1.9	12.5	−19.8	7
1997	Euphausiid	M3	9.6	0.2	−20.2	0.2			5
1998	Euphausiid	M2	10.4	1.4	−20.7	0.8	10.8	−20.5	16
1998	Euphausiid	M3	8.6	1.3	−21.8	1.1			10
1999	Euphausiid	M2	10.0	2.5	−19.0	1.1	11.2	−19.0	12
1999	Euphausiid	M3	9.3	0.9	−22.4	0.6			9
1997	Chaetognath	M2	15.2	1.1	−20.7	0.8			8
1997	Chaetognath	M3	12.9		−21.8				1
1998	Chaetognath	M2	15.0	1.4	−21.8	0.6			17
1998	Chaetognath	M3	12.6	1.6	−22.1	1.6			7
1999	Chaetognath	M2	14.6	1.2	−21.1	0.7			12
1999	Chaetognath	M3	12.6	0.8	−22.4	0.9			9
1997	Scyphozoan	M2	14.8	2.1	−20.5	0.3			7
1997	Scyphozoan	M3	10.3	0.8	−22.5	1.5			2
1998	Scyphozoan	M2	12.6	0.8	−20.1	0.9			10
1998	Scyphozoan	M3	11.0	1.2	−21.7	0.8			5
1999	Scyphozoan	M2	13.0	1.1	−19.7	0.7			8
1999	Scyphozoan	M3	10.8		−20.6				1

[a] Mean 1 is the simple average of all data for this zooplankton type at the given site and year. Mean 2 was calculated by first averaging the data for each month sampled, and then averaging those means to obtain an annual mean. September 1999 data were omitted from Mean 2, since September samples were collected only in 1999.

over *T. inermis* (M3), except in 1997, when their $\delta^{13}C$ values were equal.

Because there were only three to four sampling opportunities each year, and because sometimes one of the species normally collected was absent from the sample, it was not possible to examine seasonal changes in detail. However, at M2 copepod $\delta^{15}N$ and $\delta^{13}C$ usually decreased by 1–2‰ between February and April, May, or June, and $\delta^{15}N$ usually decreased for other zooplankton also. Such trends were absent, except in copepod $\delta^{13}C$, at M3. For copepods and euphausiids at M2, annual means (Table 1, Mean 2) were recalculated by averaging the mean values for each sampling date, to eliminate any effect of different sample

sizes at different sampling times during the year. However, means calculated in this way were nearly identical to those calculated by simple averaging of all data from the year (Table 1, Mean 1).

Zooplankton collected at M2 showed inter-annual differences in $\delta^{15}N$, especially between 1997 and 1998. The $\delta^{15}N$ values for *Calanus* and *T. raschi* were significantly greater in 1997 than 1998 or 1999 (Table 1). However, the $\delta^{15}N$ values of chaetognaths and Scyphozoa did not differ significantly between any two of the three years. Both middle shelf *Calanus* and *T. raschi* $\delta^{13}C$ increased significantly in 1999 relative to 1998. At M3 over the outer shelf, $\delta^{15}N$ values for euphausiids, chaetognaths and Scyphozoa were the same

all 3 years. Only the copepod $\delta^{15}N$ varied significantly, decreasing by 1.5‰ from 1997 to 1998. Euphausiid $\delta^{13}C$ decreased significantly from 1997 to 1998. Outer-shelf $\delta^{13}C$ values for copepods, chaetognaths, and Scyphozoa remained the same from 1997 through 1999.

3.2. SPOM and net plankton

As seen for the zooplankton, net plankton and SPOM collected in May 1998 were enriched in both ^{15}N and ^{13}C at M2 compared with M3 (Table 2). The limited number of samples from 1999 showed no difference in $\delta^{15}N$ at the two sites, but $\delta^{13}C$ was markedly lighter at M3. As seen for the copepod and euphausiid annual means at M2,

the May 1999 $\delta^{13}C$ was heavier than that for May 1998. SPOM and net plankton $\delta^{15}N$ were markedly lighter in May 1999 than in May 1998 at both M2 and M3, but that difference was not seen in the zooplankton annual means (Table 1). The $\delta^{15}N$ of the SPOM, net plankton, and contemporaneous sediment trap samples were generally similar within variability at both M2 and M3. Except in May 1999, sediment trap samples had consistently greater $\delta^{13}C$ than did SPOM and net plankton, at both sites.

3.3. Sediment trap samples

The amount of organic carbon collected by the sediment traps at M2 is shown in Fig. 1, along

Table 2
Stable isotopic composition of suspended particulate matter (SPOM) and net plankton (NP) over the southeastern Bering Sea shelf, 1997–1999

| Sampling date	Sample type	Station	$\delta^{15}N$ (‰)	s.d.	$\delta^{13}C$ (‰)	s.d.	n
June 97	NP	m2	12.6	1.2	−24.8	0.0	2
		m4	13.2	1.7	−23.2	0.2	3
April 98	NP	m2	11.4	0.7	−21.8	1.3	2
	NP	m4	12.3		−20.1		1
May 98	NP	m2	7.1		−20.6		1
April 98	SPOM	m2	13.6	1.9	−21.2	0.9	12
April 98	SPOM	m2	13.1	1.3	−21.6	0.9	3
May 98	SPOM	m2	10.4	2.2	−21.4	0.1	3
May 98	SPOM	m2	15.1	2.2	−21.5	0.5	6
May 98	SPOM	m2	12.3	1.0	−21.6	1.1	3
May 98	SPOM	m2	12.4	2.0	−21.9	0.3	3
Mean 1998	SPOM	m2	13.3	2.2	−21.4	0.7	30
May 98	SPOM	m3	10.5	1.0	−25.5	0.2	3
May 98	SPOM	m3	10.0	2.7	−24.4	0.3	3
May 98	SPOM	m3	12.7	3.0	−26.2	0.1	3
Mean 1998	SPOM	m3	11.1	2.4	−25.4	0.8	9
May 99	NP	m2	6.6	0.1	−18.2	1.4	3
	NP	m4	8.0	1.1	−19.7	1.1	3
May 99	SPOM	m2	9.1		−24.1		1
May 99	SPOM	m2	6.9	0.5	−19.8	0.1	2
May 99	NP	m3	6.7	1.2	−26.5	0.6	3
May 99	SPOM	m3	6.2		−25.8		1
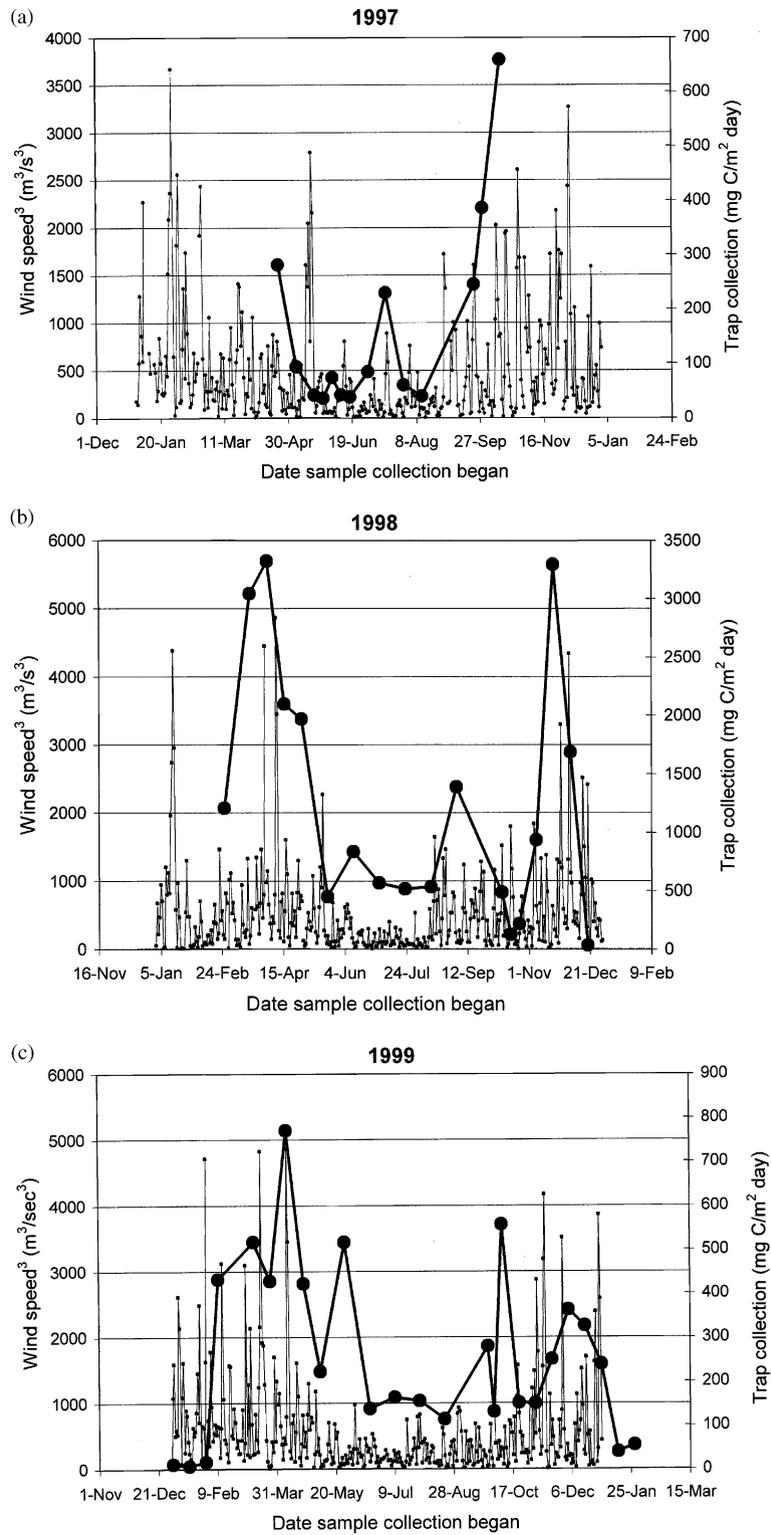
Fig. 1. Pribilof (wind speed)[3] compared with the quantity of particulate organic carbon collected by sediment traps at the middle shelf site M2 for the years 1997 through 1999.

with the cube of daily average wind speed at St. Paul Island (57°08′N, 170°18′W). St. Paul Island is about 350 km WNW of M2, but this is the only year-round wind record for the region. Since pressure areas have dimensions of about 1000 km in this region (Bond and Adams, 2002), Pribilof winds are likely a reasonable reflection of winds at the mooring site. The amount of material collected at M2 in 1998 was much greater than that in 1997 or 1999. All three years showed a similar annual pattern, with greater quantities in early spring and fall, and lesser amounts in summer and midwinter. The M2 data show some relationship with the wind patterns, i.e. the summer period of minimal collections also corresponds to the annual minimum in wind. This is not true of the winter minimum in collected material, however. Also, some of the larger quantities collected were associated with relatively calm winds, for example, late April and July 1997, early September 1999, and late May and September–October 1999.

The C/N ratio ranged from 4.8 to 9.0. There was a maximum in C/N in late May-early June during all three years (Fig. 3). Local C/N ratio minima were associated with the April 1997, July 1997, September 1997, March 1998, and March–April 1999 maxima in the amount of organic matter collected. The spring, 1998 C/N ratio of trapped material was less than that in 1997 or 1999.

The amount of material collected at M3 was much less in 1998 than in 1999 (Fig. 2) and less in both years than the quantity collected at M2. In 1998, the amount collected was less than 10 mg C/m^2 day except in March and April, when 50–100 mg C/m^2 day were trapped. The maximum value in July 1999 exceeded 300 mg C/m^2 day, and more than 50 mg C/m^2 day was collected at most times during 1999. The C/N ratio ranged from 4.5 to 7.3, and high values were found in late May–early June, as at M2 (Fig. 3). However, the C/N ratio was also high in April 1999.

The means of $\delta^{15}N$ and $\delta^{13}C$, weighted by the quantity of organic matter collected by the sediment traps, are given in Table 3. The mean for April and May sample collections is similar in all cases to the mean for April through August. The average $\delta^{15}N$ was 3‰ greater at M2 than M3 in 1997 and 1998, but the two sites had similar mean values in 1999. The $\delta^{13}C$ was 2–3‰ lighter at M3 than at M2 during both 1998 and 1999. The mean $\delta^{15}N$ at M2 was about 3‰ greater in 1997 and 1998 than in 1999. The mean $\delta^{13}C$ was similar for all three years at M2, but was about 0.5‰ heavier in 1998. M3 $\delta^{15}N$ averaged about 1‰ heavier in 1998 than 1999. The spring mean $\delta^{13}C$ was identical in 1998 and 1999, but the average for the spring–summer period was 0.6‰ lower in 1998 than 1999.

The $\delta^{15}N$ of sinking organic matter at M2 showed similar seasonal pattern of variation in all 3 years, an increase in late winter and spring, reaching a maximum in late April (1998 and 1999) to early June (1997), followed by a decrease into summer (Fig. 4). In 1997 and 1998, the decrease continued through fall, but in 1999 the values increased again after June and were greater than 13‰ in October. In 1998, a high percentage of fecal material in February–April samples was associated with high $\delta^{15}N$ values. The early 1998 sediment trap samples also contained a notably large amount of amorphous organic material. The $\delta^{15}N$ of spring and summer 1999 M2 sediment trap material was about 4‰ lower than that collected during 1997 and 1998, as also seen for the May 1999 SPOM and net plankton samples.

The M2 $\delta^{13}C$ exhibited a seasonal pattern similar to that of $\delta^{15}N$, with higher values in late winter, and a decrease through spring and summer (Fig. 5). In 1997 and 1998, the decrease continued into fall and early winter, but in 1999, as was the case for $\delta^{15}N$, the $\delta^{13}C$ increased in August through November. By late winter, $\delta^{13}C$ had decreased to the average values of previous years.

No sediment trap samples were collected at M3 in 1997. Both the $\delta^{15}N$ and $\delta^{13}C$ of sinking material at M3 showed a pattern of higher values in late winter and decreasing values into the fall of 1998, similar to the pattern at M2. This pattern did not hold in 1999, however, when the $\delta^{15}N$ and $\delta^{13}C$ had no seasonal trend. In 1998, samples from February 26 and May 21 recorded unusually low $\delta^{15}N$ and $\delta^{13}C$ values. The amount of carbon collected in these samples was very low and the C/N ratios were 7, greater than those of most other samples. As was true for zooplankton and SPOM, sediment trap samples collected at M3 were
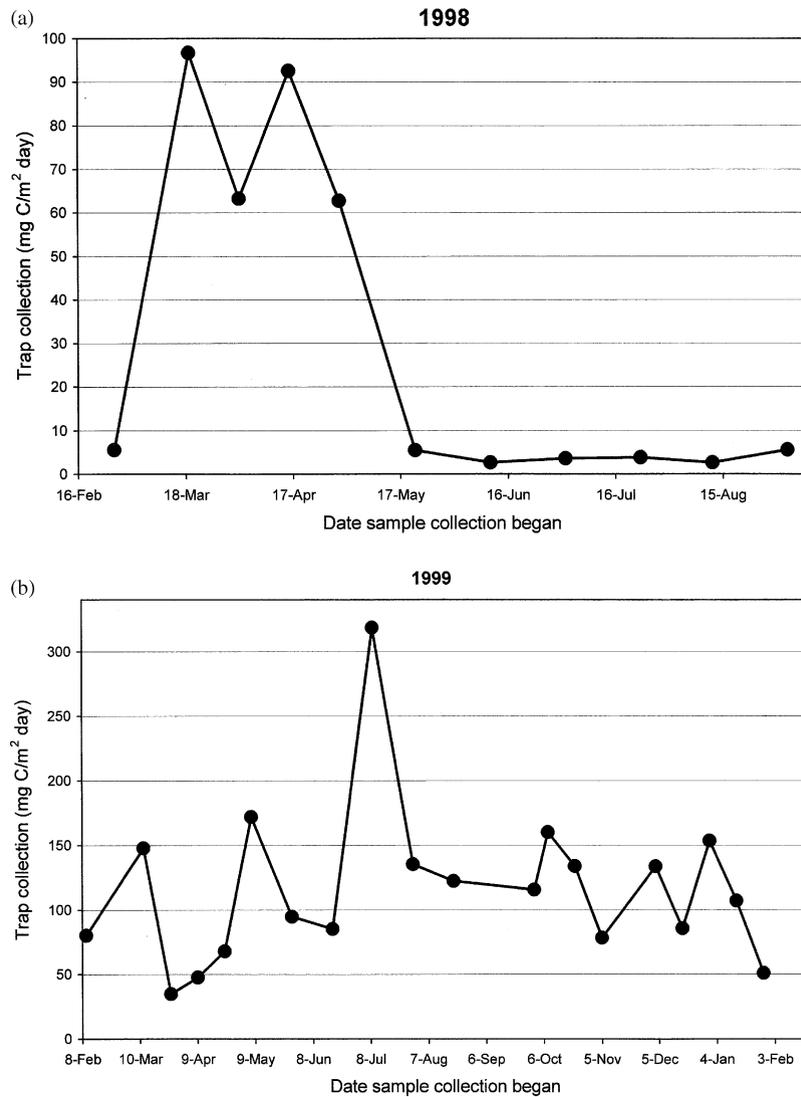
(a)

(b)

Fig. 2. The quantity of organic matter collected by sediment traps at the middle shelf site M3 for the years 1998 and 1999.

depleted in ^{15}N and ^{13}C compared with those collected at M2 in 1998 and most of 1999. In 1999 the δ^{15}N values at the two sites were equal in July, August, and December (Fig. 4).

3.4. Sediment cores

The δ^{15}N and δ^{13}C of sediments (0–2 cm) collected from middle shelf stations near M2

averaged 7.6‰ and −21.85‰, respectively, at M2 and 6.7‰ and 23.1‰ at M4. The isotopic composition of M3 sediment was similar, with an average δ^{15}N of 6.7‰ and δ^{13}C of −21.00‰.

3.5. Nutrients

The February 1997 and 1998 nitrate concentrations at M2 were very similar, from 12 to 14 µM
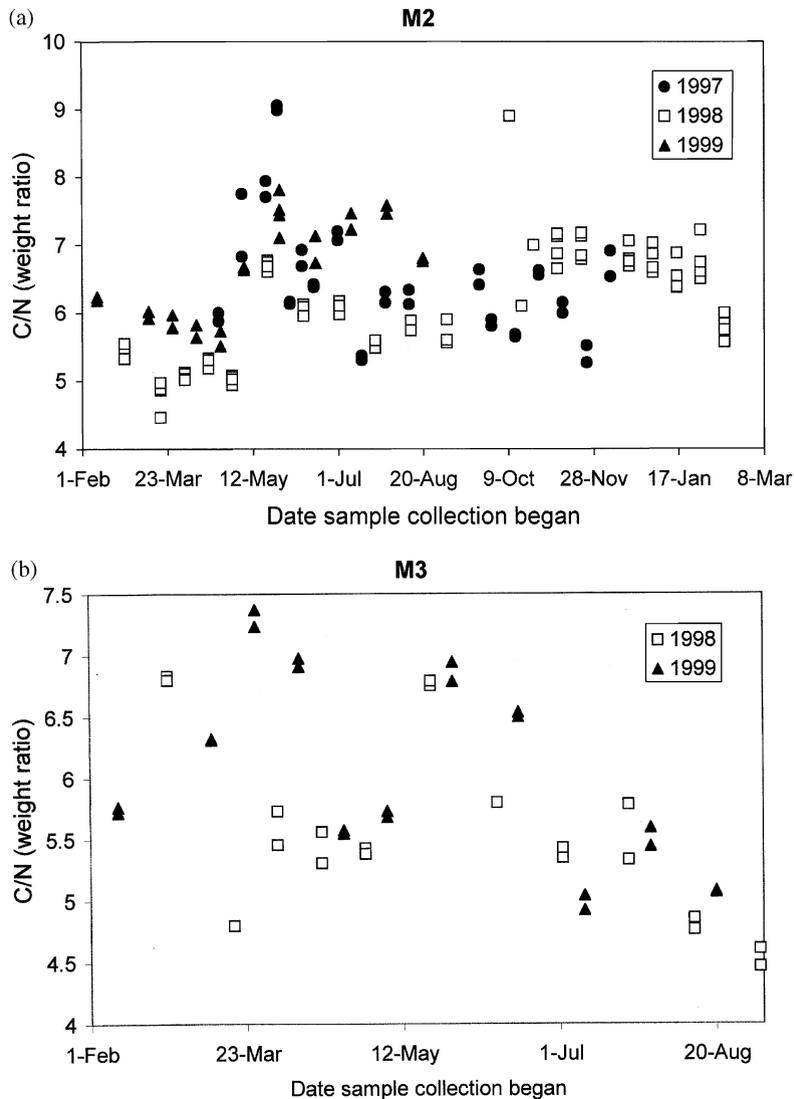
Fig. 3. C/N (weight ratio) of organic matter collected by sediment traps located over the middle (M2) and outer (M3) shelf of the southeastern Bering Sea.

throughout the water column; they were slightly lower, 9–11 µM, in February 1999 (Fig. 6). (February ammonium data are unavailable). In 1997 euphotic zone nitrate was depleted at M2 by early May, and in June there was substantial utilization of nitrate below the pycnocline, reducing the concentrations near the bottom to only 2 µM. The ammonium concentration, which was

8–10 µM in early May, decreased to less than 1 µM in surface waters by late June. The 1997 data contrast sharply with May 1998 when the nitrate concentration was about 11–12 µM throughout the water column, only slightly less than February and April values. However, the ammonium concentration had increased markedly over April values to 6–10 µM. On May 2, 1999, nitrate concentrations

were 9–11 μM throughout the water column. This water sample was taken prior to the advance of ice over the mooring site about May 7, which prompted a bloom (Rho, 2000). The May 1999 ammonium concentration was much less than that in 1997 and 1998.

Table 3
Weighted mean of sediment trap $\delta^{15}N$ and $\delta^{13}C$ for spring and summer periods. The isotopic data were weighted by the quantity of organic carbon collected by the trap during each sampling period

Station	Sampling period[a]	Mean $\delta^{15}N$ (‰)	Mean $\delta^{13}C$ (‰)
M2	4/22/97–5/27/97	13.0	−20.8
M2	4/22/97–8/12/97	13.6	−21.1
M2	4/2/98–5/21/98	13.9	−20.1
M2	4/2/98–8/13/98	13.8	−20.3
M2	4/9/99–5/7/99	10.4	−20.6
M2	4/9/99–8/20/99	9.7	−20.9
M3	4/2/98–5/21/98	10.9	−23.0
M3	4/2/98–9/2/98	10.8	−22.9
M3	4/9/99–5/7/99	9.6	−23.0
M3	4/9/99–8/20/99	9.4	−22.3

[a] The dates sediment trap sample collection began, i.e., the last sample was collected for 1–2 weeks after the final date shown.

No February data are available for M3. The early May 1997 nitrate concentrations were 3–6 μM in the mixed layer, but by mid-June, surface water nitrate had decreased to 0 μM (Fig. 7). Ammonium increased throughout the water column between May and mid-June, but by late June, it was almost depleted near the surface. The 1998 nutrient profiles at M3 were similar to those at M2; nitrate was high, 14–15 μM, as late as mid-May. In early May 1999, the nitrate concentration was about 18 μM–70 m depth, but at 120 m depth the nitrate concentration was 28 μM, indicating an influx of nutrients from slope water.

4. Discussion

4.1. Sediment traps and the quantity of material collected

In the upper ocean, swimmers (zooplankton that enter traps actively rather than by passive sinking) often constitute most of the collected material, and are very difficult to quantitatively separate from other particles (Lee and Hedges, 1988; Lee et al., 1992). However,
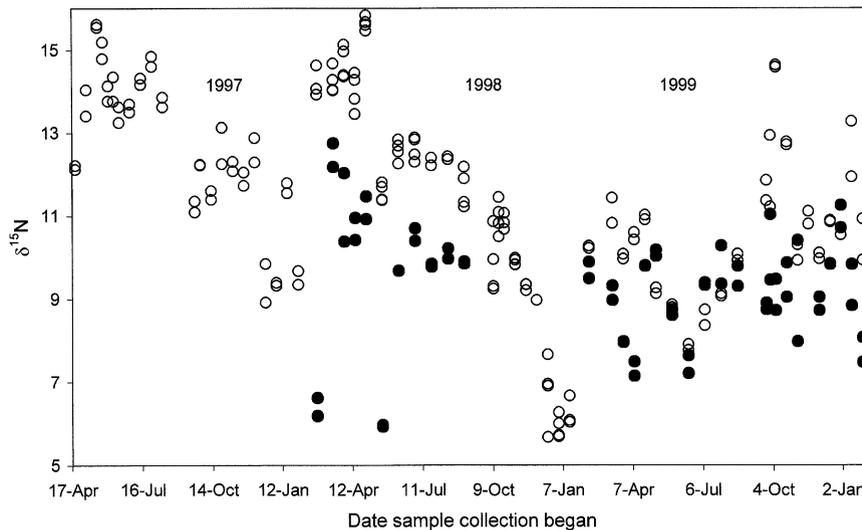

Fig. 4. $\delta^{15}N$ (‰) of sediment trap samples collected at the middle shelf site M2 (○) and the outer shelf site M3 (●), April 1997 through January 2000. No samples were collected at M3 during 1997. Multiple symbols at a single time represent replicate analyses of a single sediment trap sample.
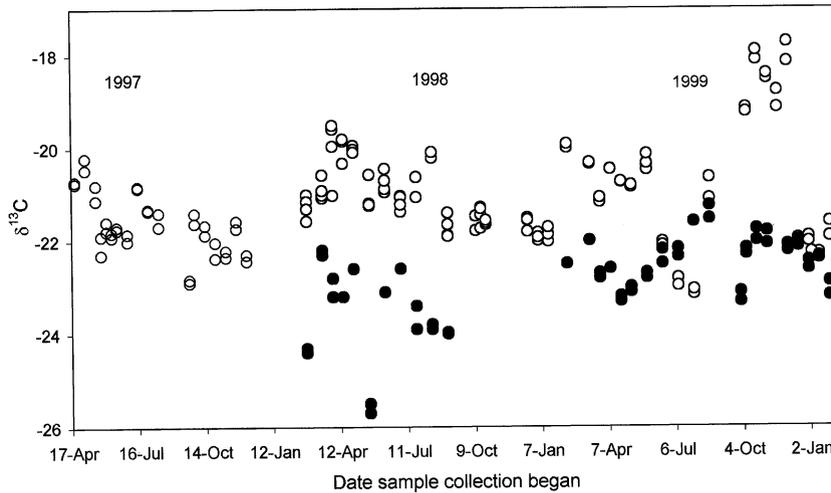
Fig. 5. $\delta^{13}C$ (‰) of sediment trap samples collected at the middle shelf site M2 (○) and the outer shelf site M3 (●), April 1997 through January 2000. No samples were collected at M3 during 1997. Multiple symbols at a single time represent replicate analyses of a single sediment trap sample.

swimmer-excluding traps (Peterson et al., 1993) were used in this study. Samples were carefully examined for intact zooplankton, but these were usually absent. Occasionally, one or two small copepods were found and picked out. In a single event, a large number of pteropods was present in the M2 September 1999 sample. Pteropods were extremely abundant in the water at that time, and it's uncertain whether the trapped animals were swimmers or sank into the trap.

Sediment traps often do not collect sinking particles quantitatively, and the shallow southeast Bering Sea sites where the moorings were deployed are not ideal for quantitative particle trapping. Even in favorable locations (deep water with relatively weak currents), radioisotopic calibrations indicate that trapping efficiency is often not 100% and that under-trapping is most common (Buessler, 1991; Cochran et al., 1993). Tidal currents over the Bering Sea middle shelf can approach 20 cm/s, although net currents are much slower, and this could affect efficiency (Gardner et al., 1983, 1996). Also, particularly for the middle shelf trap, resuspended bottom sediment is a potential contributor to the samples, though there is no evidence that it was a major component

during most of the year. For example, the $\delta^{15}N$ of the underlying sediment at M2 (7–8‰), collected with a box corer, was much less than that of typical sediment trap samples. When resuspended sediment was expected, after very severe winter storms, M2 sediment trap samples contained numerous diatom fragments. This differed notably from the typical sample, in which intact diatom frustules, intact or broken fecal pellets, amorphous aggregates, and sometimes coccoliths were the major identifiable components. M3 samples never contained predominantly broken diatom tests. Given the uncertainties in trapping efficiency and the potential for collection of resuspended sediments, at least after severe storms, we do not claim that the quantity of organic matter collected by the traps was equal to the vertical flux of sinking particles. Rather, this paper emphasizes the composition of the sediment trap samples and how temporal and spatial variations in collected material relate to conditions in the water column.

Some especially severe storm events did correspond to unusually high amounts of material collected by the M2 trap (Fig. 1). Sustained wind speeds in excess of 15 m/s ($3375 m^3/s^3$) were associated with large collections of organic
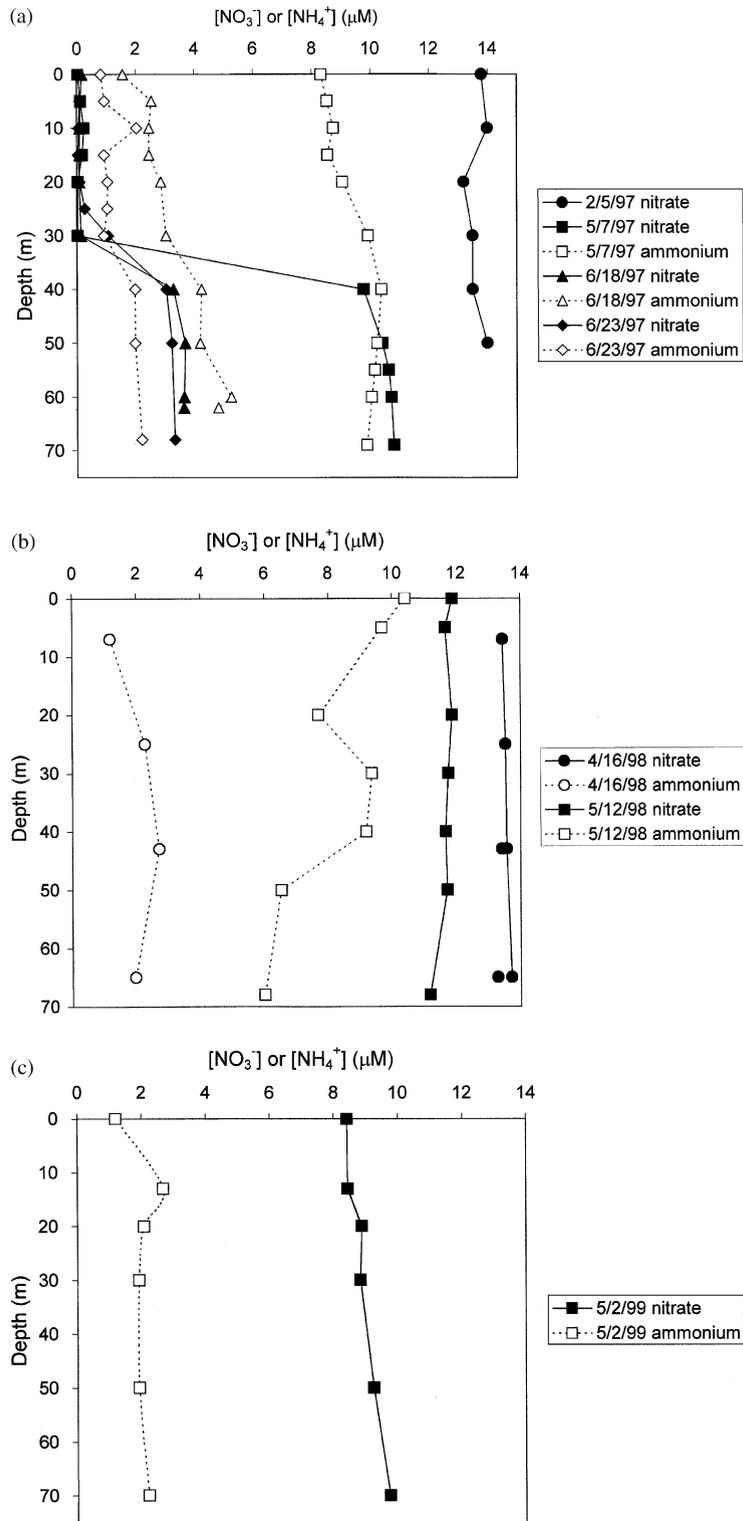
Fig. 6. Nitrate and ammonium concentrations at middle shelf site M2, 1997–1999. Data are courtesy of Terry Whitledge, University of Alaska Fairbanks.
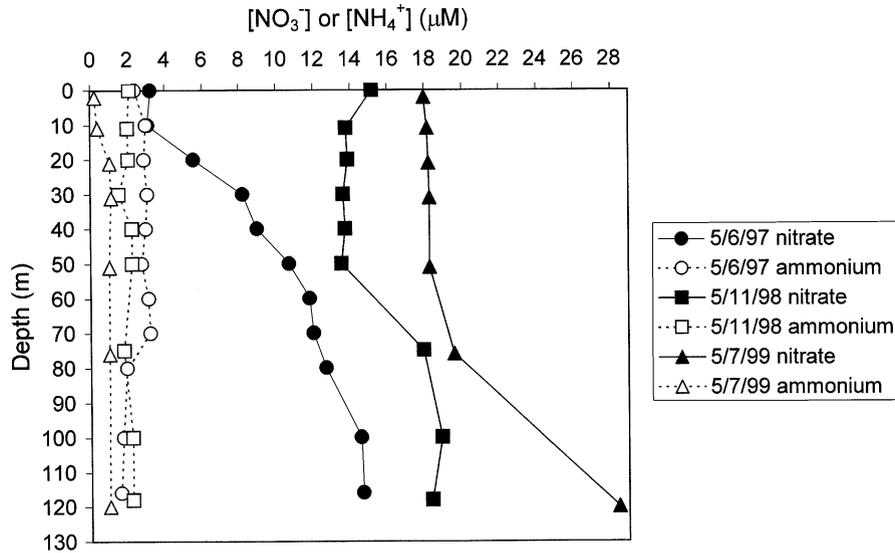
Fig. 7. Nitrate and ammonium concentrations at outer shelf site M3, 1997–1999. Data are courtesy of Terry Whitledge, University of Alaska Fairbanks.

material during February through April, 1998 and 1999 and November 1998. Substantial primary production is unlikely at these times except, perhaps, in April. In November 1999, both microscopic and lipid analyses indicated that the material collected consisted mainly of intact diatoms, which suggests that if the collected material was resuspended, it consisted of recently settled phytoplankton. In February through April of 1998 and 1999, the collections had numerous intact fecal pellets in addition to amorphous material, again suggesting resuspension of a recently deposited layer.

However, high rates of organic matter collection by the M2 trap also occurred at times when winds were relatively calm. These include late April 1997, late April–early May 1998, and late May 1999, probably associated with spring phytoplankton blooms. In July 1997, a small wind event during an otherwise very calm period was associated with increased particle collection by the M2 trap, likely due to productivity spurred by nutrients supplied to surface waters via wind mixing (Sambrotto et al., 1986). There were also late summer–early fall maxima in the quantity col-

lected, associated with moderate winds, which were probably due to increased fall productivity associated with mixing and nutrient influx to the photic zone. Some of these fall samples had very high numbers of coccoliths, but diatoms and fecal pellets were also numerous. The data suggest that fall blooms are important contributors to annual primary production in the southeastern Bering Sea.

One approach to assessing the quantity of the material the sediment trap collected is to compare it to rates of carbon, nitrate, and ammonium uptake by phytoplankton. As yet, data are available only for 1997 and 1998 (Rho, 2000). The measurements were made almost entirely in the spring, and primarily at times and places where phytoplankton biomass (chorophyll) was low. Measured carbon and ammonium uptake rates over the middle shelf were much greater in 1998 than 1997, as was the amount of material collected by the sediment trap. However, there was no clear difference in nitrate uptake rate, either as measured by a tracer or as estimated by disappearance of nitrate from the mixed layer during the spring and summer.

Under the conventional paradigm for the open ocean (Eppley et al., 1979), the amount of nitrogen collected by the sediment trap should equate to the amount of nitrate removed from the photic zone. For late April through August 1997, the sediment trap collection was about $2.2\,g\ N/m^2$, while the estimated nitrate consumption for April through August was $58\,g\ N/m^2$ (Rho, 2000), greater as expected because the trap was not deployed for the whole period nor at the time (the first part of April) when most nitrate consumption occurred. Further, because of the unusually deep nutricline in summer 1997, some of the nitrate uptake and primary production occurred below the depth of the trap. In 1998, $33\,g\ N/m^2$ were collected during April through August, less than but comparable to the $53\,g$ of nitrate nitrogen uptake (Rho, 2000). However, there was also substantial ammonium consumption during this period, at rates more than 10 times the nitrate uptake rate. Because a substantial quantity of ammonium appeared between April and May without an equivalent net consumption of nitrate, it appears to constitute a new, rather than regenerated, nitrogen input to the pelagic system. The amount of material collected from April through August 1999, was similar to that in 1997, $3.4\,g\ N/m^2$. It is not entirely clear why the amount of material collected by the M2 trap in 1998 was so much greater than that collected in 1997 or 1999. Monthly mean (wind speed)[3] was unusually high in April and August 1998 relative to the other 2 years, but the mean values were similar and low for May through July of all 3 years. High winds in spring 1998 were associated with high concentrations of nitrate in surface waters that persisted through May (Fig. 6). The other unusual conditions in spring 1998 were the high ammonium concentrations (Fig. 6) and consumption rates (Rho, 2000). Hence, there is some evidence that the nutrient supply to the photic zone was greater in 1998 than in the other 2 years.

4.2. Cross-shelf variation of the stable isotopic composition of SPOM, plankton, and sediment trap samples

The greater middle shelf $\delta^{15}N$ of SPOM, zooplankton, and particles collected by sediment traps, relative to that found for outer shelf samples, reflects variations in the isotopic composition of phytoplankton that ramify throughout the food web. Schell et al. (1998) reported a similar pattern in zooplankton $\delta^{15}N$ across the Bering Sea shelf, which they attributed to progressive cross-shelf nutrient depletion. Because phytoplankton preferentially assimilate the lighter isotope, the residual inorganic nitrogen pool becomes progressively heavier as it is consumed (Wada and Hattori, 1981; Altabet, 2001). Previous work has shown that the main source of nutrients for the southeastern Bering Sea shelf is the high-nutrient water overlying the bordering continental slope. Calculated tidally driven horizontal diffusive nutrient fluxes appear to be large enough to provide the nitrogen required to sustain shelf primary production (Coachman and Walsh, 1981; Whitledge et al., 1986). Horizontal advection of nutrients was estimated to be small (Coachman, 1986), but recent observations of rapid but intermittent cross-shelf flows indicate the potential for advective transport as well (Stabeno et al., 2003). As a consequence of the offshore nutrient source, the middle shelf can be described as nutrient depleted, while outer-shelf nutrients are more rapidly replenished by the on-shelf transport from slope water (Hattori and Goering, 1981; Whitledge et al., 1986).

However, both the outer-shelf site and the middle-shelf site M2 typically exhibit complete depletion of surface-water nitrate during the spring bloom (Whitledge et al., 1986; Rho, 2000). If the initial nitrate $\delta^{15}N$ at the two sites was the same, the weighted average $\delta^{15}N$ of sediment trap particles over the productive season (Table 3) should be the same also, but that was observed only in 1999. One potential reason for the difference between M2 and M3 in 1997 and 1998 was that, while surface water nitrate is ultimately depleted at both sites, nitrogen utilization, estimated based on the quantity of organic material collected by the sediment traps (Figs. 1 and 2), was greater at M2. The additional nitrogen apparently came from below the thermocline at M2, ultimately substantially decreasing nitrate and ammonium concentrations throughout the water column. At the outer-shelf site (M3) subsurface

waters can mix more readily with nutrient-rich waters offshore, adding fresh (and isotopically lighter) nitrate throughout the productive season. Hence, nitrate supplied to surface waters by vertical mixing would not become enriched in ^{15}N, as probably occurs at M2. Another possible explanation is that the initial isotopic composition of the inorganic nitrogen supplied at the two sites differed. Since the isotopic composition of nitrate supplied from offshore should have been uniform, and coastal waters are not a likely nitrogen source, isotopically heavy inorganic nitrogen would have to be supplied on the shelf, perhaps via regeneration from sediments. Regenerated ammonium should be isotopically lighter than the decomposing or digested organic matter (Checkley and Miller, 1981), but if material decomposing at the sediment–water interface in the winter and spring were similar to the isotopically heavy sediment trap samples collected during 1997 and 1998, the released inorganic nitrogen could have a δ^{15}N of about 10‰.

The δ^{15}N also indicated differences in trophic level of certain organisms between the middle and outer shelf regions. At M2, chaetognaths were enriched 2–5‰ over both copepods and euphausiids for the period 1997–1999. At M3, chaetognaths were heavier by 3–4‰ than euphausiids, which were enriched 1–1.5‰ over copepods. This is consistent with a more omnivorous diet for euphausiids at M3.

Geographic trends for δ^{13}C were similar to those for δ^{15}N. Middle shelf zooplankton were usually enriched in ^{13}C over their outer shelf counterparts, and the particulate matter collected by sediment traps had consistently greater δ^{13}C at M2 than at M3. This cross-shelf δ^{13}C trend is opposite to that reported by Schell et al. (1998), who attributed a pattern of progressively lighter δ^{13}C of copepods from the outer to the inner shelf to decreasing primary productivity associated with nutrient depletion. As discussed in greater detail later, δ^{13}C of phytoplankton is affected by many factors, of which growth rate is only one. However, the data reported here are consistent with substantially greater rates of primary production over the middle shelf than the outer shelf. In particular, the sediment trap at M2 collected substantially more organic matter than the trap at M3, and SPOM, zooplankton, and sediment trap particles all had greater δ^{13}C at M2 also.

4.3. Seasonal and inter-annual variation of the stable isotopic composition of SPOM, plankton, and sediment trap samples

In 1997, the Bering Sea had much less cloud cover and higher atmospheric and water temperatures than normal. In early spring, sea ice was present over M2 and the retreat of sea ice early April resulted in melt-water salinity stratification of the water column and an ice-edge bloom (Stabeno et al., 2001). The bloom ended when nutrients were stripped from the surface layer by late April (Fig. 6), and from late April through late May little regenerated production occurred, since ammonium was depleted as well (Rho, 2000). Therefore, net plankton collected in June sinking organic matter and zooplankton were all enriched in ^{15}N (Tables 1 and 3; Fig. 4). Microscopic analysis showed that the April sediment trap sample consisted mainly of sinking diatoms. At the end of May, the C/N ratio of sinking material was 9, and δ^{15}N values had increased to greater than 15‰.

By June, a subsurface phytoplankton bloom depleted nitrate at depth (Stockwell et al., 2001). Slightly lower June δ^{15}N values in sediment trap material may correspond to phytoplankton growth near the base of the euphotic zone. In September fall mixing commenced, which brought nutrients to the surface and coincided with the sinking of coccoliths into the sediment trap. Owing to new nitrate input, the δ^{15}N decreased in the September samples (Fig. 4), which contained diatoms and fecal material in addition to the coccoliths. A coccolithophorid bloom had been present over the middle shelf since July, and SeaWIFS imagery showed that the bloom covered most of the middle and outer shelf south of Nunivak Island in September (Stockwell et al., 2001).

The δ^{15}N of SPOM and sinking organic material collected in 1998 was initially high, similar to that in 1997. Nutrient concentrations and their temporal variation differed markedly

from 1997, with nitrate concentrations in surface waters remaining high through May. Much more organic matter was collected by the sediment traps in 1998 than in 1997, and microscopic analysis of the trapped material revealed numerous fecal pellets. Zooplankton feces are isotopically enriched compared with their food, but can be either heavier or lighter than their bodies (Checkley and Entzeroth, 1985; Checkley and Miller, 1989; Altabet and Small, 1990). However, in 1998 the sediment trap particles were a remarkable 3–4‰ heavier than the copepods and euphausiids, rather than being similar as they were in 1997. Detrital aggregates and unidentified flagellates, most likely heterotrophs, also were found in abundance. Many heterotrophic flagellates are known to be bacteriovores that attach to sinking detrital matter (Caron, 1991). Since the water column's heat content was higher than ever previously recorded (Stabeno et al., 2001) rates of bacterial decomposition may have been accelerated (Rho, 2000), resulting in elevated flagellate biomass. Consistent with this idea, the ammonium concentration across the middle shelf was elevated in early spring (Rho, 2000). The abundance of fecal matter in the sediment trap samples suggests that zooplankton grazing was also an important factor in high ammonium concentrations. As in 1997, the $\delta^{15}N$ of sediment trap samples decreased in fall, 1998, associated with increased vertical mixing and new nutrient supply to surface waters.

In 1999, the $\delta^{15}N$ of SPOM (Table 2) and sinking organic matter (Fig. 4) was much lower than in 1997–1998, although that of zooplankton was essentially unchanged from 1998 (Table 1). A lower flagellate to diatom ratio and less fecal material and detritus were observed in all 1999 spring and summer samples, compared with those from 1997 and 1998, consistent with the difference in $\delta^{15}N$. Another important difference was the relatively low ammonium concentrations in spring, 1999, compared with 1997 and 1998 (Fig. 6). As discussed in the previous section, if the source of some of this ammonium were winter regeneration from sediment organic matter with high $\delta^{15}N$, it could explain the heavier $\delta^{15}N$ of sediment trap material in 1997 and 1998. The lower ammonium in 1999 could have resulted from unusually cold

bottom water temperatures during spring (Stabeno et al., 2003). The $\delta^{13}C$ and $\delta^{15}N$ both decreased from February through the spring and summer, as in earlier years. But in fall 1999, $\delta^{15}N$ values were higher than in February. An alternative explanation is that the $\delta^{15}N$ of nitrate supplied from the outer shelf was lower in 1999; the slightly lower trap sample and SPOM $\delta^{15}N$ at M3 suggests that this could have been a factor, but it can not account for the much larger change at M2. Also counter to this idea is the fact that the bottom water salinity at M2 was nearly the same in spring of each of these years (Stabeno et al., 2003).

M3 was also nutrient-depleted in 1997 (Fig. 7), but zooplankton $\delta^{15}N$ values were much less than those at M2. In 1998, similar to M2, nutrient profiles show high nitrate concentrations in mid-May throughout the entire water column. The $\delta^{15}N$ of SPOM collected in early May was equal to that of sinking material, as also was observed at M2. Large fecal pellets from *N. cristatus* and *N. plumchrus* and flagellates composed a major portion of the sinking organic matter in March through May 20. The 1998 sediment trap samples were slightly more enriched in ^{15}N than in 1999 (Table 3). Much less material, especially diatoms, sank into the trap at M3 compared with M2, and in contrast to M2 the amount of material collected by the sediment trap at M3 was less in 1998 than 1999. More phytoplankton were present in the 1999 trapped material.

The $\delta^{13}C$ values of M2 copepods and euphausiids were slightly heavier in 1999 than in 1997 and 1998, while the weighted average of spring–summer sediment trap samples was slightly heavier in 1998 than in 1997 or 1999. The latter is consistent with the greater quantity of organic matter collected in 1998, if $\delta^{13}C$ reflects primary productivity. However, if this were the case, consistency between the zooplankton and sediment trap samples would be expected. The $\delta^{13}C$ of M3 copepods and euphausiids was statistically the same in 1998 and 1999, while the weighted mean of sediment trap samples was slightly heavier in 1999. Again, the latter is consistent with the greater quantity of organic matter collected in 1999, if $\delta^{13}C$ reflects primary productivity, but a corroborating pattern in zooplankton is lacking. However,

zooplankton sampled mainly in spring do not represent processes over the entire time frame sampled by the sediment traps.

Schell et al. (1998) reported zooplankton δ^{15}N and δ^{13}C for the Bering, Chukchi, and Beaufort Seas, from samples collected during 1985–1990 and 1993–1995. In their report, data from the outer shelf of the southeastern Bering and the middle shelf of the northern Bering Sea are combined as an "Eastern Bering Sea" region. The mean for $n = 64$ copepod samples in this region was $9.8 + 0.22$‰, and for 33 euphausiids was $10.0 + 0.22$‰, lighter than the mean of our 1997 middle and outer shelf samples, but comparable to the 1998 and 1999 values. This is consistent with a variety of indicators that 1997 nutrient depletion was unusual compared to all other years sampled. Our 1997–1999 chaetognath data, however, are all distinctly heavier than those of Schell et al. (1998), which averaged $12.9 + 0.30$‰ for their northern middle and southern outer shelf stations. This suggests that 1997–1999 chaetognaths were feeding at a higher trophic level than before.

Our M3 copepods are distinctly lighter in δ^{13}C than those reported by Schell et al. (1998), which averaged $-22.2 + 0.18$‰ for 72 samples from the eastern Bering. Our δ^{13}C values for euphausiids and chaetognaths were similar to those reported by Schell et al. (1998), however. Schell (2000) reported a decreasing trend in the δ^{13}C of bowhead whale baleen over the past 30 years, which he attributed to decreasing primary productivity in the Bering Sea. The decreased copepod δ^{13}C in 1997–1999, compared with that of copepods collected during 1985–1990 and 1993–1995, is consistent with his observation, but the trend is not necessarily due to primary productivity changes. If the difference was due to a change in phytoplankton δ^{13}C, it should have been seen in euphausiids and chaetognaths also.

The controls on δ^{13}C of phytoplankton have been investigated in culture (Laws et al., 1995; Popp et al., 1998). Phytoplankton carbon isotopic fractionation is a function of the ratio of algal growth rate to the concentration of dissolved carbon dioxide, $\mu/[CO_2]_{aq}$, for particular species. As growth rate μ increases or $[CO_2]_{aq}$ decreases, carbon isotopic fractionation decreases, leading to

cells with increasing δ^{13}C. However, the slope of this function varies more than twenty fold for different phytoplankton species, according to the ratio of cell surface area to volume. Although cell geometry as well as size is important, for cells with similar shapes, carbon isotope fractionation is greater for small cells. Hence their δ^{13}C is lower than that of large cells at a given $\mu/[CO_2]_{aq}$. In the field, μ, $[CO_2]_{aq}$, cell surface area/volume, and the δ^{13}C of the inorganic carbon pool can all vary temporally and spatially (Popp et al., 1998; Villinski et al., 2000).

Our cross-shelf patterns in zooplankton, SPOM, and sediment trap samples, and seasonal changes in sediment trap samples, show very consistent positive correlations between δ^{13}C and δ^{15}N, opposite to the trend reported by Schell et al. (1998), but similar to patterns observed by Goering et al. (1990) and Wu et al. (1999). As yet we have no definitive explanation for the spatial and temporal patterns of stable carbon and nitrogen isotope composition. Our data are consistent with any of the following interpretations.

First, higher δ^{15}N in spring relative to fall, over the middle shelf compared with the outer shelf, and during 1997 and 1998 compared with 1999, were mainly due to isotopically heavy ammonium regenerated from sediment organic matter during winter and spring. This would be an added nutrient source for the year being examined, although derived from earlier years, and hence could drive elevated rates of primary production and higher δ^{13}C.

Second, high rates of primary production resulted in decreased $[CO_2]_{aq}$, causing the ratio $\mu/[CO_2]_{aq}$ to increase and isotopic fractionation to decrease, and leading to increased δ^{13}C of phytoplankton. The δ^{15}N of phytoplankton increased as fractional utilization of the available nitrate (or nitrate plus ammonium) pool increased, but, at least while the bulk of the organic matter production was occurring, phytoplankton growth rates and δ^{13}C remained high. For example, conditions that favored utilization of more of the total water-column inventory of dissolved inorganic nitrogen at M2 could increase μ, δ^{13}C, and δ^{15}N. Such conditions include those in 1997, when

utilization of most of the nitrate below the thermocline occurred, and 1998, when increased mixing supplied more nutrients from subsurface to surface waters.

Third, temporal and spatial changes in phytoplankton species composition also could result in the observed patterns. In this scenario, smaller cells with greater surface area/volume ratio are more important primary producers over the outer shelf than over the middle shelf and in fall compared with spring. Such consistent patterns in phytoplankton species composition were not apparent from the microscopic examination of sediment trap samples, i.e. the species composition was highly variable in time and space. Therefore, one or both of the first two explanations is more likely.

5. Conclusions

- The quantity of material collected by the sediment traps was greater in both spring and late summer-fall than in early and mid summer. In spring, greater quantities of material collected were associated with increases in phytoplankton production and draw down of nutrients. The increased quantity of organic matter in sediment traps in late summer and early fall coincided with increasing wind mixing and supply of nutrients to the photic zone.
- The $\delta^{15}N$ and $\delta^{13}C$ values of SPOM, sediment trap material and zooplankton from the middle shelf site were usually heavier than sediment trap material and zooplankton from the outer shelf. This pattern could be explained greater productivity over the middle shelf, associated with either isotopically heavy nitrogen being regenerated from sediments, or with utilization of a greater fraction of the available inorganic nitrogen pool.
- Seasonal and inter-annual variability of $\delta^{15}N$ at the middle shelf site M2 were pronounced. Interannual and seasonal changes in nutrient supply are probably responsible for much of the variability in $\delta^{15}N$.
- Our data are consistent with a relationship between $\delta^{13}C$ and primary productivity, and

hence lend some support to the Schell (2000) inference that decreasing $\delta^{13}C$ of bowhead whale baleen indicates declining Bering Sea productivity over the past 30 years. However, we can not rule out other factors influencing $\delta^{13}C$, such as phytoplankton species effects.

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