

Organic matter pathways to zooplankton and benthos under pack ice in late winter and open water in late summer in the north-central Bering Sea

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ABSTRACT: On continental shelves in arctic and subarctic seas, much of the production from spring blooms at the retreating ice edge may sink to the bottom with little grazing by zooplankton, thereby supporting abundant benthic communities. The importance of this settled phytoplankton to macrobenthos throughout the year may partly determine effects of long-term changes in ice cover. We studied organic matter (OM) pathways to macrobenthos and macrozooplankton under ice cover in late winter (March–April) and open water in late summer (September) in the north-central Bering Sea. In late winter 2001, only a very small fraction of OM in the water column was particulate. C:N ratios, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ in suspended particulate organic matter (SPOM), and sediments indicated very little recent input of fresh ice algae or phytoplankton in ice-covered areas. For the 3 main deposit-feeding bivalves, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ indicated similar diets among species, with minimal change in food quality between late summer and late winter, and between late winters with very different ice cover (1999 vs. 2001). In winter 2001, there were large increases in $\delta^{13}\text{C}$ from SPOM to bulk sediments (+3.2‰) and from sediments to near-surface deposit-feeders (+1.6 to +3.0‰), but small differences in $\delta^{15}\text{N}$ from SPOM to sediments (+1.2‰) and from sediments to deposit-feeders (–0.3 to +1.6‰). These values suggest that the diet of near-surface deposit-feeders during these non-bloom periods included substantial amounts of the cells or products of bacteria that had assimilated well-reworked carbon and isotopically light dissolved inorganic nitrogen (DIN). By late summer and through winter, 4 to 11 mo after the spring bloom, products of bacterial activity appeared to be an important route of OM into the benthic food web. Due to bacterial dependence on annual carbon inputs, and unique nutrient content of fresh phytoplankton for breeding invertebrates, ice-edge blooms might be an important determinant of annual variations in macrobenthic abundance.

KEY WORDS: Food webs · Organic matter sources · Sea ice · Spring bloom · Stable isotopes

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INTRODUCTION

In recent years, much research has focused on climate-related changes in the annual and seasonal extent of ice cover in arctic and subarctic seas (e.g. Niebauer et al. 1999, Parkinson & Cavalieri 2002, Shapiro et al. 2003). Despite variation among regions, the overall trend is of decreasing maximum extent, as

well as earlier and more extensive melting (Vinje & Kvambekk 1991, Stabeno & Overland 2001, Parkinson & Cavalieri 2002, Overland & Stabeno 2004). As explained below, such changes may substantially reduce the amount of the spring bloom that settles directly as food for benthic communities. The consequences of such effects depend in part on the trophic importance, throughout the year, of fresh phytoplank-

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ton versus longer-term organic pools in the sediments. In this study, we investigated sources and flows of organic matter in the Bering Sea during open water in late summer and under pack ice in late winter, 4 to 11 mo after the spring bloom.

How does ice cover affect the supply of organic matter to the benthos? Species of ice algae differ from algal species in the main ice-edge bloom, and the ice algal fraction of total annual primary production over shallow continental shelves with winter-only pack ice is variable but often just a few percent (Horner 1985, Gosselin et al. 1997). This fraction is higher in deep oligotrophic areas with year-round ice cover than in shallow nutrient-rich areas such as the Bering shelf, where the period between freezing and melting of southward-flowing pack ice is mostly <5 wk, and ice cover lasts <6 mo (cf. central Arctic Ocean versus peripheral shelves, Gosselin et al. 1997). Far more important than ice algal production, under thinning ice and in the broken marginal ice zone, input of low-salinity meltwater and suppressed wind mixing cause the water column to stratify, fostering an intense bloom that follows the ice edge as it recedes over large areas (Sakshaug & Slagstad 1992, Niebauer et al. 1995, Engelsen et al. 2002). A number of weeks later, the water column stratifies by solar heating, allowing an open-water bloom if adequate nutrients remain or are replenished (Niebauer et al. 1995). In areas that were free of pack ice, there is only an open-water bloom that is later and occurs with less intensity over a longer period. In the Bering Sea, earlier melting tends to result in lower phytoplankton biomass during the bloom (Saitoh et al. 2002). Based on work in other regions, interpretations differ as to whether total primary production when an ice-edge bloom occurs exceeds that from an open-water bloom alone (Sakshaug & Slagstad 1992, Strass & Nöthig 1996, Ramseier et al. 1999, Engelsen et al. 2002). Regardless of such disparities, the fate of production from the 2 bloom types is thought to be quite different.

On the continental shelf of the northern Bering Sea, particles produced during an ice-edge spring bloom often have only 30 to 100 m to sink to the bottom. Zooplankton populations are very low after a dark winter under the ice with minimal primary production, and with very low temperatures. Consequently, the very large but brief pulse of carbon from an ice-edge bloom mostly sinks to the bottom without being grazed by zooplankton (Coyle & Cooney 1988, Grebmeier et al. 1988). If pack ice does not extend over an area so that there is no ice-edge bloom, then the open-water bloom occurs a number of weeks later, and is grazed heavily by zooplankton whose populations have increased by that time (Coyle & Pinchuk 2002, Hunt et al. 2002, Olli et al. 2002). As a result, much less of the bloom reaches the bottom to sup-

port benthic communities. The ability of well-developed macrozooplankton populations to graze most of the production from an open-water bloom may vary among regions of the shelf (Cooney & Coyle 1982), and grazing by protists may also be important (Hansen et al. 2003). However, it appears that food reaching the benthos might be reduced by decreased ice extent, and by earlier melting under shorter daylight conditions.

How much and how quickly would benthic communities be affected by ice-mediated changes in the supply of fresh phytoplankton? Answers depend partly on how long phytoplankton persists alive in aphotic sediments, and on relative consumption of fresh phytoplankton versus products of bacteria derived from longer-term organic pools. Studies from various areas indicate that living phytoplankton, and chlorophyll which is contained mainly within living phytoplankton (Hansen & Josefson 2004), can persist in sediments for months (Kanneworff & Christensen 1986, Hansen & Josefson 2001). However, gut contents and experiments on macrobenthos have often revealed little direct consumption of living phytoplankton or chlorophyll, even during and after sedimentation of spring blooms (Blegvad 1914, Webb 1993, Johnson 1987, van de Bund et al. 2001). One study found substantial phaeopigment in the guts of bivalves and a polychaete during and just after a spring bloom, but far less such material at other times (Christensen & Kanneworff 1985). In the deep sea, some sedimenting chlorophyll *a* was ingested selectively with newly settled deposits, whereas some chlorophyll *a* was consumed in a mix with older sediments (Miller et al. 2000).

Some recent studies on a range of macroinvertebrates suggest that living phytoplankton are not assimilated directly (Nichols & Garling 2000, Hansen & Josefson 2004); instead, phytoplankton persisting in the sediments may become gradually available to deposit-feeders only after the phytoplankton die and undergo microbial processing (Hansen & Josefson 2004). Some polychaetes (but not others) showed rapid uptake of ^{13}C from labeled diatoms, but these diatoms were freeze-dried (killed) before being applied to sediments (Levin et al. 1999). On continental shelves, respiration rates of sediments (including macrofauna) are often high during periods of high phytoplankton production (Graf et al. 1982, Kanneworff & Christensen 1986, Grebmeier & McRoy 1989, Grebmeier & Cooper 1995, Cooper et al. 2002). However, such rates may result from rapid metabolism of a labile fraction of sedimenting particles that includes non-living phytodetritus and microbial products, while much of the living phytoplankton that settles is degraded only gradually (Hansen & Josefson 2004).

The trophic importance of fresh phytodetritus versus material processed by and derived from bacteria

appears to vary among macroinvertebrate taxa (Graf et al. 1982, Christensen & Kannevorf 1985, Johnson 1987, Lopez & Levinton 1987, Carey & Mayer 1990, Webb 1993, Levin et al. 1999, Josefson et al. 2002, Thomas & Blair 2002). Consequently, ice-mediated changes in bloom sedimentation might affect not only the total food supply, but also the relative dominance of species with varying dependence on newly deposited versus longer-term organic pools in the sediments. The reproductive schedules of a number of benthic invertebrates appear to be related to bloom pulses, but pulses occur variously during adult conditioning, gamete formation, or juvenile growth, and correlations are not apparent in all taxa (Graf et al. 1982, Tyler et al. 1992, Ambrose & Renaud 1997). Thus, food sources during non-bloom periods, when fresh phytoplankton may not be abundant or rapidly assimilated, may be critical to reproduction, growth, and survival of different macroinvertebrates with differing annual phenologies.

To provide insight into these questions in the north-central Bering Sea, we used C:N ratios and stable isotopes of carbon and nitrogen to evaluate the sources of organic particles in the water column and sediments, and the sources and flows of organic matter for pelagic and benthic macroinvertebrates. South of St. Lawrence Island, sampling was conducted under the ice in April 1999 and March 2001 before the ice-edge bloom, and during the ice-free season in September 1999, long after the spring bloom. To assess the availability of particulate versus dissolved organic matter to planktonic food webs, and the potential for organic sedimentation to the benthos, we also measured concentrations of dissolved and particulate organic matter in the water column in March 2001. All these data were used to infer the direct importance of fresh phytoplankton from the spring bloom to food webs at other times of year.

MATERIALS AND METHODS

Study area. From late December through April in the Bering Sea, pack ice forms north of St. Lawrence Island and is advected southward by prevailing winds at typical speeds of 17 to 22 km d⁻¹ to as fast as 28 to 32 km d⁻¹ (Niebauer et al. 1999). Maximum ice extent and chronology of extent vary widely among years. This study was conducted south of St. Lawrence Island (61.2° to 63.3° N, -170.0 to -175.3° W) from 13 to 27 April and 16 to 26 September 1999, and 17 March to 1 April 2001. During ice cover in March–April, samples were collected from the US Coast Guard icebreakers ‘Polar Sea’ (1999) and ‘Polar Star’ (2001). September samples during the ice-free season were collected from the RV ‘Alpha Helix’.

Samples were collected at the same stations on a grid used by our research group since 1988; see Clement et al. (2004) for a map of the grid and study area. Water depth ranged from 30 to 100 m.

Total and dissolved organic carbon in the water column. In March 2001, water samples were collected with 10 l Niskin bottles from 2 m below the water surface, mid-depth (mean 27 m), and 5 m above the bottom. Water samples were transferred to amber borosilicate bottles (previously baked for 2 h at 500°C), which were capped tightly and immediately frozen for later analysis. In the laboratory, aliquots to be analyzed for dissolved organic carbon (DOC) were filtered through pre-combusted, 0.7 µm, glass-fiber filters (Whatman GF/F) that were pre-rinsed with 1 l of 18 MΩ water. The latter samples, and unfiltered samples to be analyzed for total organic carbon (TOC), were 0.1% acidified with reagent-grade 85% H₃PO₄ before 3 replicate subsamples were analyzed by high-temperature catalytic oxidation (Shimadzu TOC analyzer, model 5000A). At the start of each analytical run, consensus reference materials were analyzed. Reference materials were low carbon water (lot #05-00-4) and deep Sargasso Sea water (lot #06-00; www.rmas.miami.edu/groups/organic-biogeochem/crm.html) provided by the laboratory of D. A. Hansell at the University of Miami, Florida, USA.

Particulate organic matter in ice algae, the water column, and sediments. During all 3 sampling periods, water samples were collected with Niskin bottles at 3 depths per station as described in the preceding section. Free-floating chunks of ice that were colored with ice algae were retrieved from beside the ship with a metal bucket lowered on a rope, and melted at room temperature under shaded conditions on the ship. Water from both Niskin bottles and melted ice was filtered on the ship through pre-combusted, 0.7 µm, glass-fiber filters (Whatman GF/F), which were frozen for later analysis. To remove inorganic carbonates, filters were acid-fumed by placing them in a large desiccator on a perforated ceramic platform over a pool of 10% HCl for 20 min. Samples of each dried filter plus residue were taken with a hole punch. Also at each station, surface sediments (1 cm³, 1.54 cm² surface area) were collected from the top of a sample taken with a van Veen grab before the grab was opened. Sediments were oven-dried at 60°C, ground, and acidified with 0.1 N HCl to remove inorganic carbonates. Both filter and sediment samples were analyzed for carbon and nitrogen content, δ¹³C and δ¹⁵N.

Zooplankton and macrobenthos. Macrozooplankton was collected with a ring net (1 m diameter) with 0.5 mm mesh, lowered to 5 m above the bottom and raised vertically at a speed of 0.5 m s⁻¹. Retained organisms were frozen in salt water until later analysis.

In the laboratory, thawed samples were sorted by species, pooled within sample station, rinsed with distilled water onto pre-combusted glass-fiber filters, and oven-dried at 55°C. Lipids can become depleted in ^{13}C during synthesis (DeNiro & Epstein 1977), so that body lipids can have lower $\delta^{13}\text{C}$ values than other major body components (proteins and carbohydrates) (see references in Wada et al. 1987); thus, whole-body $\delta^{13}\text{C}$ can vary appreciably with lipid levels even if the diet does not change. Consequently, before isotope analysis, lipids were extracted from tissue samples with petroleum ether (Focken & Becker 1998). Each dried filter was immersed in a jar of ether, which was stirred during the day about twice per hour, and replaced every 24 h over 3 d of immersion. To remove inorganic carbonates, the filters were placed in a glass desiccator on a perforated ceramic platform above a pool of 10% HCl, and removed after 20 min. Each sample was then scraped off its filter into a mortar immersed in a jacket of liquid nitrogen, which froze the sample as it was ground with a pestle into a fine powder.

Benthic macroinvertebrates were collected with a van Veen grab (area of each sample was 0.1 m²). Samples were washed over a 1 mm sieve, and retained organisms were frozen for later analysis. In the laboratory, organisms were sorted by species and pooled by sample station. Worms were extracted from tubes and their gut contents removed; for stations included in analyses, there were typically 3 to 4 individuals per station. Gut contents were removed from amphipods, and there were typically 5 to 6 individuals per station. For bivalves, we analyzed muscle tissues only (adductors and foot), with typically 8 to 15 individuals per station. For ophiuroids, we analyzed 1 proportionate leg from each specimen, usually with 4 to 8 individuals per station. Samples were oven-dried at 55°C and ground with a mortar and pestle. To extract lipids, each dried sample was immersed in a jar of petroleum ether for 3 d as described above for zooplankton. To remove inorganic carbonates, samples were immersed in 10% HCl and re-dried. We present data only for species and stations with enough material for analysis.

Elemental and isotope analyses. Samples were combusted in an elemental analyzer (ANCA g/s/l sample preparation module) interfaced with a Europa 20:20 continuous-flow isotope-ratio mass spectrometer (Europa Scientific). Stable isotope values are reported in δ notation as the deviation from standards in parts per thousand (‰) by the equation $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where X is ^{13}C or ^{15}N and R is the ratio of $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. Standard values were based on Vienna-PeeDee Belemnite for ^{13}C and atmospheric N_2 for ^{15}N . Precision based on repeated measurements of internal laboratory standards of albumen was $\pm 0.1\%$ for $\delta^{13}\text{C}$ and $\pm 0.3\%$ for $\delta^{15}\text{N}$. The notation $\Delta^{13}\text{C}$ and

$\Delta^{15}\text{N}$ refers to differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. C:N ratios were calculated in terms of the numbers of atoms of each element.

Statistical analyses. With SAS software (SAS Institute), t -tests, analyses of variance (ANOVAs), and Bonferroni pairwise comparisons were used to test for differences. Differences where $p < 0.05$ were considered significant.

RESULTS

The maximum extent and chronology of ice cover in the study area varied dramatically between 1999 and 2001. In 1999, ice cover was extensive throughout winter, reaching the shelf break from at least February through April. Thus, during our sampling in April, relatively thick ice with much ice algae still covered the study area. In contrast, in 2001, ice cover was unusually absent for most of winter, and extended south over the study area for the first time only the week before we arrived in mid-March. Thus, compared to April 1999, the ice in March 2001 was generally thinner, was more recently formed, and contained relatively little ice algae; any effects of ice cover on pelagic and benthic communities had had only 1 to 3 wk to develop.

Water-column TOC and DOC

In the well-mixed water column during March 2001, there were no differences (1-way ANOVAs) between near-surface, mid-depth, and near-bottom water samples in TOC ($p = 0.47$) or DOC ($p = 0.57$). TOC did not differ significantly from DOC at any depth (paired t -tests, all $p > 0.75$), i.e. concentrations of particulate organic carbon ($\text{POC} = \text{TOC} - \text{DOC}$) were so small as to be within measurement errors of TOC and DOC. The mean ($\pm \text{SE}$) DOC concentration at mid-depth was $65 \pm 2 \mu\text{mol l}^{-1}$ (range 48 to 94 $\mu\text{mol l}^{-1}$, $n = 27$ stations with viable samples).

Stable isotope and C:N ratios of ice particulate organic matter (POM), POM suspended in water column (SPOM), and sediments

Neither $\delta^{13}\text{C}$ nor $\delta^{15}\text{N}$ values of SPOM varied appreciably with depth during any sampling period, except for $\delta^{13}\text{C}$ near the bottom in September 1999 when stormy conditions probably caused more resuspension of sediments on this shallow shelf (Fig. 1, Table 1). $\delta^{13}\text{C}$ of SPOM was 1.1 to 2.1‰ higher in April 1999 than in March 2001. This difference might have resulted from greater input of ice POM, as well as 3.3‰ higher $\delta^{13}\text{C}$

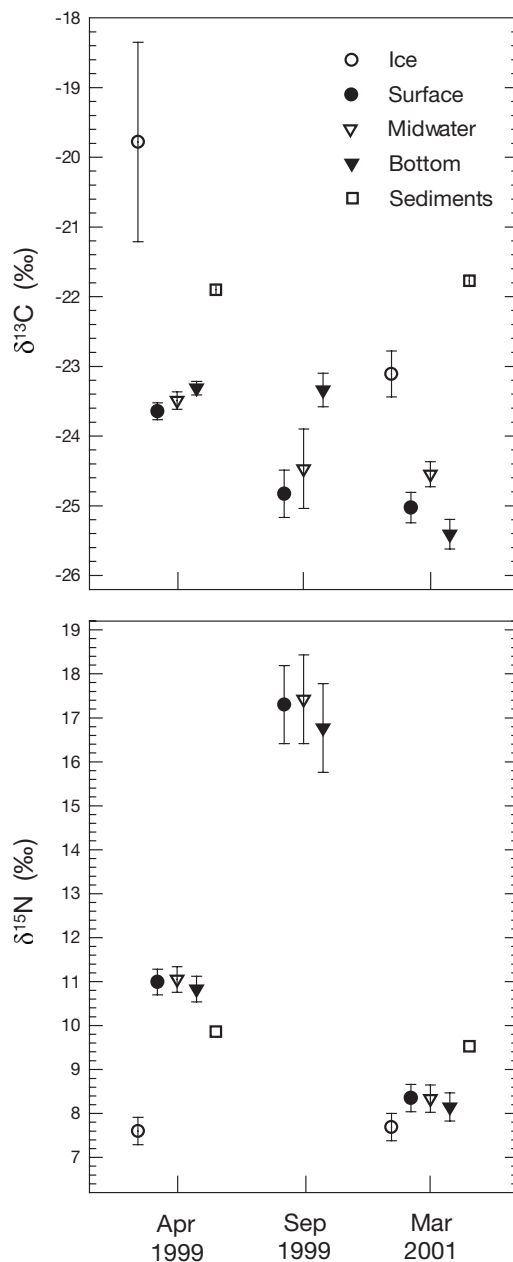


Fig. 1. Mean (\pm SE) stable isotope values ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of particulate organic matter (POM) in surface sediments, in pack ice (ice POM), and suspended in the water column (SPOM) ~2 m below the water surface (surface), halfway to the bottom (midwater), and 5 m above the bottom (bottom) south of St. Lawrence Island in the Bering Sea in April 1999 (32 stations), September 1999 (24 stations), and March 2001 (41 stations). For $\delta^{13}\text{C}$, means for surface and midwater SPOM were 1.0 to 1.4‰ heavier in April 1999 than in the other time periods, which did not differ (Bonferroni pairwise comparisons, $\alpha = 0.05$). Mean $\delta^{13}\text{C}$ of SPOM at 5 m above the bottom averaged 2.1‰ heavier in April 1999 than in March 2001 ($p < 0.05$; bottom samples in September 1999 were influenced by very stormy conditions). Mean $\delta^{15}\text{N}$ of SPOM differed between periods at each depth ($p < 0.05$). POM in ice differed between April 1999 and March 2001 in $\delta^{13}\text{C}$ (t -test, $p < 0.001$) but not in $\delta^{15}\text{N}$ ($p > 0.90$). Error bars for sediments are too small to be seen

of ice POM, in 1999. However, $\delta^{15}\text{N}$ values of SPOM were also 2.6 to 2.7‰ higher in April 1999 than March 2001, when there was no difference in $\delta^{15}\text{N}$ of ice POM. Different patterns in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of SPOM compared to ice POM in 1999 versus 2001 suggest that inputs of ice POM were not the main determinant of isotope values in SPOM. Isotope values of SPOM in late winter were more consistently related to C:N ratios, whereby higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were associated with lower C:N ratios (cf. Figs. 1 & 2). This pattern might indicate more heavily reworked particles with higher bacterial content (lower C:N ratios) in April 1999 than in March 2001 (in other studies, C:N ratios of bacteria have been about 4, versus Redfield values for phytoplankton of around 6.6, Hedges et al. 1997, Daly et al. 1999).

In our study, the $\delta^{15}\text{N}$ values of SPOM (Fig. 1) were much heavier in September (mean = 17.1‰) than during late winter of both years; our values were in fact much higher than values of 5 to 10‰ during early to mid-summer reported for other regions (Owens 1987, Hobson et al. 1995, 2002). Our high values of $\delta^{15}\text{N}$ in late September may reflect a large fraction of fecal pellets relative to phytoplankton in SPOM at that time, when zooplankton have reached peak abundance and phytoplankton production has declined. Other studies have shown copepod fecal pellets to be enriched by ~8‰ in $\delta^{15}\text{N}$ relative to SPOM during productive periods (Checkley & Entzeroth 1985), and report an absolute value of 8‰ for the portion of SPOM that was consumed (Mariotti et al. 1984, Butler & Dam 1994). Based on those published results, our values of $\delta^{15}\text{N}$ in September are near those expected for bulk SPOM dominated by fecal pellets after the productive season.

The mean (\pm SE) C:N ratio of bulk sediments (Fig. 2) was 7% higher in April 1999 (7.77 ± 0.03) than at the same stations in March 2001 (6.98 ± 0.06) (paired t -test, $p < 0.001$, $n = 27$). Bulk sediment values of $\delta^{13}\text{C}$ did not differ between winters at the same stations (paired t -test, $p = 0.07$). Mean winter values of $\delta^{15}\text{N}$ did not differ between years by more than analytical error, emphasizing the very small variation between years at the same stations. The small within-year variation among stations in C:N ratios, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ in sediments during both winters (Figs. 1 & 2) also indicates that these soft, unconsolidated sediments were well mixed horizontally, perhaps suggesting frequent resuspension and transport together with bioturbation. Compared to marked changes between winters in stable isotope signatures of SPOM, values in bulk sediments stayed relatively constant (Fig. 1). In addition, while the C:N ratio of SPOM was higher in March 2001 than in April 1999, that of sediments showed the reverse trend (Fig. 2). These patterns suggest that stable isotope values and C:N ratios of the bulk organic

Table 1. Mean (\pm SE) C:N ratios (by atoms) and stable isotope values ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, ‰) in particulate organic matter (POM) in pack ice, in the sediments, and suspended in the water column (SPOM) south of St. Lawrence Island in the Bering Sea

Sample type	No. of stations	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C:N
Ice POM, Apr 1999	18	-19.8 ± 1.4	7.6 ± 0.3	8.4 ± 0.2
Ice POM, Mar 2001	28	-23.1 ± 0.3	7.7 ± 0.3	9.5 ± 0.5
Sediment POM, Apr 1999	30	-21.9 ± 0.1	9.9 ± 0.1	7.8 ± 0.1
Sediment POM, Mar 2001	37	-21.8 ± 0.1	9.5 ± 0.1	7.0 ± 0.1
SPOM, Apr 1999				
2 m below surface	32	-23.6 ± 0.1	11.0 ± 0.3	7.3 ± 0.1
Mid-depth	32	-23.5 ± 0.1	11.0 ± 0.3	7.2 ± 0.1
5 m above bottom	32	-23.3 ± 0.1	10.8 ± 0.3	7.3 ± 0.1
SPOM, Sep 1999				
2 m below surface	24	-24.8 ± 0.3	17.3 ± 0.9	7.7 ± 0.3
Mid-depth	24	-24.5 ± 0.6	17.4 ± 1.0	7.8 ± 0.3
5 m above bottom	24	-23.3 ± 0.2	16.8 ± 1.0	8.3 ± 0.2
SPOM, Mar 2001				
2 m below surface	41	-25.0 ± 0.2	8.3 ± 0.3	10.3 ± 0.4
Mid-depth	41	-24.6 ± 0.2	8.3 ± 0.3	9.0 ± 0.4
5 m above bottom	41	-25.4 ± 0.2	8.2 ± 0.3	11.5 ± 0.6

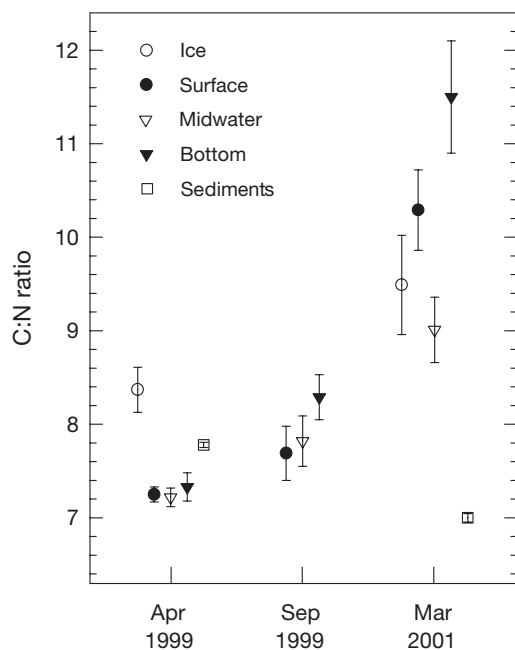


Fig. 2. Mean (\pm SE) carbon:nitrogen ratios (C:N, by atoms) of particulate organic matter (POM) in surface sediments, in pack ice (ice POM), and suspended in the water column (SPOM) ~2 m below the water surface (surface), halfway to the bottom (midwater), and 5 m above the bottom (bottom) south of St. Lawrence Island in the Bering Sea in April 1999 (32 stations), September 1999 (24 stations), and March 2001 (41 stations). Error bars for sediments are smaller than the symbols

pool in sediments were relatively uncoupled from concurrent values in SPOM as well as ice POM. Values of $\delta^{13}\text{C}$ averaged 1.4 to 1.7‰ higher in sediments than in SPOM in April 1999, and 2.8 to 3.6‰ higher in March 2001. The difference was less for $\delta^{15}\text{N}$, with values

being only 1.0 to 1.2‰ heavier in sediments than in SPOM in 1999, and 1.2 to 1.4‰ higher in 2001.

Stable isotope ratios in deposit-feeding bivalves

For the 3 main deposit-feeding bivalves *Nuculana radiata*, *Macoma calcaria*, and *Nucula belloti*, $\delta^{13}\text{C}$ values in muscle did not differ significantly among species ($p = 0.38$, Fig. 3, Table 2). Values of $\delta^{13}\text{C}$ also did not differ among sampling periods ($p > 0.05$), except between April and September 1999 for *M. calcaria*, when the largest difference occurred but was still only 0.8‰ (other differences were < 0.4 ‰).

Tests for species and sampling periods were from 2-way ANOVA with Bonferroni comparisons; there were no interactions. For $\delta^{15}\text{N}$, there were no differences between sampling periods ($p = 0.26$), nor between *N. radiata* and *N. belloti* ($p > 0.05$); *M. calcaria* differed from *N. radiata* by 1.0 to 1.1‰, and from *N. belloti* by 0.4 to 0.8‰ ($p < 0.05$). These patterns indicate that these species consumed very similar foods, and that the isotope ratios of those foods showed minimal variation between September and March–April, and between winters with very different ice cover.

Stable isotope ratios among all macroinvertebrates

Other studies of a range of aquatic food webs have found mean increases of ≤ 1 ‰ $\delta^{13}\text{C}$ and ~ 3.4 ‰ $\delta^{15}\text{N}$ per trophic transfer (see 'Discussion'). In our study, in March 2001, the copepod *Metridia pacifica* and pelagic amphipod *Themisto pacifica* were 2.6 to 2.8‰ higher in $\delta^{13}\text{C}$, but only 0.8 to 1.5‰ higher in $\delta^{15}\text{N}$, than SPOM (Fig. 4, Table 2). The copepod *Calanus marshallae* and euphausiid *Thysanoessa inermis* were 2.8 to 3.7‰ higher in $\delta^{13}\text{C}$, and 2.8 to 3.4‰ higher in $\delta^{15}\text{N}$, than SPOM (Fig. 4), perhaps reflecting a more carnivorous diet. The chaetognath *Sagitta elegans* had just over 1‰ higher $\delta^{13}\text{C}$, and 3.6 to 5.6‰ higher $\delta^{15}\text{N}$, than potential copepod prey.

Among benthic deposit-feeders (for details of feeding modes see Table 2), 4 bivalve species were all about 6‰ higher in $\delta^{13}\text{C}$ than SPOM, and 2.8‰ higher than sediments (Fig. 4, Table 2). For $\delta^{15}\text{N}$, the bivalves *Macoma calcaria* and *Yoldia hyperborea* were only 0.9 to 1.5‰ higher than SPOM, and differed from sediments by only -0.3 to 0.3‰; these infaunal species have long siphons and can stay buried while still feeding on surface de-

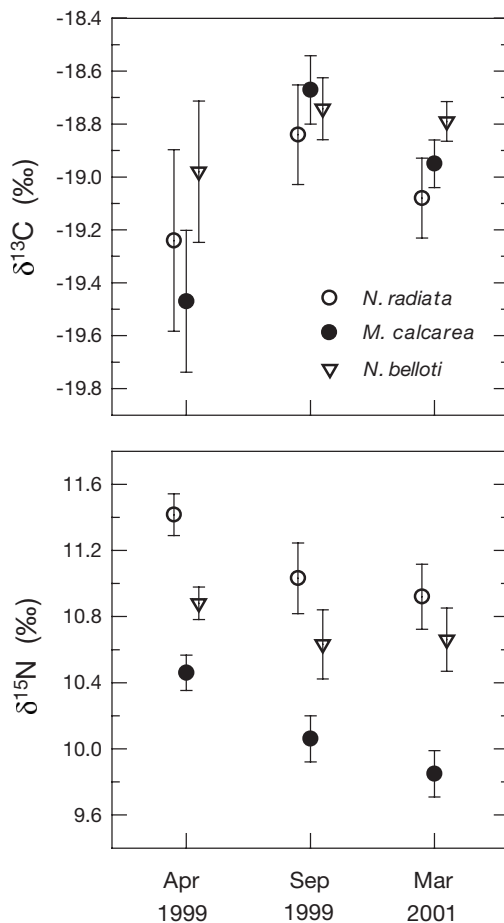


Fig. 3. *Nuculana radiata*, *Macoma calcareea*, and *Nucula belloti*. Mean (\pm SE) stable isotope values ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) in muscle tissue of the bivalves *N. radiata*, *M. calcareea*, and *N. belloti* south of St. Lawrence Island in the Bering Sea in April 1999 ($n = 3$ to 5 stations per species), September 1999 ($n = 18$ to 22 stations per species), and March 2001 ($n = 23$ to 35 stations per species). For statistical comparisons, see text

posits via their incurrent siphons (*M. calcareea*) or long labial palps (*Y. hyperborea*). The $\delta^{15}\text{N}$ of *Nucula belloti* and *Nuculana radiata* was 2.4 to 2.6‰ higher than in SPOM, and 1.1 to 1.4‰ heavier than in sediments. The latter species have very short siphons and cannot access the actual surface of sediments when buried; thus, their diet may include a larger mix of subsurface sediments with higher $\delta^{15}\text{N}$ values than was ingested by the other 2 bivalve species. The amphipod *Pontoporeia femorata* was about 1‰ less fractionated in ^{13}C than the bivalves, but was similar to *Nucula* and *Nuculana* in $\delta^{15}\text{N}$. *Pontoporeia*'s lighter $\delta^{13}\text{C}$ than in the bivalves, and more similar $\delta^{15}\text{N}$ to *Nucula* and *Nuculana*, might result from the more subsurface feeding of *P. femorata*, with greater consumption of phytoplankton detritus than of bacterial production. This trend was even more apparent in the polychaete *Pectinaria hyperborea*, whose $\delta^{13}\text{C}$ was

~1.6‰ lower, and $\delta^{15}\text{N}$ was 3.4 to 5.1‰ higher, than in the bivalves (Fig. 4); *Pectinaria* is an obligate subsurface feeder.

Other macrobenthos (Fig. 4) included the brittle star *Ophiura sarsi*, whose isotope ratios appeared to reflect scavenging of animal tissues from the bivalve-dominated community. Isotope ratios for the gastropod *Natica clausa* supported previous reports that it preys mainly on bivalves (Table 2). Ratios for the worms *Priapululus caudatus* and *Lumbrinereis fragilis* indicated more general predatory habits (Table 2).

DISCUSSION

Sources of SPOM

Under pack ice in March 2001, only a very small fraction of carbon in the water column was particulate. Chlorophyll *a* concentrations integrated over the water column were quite low, ranging from 3.11 to 54.22 mg m^{-2} in March 2001, and from 9.43 to 78.20 mg m^{-2} in April 1999 (Clement et al. 2004). Ice POM had much higher $\delta^{13}\text{C}$, and lower $\delta^{15}\text{N}$, than SPOM (Fig. 1). Thus, the contribution of living ice algae to SPOM appeared minimal in March–April of both years.

The SPOM that remains suspended might not be the same as the POM that settles to the sediments. It has been suggested that the often large difference in $\delta^{13}\text{C}$ values between SPOM and polar sediments results from sedimentation of isotopically heavy ice algae (e.g. Wada et al. 1987, Nyssen et al. 2002). However, during studies in the SE Bering Sea, algae did not become abundant in the ice until March–April, when the daylight period increased (McRoy & Goering 1974). At the time of our cruises before the ice had melted, it appeared that a relatively small fraction of this late-forming ice algae had been released. Moreover, $\delta^{13}\text{C}$ values in different bivalve species (Fig. 3) were actually 0.2 to 0.5‰ lighter in April 1999 when there were large amounts of isotopically heavier ice algae (−19.8‰, Fig. 1) than in March 2001, when there were only small amounts of isotopically lighter ice algae (−23.1‰). This pattern suggests that diagenetic processes were more important than ice algal sedimentation in yielding the 3.2‰ higher $\delta^{13}\text{C}$ in sediments than in SPOM (Fig. 4, cf. Canuel & Martens 1993).

Seasonal diet of deposit-feeding bivalves

Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ indicate that the 3 main deposit-feeding bivalves consumed very similar foods, with minimal change in food quality between late summer and late winter, and between late winters with

Table 2. Feeding mode and mean (\pm SE) stable isotope values ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, ‰) of pelagic and benthic invertebrates south of St. Lawrence Island in the Bering Sea. For invertebrates, multiple individuals were pooled within stations at which the species occurred in adequate biomass for analysis. All data are from March 2001 except for *Pectinaria hyperborea*, *Lumbrinereis impatiens*, and *Priapulus caudatus*, which are from September 1999

Sample type	No. of stations	Feeding mode ^a	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Bivalves				
<i>Nuculana radiata</i>	23	Subsurface deposits ^{1,2,3}	-19.1 ± 0.2	10.9 ± 0.2
<i>Macoma calcarea</i>	30	Fine surface deposits, often top mm ^{4,5,6}	-19.0 ± 0.1	9.8 ± 0.1
<i>Nucula belloti</i>	35	Subsurface deposits ^{1,2,3}	-18.8 ± 0.1	10.7 ± 0.2
<i>Yoldia hyperborea</i>	6	Surface and subsurface deposits ^{7,8}	-18.9 ± 0.3	9.2 ± 0.4
Crustaceans				
<i>Calanus marshallae</i>	30	Suspended particles/microzooplankton ^{9,10,11}	-22.2 ± 0.1	11.1 ± 0.2
<i>Metridia pacifica</i>	8	Suspended particles/microzooplankton ^{9,10,11}	-22.2 ± 0.3	9.1 ± 0.5
<i>Themisto pacifica</i>	8	Suspended particles/copepodids ^{12,13}	-22.4 ± 0.3	9.8 ± 0.5
<i>Pontoporeia femorata</i>	6	Near-surface deposits ^{14,15}	-20.2 ± 0.5	11.2 ± 0.7
<i>Thysanoessa inermis</i>	25	Suspended particles ¹⁶	-21.3 ± 0.1	11.7 ± 0.2
Gastropod				
<i>Natica clausa</i>	6	Predator, especially on bivalves ^{17,18}	-18.4 ± 0.3	14.3 ± 0.8
Echinoderm				
<i>Ophiura sarsi</i>	12	Surface omnivore/detritivore ^{19,20}	-19.0 ± 0.6	15.5 ± 0.7
Polychaetes				
<i>Lumbrinereis fragilis</i>	3	Predator, including ophiuroids, polychaetes, small bivalves and crustaceans ²¹	-17.2 ± 0.2	15.6 ± 0.1
<i>Pectinaria hyperborea</i>	2	Subsurface deposits ²²	-20.6 ± 0.4	14.3 ± 0.7
Priapulid				
<i>Priapulus caudatus</i>	2	Predator, including ophiuroids and worms ²³	-17.7 ± 0.6	16.5 ± 0.2
Chaetognath				
<i>Sagitta elegans</i>	4	Predator, mainly on copepods ²⁴	-21.1 ± 0.5	14.7 ± 0.7

^aReferences for feeding modes: ¹Levinton (1982), ²Cheng (1983), ³Lopez & Cheng (1983), ⁴Reid & Reid (1969), ⁵Hylleberg & Gallucci (1975), ⁶Rossi et al. (2004), ⁷Bender & Davis (1984), ⁸Stead et al. (2003), ⁹Runge et al. (1991), ¹⁰Atkinson (1996), ¹¹Levinsen et al. (2000), ¹²Bradstreet & Cross (1982), ¹³Auel & Werner (2003), ¹⁴Lopez & Elmgren (1989), ¹⁵Byrén et al. (2002), ¹⁶Falk-Petersen et al. (2000), ¹⁷Bernard (1967), ¹⁸Barnes (1980), ¹⁹MacGinitie (1949), ²⁰Warner (1982), ²¹Blegvad (1914), ²²Dobbs & Scholly (1986), ²³Lang (1948), ²⁴Terazaki (1998)

very different ice cover (Fig. 3). Although turnover rates of stable isotopes in organic tissues of subarctic bivalves have not been measured, a number of studies in north-temperate regions indicate that turnover rates in bivalves are high enough for seasonal variations in organic matter sources to be detectable (e.g. Lorrain et al. 2002, Rossi et al. 2004).

Diet of deposit-feeders: inference from $\delta^{13}\text{C}$

The average fractionation of $\delta^{13}\text{C}$ per trophic level is widely accepted as being $\leq 1\text{‰}$ (Vander Zanden & Rasmussen 2001). Thus, the large increase in $\delta^{13}\text{C}$ from SPOM to bulk sediments (3.2‰) suggests that the organic matter available to deposit-feeders was well reworked (Fischer 1991, Nyssen et al. 2002). However, the large increase in $\delta^{13}\text{C}$ from sediments to deposit-feeders (1.6 to 3.0‰, Fig. 4) indicates a smaller labile portion in sediments that is selectively assimilated (hence the large fractionation) by bivalves and the amphipod *Pontoporeia*. A review by Mayer (1993) sug-

gested that 30% or more of organic matter deposited in sediments is soon converted into new biomass of bacteria and their products. Thus, the labile pool during late summer and late winter, 4 to 11 mo after the spring bloom, may include substantial new biomass of bacterial origin, in addition to incompletely decomposed algal detritus (Moriarty 1982, Turley & Lochte 1990, Canuel & Martens 1993, Mayer 1993). Isotope fractionation during production of bacterial biomass can vary widely with substrate, but averaged 2.3‰ in $\delta^{13}\text{C}$ over that of the carbon source (Coffin et al. 1990). Thus, cells and products of bacteria could have high $\delta^{13}\text{C}$ relative to bulk sediments, but still be far more labile to macrobenthos than the more refractory bulk pool.

The idea that deposit-feeder diets include bacterial production from a larger pool of less labile organic matter is consistent with experimental studies. Another *Macoma* species and 2 other *Nucula* species fed selectively on bacteria and nonselectively on detritus, with higher absorption efficiencies for bacteria (Newell 1965, Cheng 1983, Lopez & Cheng 1983). In various areas including the SE Bering Sea, much of sediment-

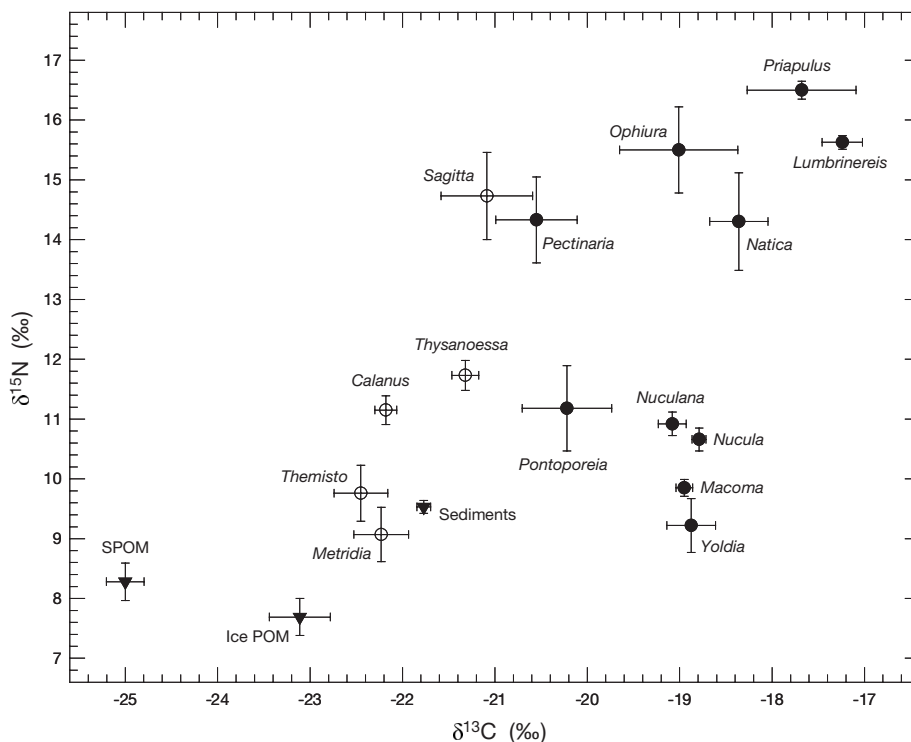


Fig. 4. Mean (\pm SE) stable isotope values ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of particulate organic matter in pack ice (Ice POM) and suspended in the water column (SPOM, near-surface, midwater, and near-bottom samples combined), of organic matter in the sediments, and of pelagic and benthic invertebrates south of St. Lawrence Island in the Bering Sea. All data are from March 2001 except for *Pectinaria hyperborea*, *Lumbrineris fragilis*, and *Priapulus caudatus* (September 1999). \blacktriangledown : potential inputs of organic matter; \circ : zooplankton; \bullet : benthos. Other species shown are *Calanus marshallae*, *Themisto pacifica*, *Metridia pacifica*, *Thysanoessa inermis*, *Sagitta elegans*, *Pontoporeia femorata*, *Natica clausa*, *Nuculana radiata*, *Nucula belloti*, *Macoma calcarea*, and *Yoldia hyperborea*. Feeding modes, isotope values, and sample sizes are in Table 2

ing phytoplankton was not metabolized by deposit-feeders immediately, but only after a period of conditioning that perhaps allowed intermediate processing by bacteria (cf. Kannevorff & Christensen 1986, Rudnick 1989, Rowe & Phoel 1992, Webb 1993, Josefson et al. 2002). Persistence in the sediments of living phytoplankton and the chlorophyll it contains, despite extensive reworking of sediments (see below), further suggests that these living cells are not immediately labile to heterotrophs (Hansen & Josefson 2004). Much of the organic matter in sediments that is indigestible by macrobenthos is labile to bacteria, which can therefore be critical to making the large pool of reworked carbon available to deposit-feeders (Marzolf 1965, Newell 1965, Levinton 1972). Consumption by macrobenthos of protists that have fed on bacteria or directly on deposited phytoplankton may also be important (Kemp 1990, Kreeger & Newell 2000).

As examples of the extent of reworking, *Nucula proxima* reworked 1 to 5 times per day the amount of permanent annual deposits (Levinton 1972), and *Yoldia* sp. processed up to 8 times their body mass of sediments hourly (Bender & Davis 1984, review in Lopez & Levinton 1987). At a density of 100 ind. m^{-2} (much lower than is typical of *Macoma calcarea* in our area), *M. balthica* processed about 994 g of sediment $\text{m}^{-2} \text{mo}^{-1}$ (Bubnova 1972); similar values are reported for the polychaete *Pectinaria* sp. (Nichols 1974). These values for only a few species of a diverse macrobenthos (Grebmeier et al. 1989) emphasize the key role of a

renewable, labile component, compared to a much larger pool of residual, refractory materials.

It is often asserted that deposit-feeder diets include a large fraction of bacteria and their products rather than just plant detritus or living algal cells; however, it is also noted that the biomass of bacterial cells in sediments is often inadequate to support the biomass of consumers (Lopez & Levinton 1987, Kemp 1990). Most organic matter in detritus must be digested extracellularly before absorption by bacteria, requiring release of large amounts of exoenzymes (Meyer-Reil 1983, Boetius & Lochte 1996). Sediment bacteria may also secrete a substantial matrix of mucoid exopolymer, which in turn may be consumed by macroinvertebrates (Hobbie & Lee 1980, Decho 1990, Decho & Moriarty 1990, Hoskins et al. 2003, but see Harvey & Luoma 1984). Such secretions might greatly enhance the amount of bacteria-derived organic matter in sediments, which could support a much larger biomass of consumers than would bacterial cells alone (Hobbie & Lee 1980, Cammen 1982). For example, the estimated carbon content of exopolymer particles in sea ice was 10 to 20 times greater than that of bacterial cells (Meiners et al. 2004); a similar situation may exist in sediments (Mayer & Rice 1992).

In shallow inland waters, stable isotopes indicate that some dominant deposit-feeders (the amphipod *Hyalella azteca* and chironomid larvae) consume mainly amorphous detritus of microalgal origin, although algal cells are not detectable in their guts (Hart

& Lovvorn 2003, see also Nichols & Garling 2000). A number of studies have found similarly large fractions of amorphous matter, with only minimal occurrence of algal cells, in guts of the amphipod *Pontoporeia* (e.g. Johnson 1987). In a labeling experiment to simulate a spring bloom, *Pontoporeia femorata* consumed almost negligible amounts of deposited diatoms (van de Bund et al. 2001). The amorphous material consumed might be mainly exudates of microalgae, or of bacteria feeding on such exudates (see also Hoskins et al. 2003). In our study, 4 to 11 mo after the spring bloom, the large increase in $\delta^{13}\text{C}$ from SPOM to deposit-feeders suggests that most carbon they consumed was not recently settled microalgae or their exudates, but rather was algal-derived carbon reworked after sedimentation. Both observational and experimental findings of very rapid degradation of the labile fraction of bloom deposits support this view (Turley & Lochte 1990, Mayer & Rice 1992, Canuel & Martens 1993, Levin et al. 1999). Note that phytoplankton may have persisted alive in the sediments for a number of months before degradation, gradually yielding more labile materials with bacterial isotopic signatures (cf. Hansen & Josefson 2004).

Diet of deposit-feeders: inference from $\delta^{15}\text{N}$

A number of authors have suggested that the large increase in $\delta^{13}\text{C}$ in deposit-feeders relative to both SPOM (4.8 to 6.2‰) and bulk sediments (1.6 to 3.0‰) results from consumption of a labile fraction derived from heterotrophic microbes subsisting on a reworked carbon pool (McConnaughey & McRoy 1979, Hobson et al. 1995, Nyssen et al. 2002). Standing stocks and mineralization rates by bacteria and protists in cold polar sediments are at least as high as those in temperate marine sediments (Glud et al. 1998, Rysgaard et al. 1998). Fractionation of ^{15}N is variable, but averages 3.4‰ per trophic transfer (Vander Zanden & Rasmussen 2001). Given this mean fractionation, why was the difference in $\delta^{15}\text{N}$ between near-surface deposit-feeders and both SPOM (0.9 to 2.9‰) and bulk sediments (–0.3 to 1.6‰) so low? This anomaly suggests 2 alternatives. First, if nitrogen were limiting, it might be tightly recycled with little fractionation. Second, the food sources of deposit-feeders might have been derived from bacteria that had incorporated dissolved inorganic nitrogen (DIN), rather than particulate organic nitrogen (PON) that is isotopically heavier (Keil & Fogel 2001).

Regarding the first alternative, C:N ratios in sediments were low during winter (7 to 7.8, Fig. 2), as they were from July to September in similar areas of the northern Bering and Chukchi Seas (mostly 6 to 9, Blackburn 1987, Grebmeier et al. 1988, Naidu et al.

1993, 2004). These low C:N ratios suggest that nitrogen should not be limiting to potential bacterial foods of the macrobenthos. It is possible that organic and inorganic nitrogen that is otherwise labile could be protected from bacterial uptake by sorption to mineral surfaces (Keil et al. 1994), or that appreciable amounts of organic nitrogen in sediments are indigestible (Dauwe et al. 1999). However, high concentrations of NH_4^+ and hydrolyzable urea in sediments of the northern Bering Sea shelf (Lomstein et al. 1989) suggest abundant available nitrogen for bacteria.

With inorganic nitrogen seemingly abundant, we are left with the second alternative for low $\Delta^{15}\text{N}$ between sediments and deposit-feeders: incorporation of isotopically light DIN (NH_4^+) into bacteria (Caraco et al. 1998). In the northern Bering Sea, it appears that microbial cells or their products are consumed by the abundant macrofauna, producing urea which is hydrolyzed to NH_4^+ , which in turn is taken up by bacteria (Blackburn 1987, Lomstein et al. 1989). Bacteria preferentially assimilate $^{14}\text{NH}_4^+$ over $^{15}\text{NH}_4^+$, with a resulting increase of $\delta^{15}\text{N}$ in residual materials (Wada 1980). In experiments with natural assemblages of marine bacteria, mean fractionation of NH_4^+ during uptake by bacteria was –10‰, ranging from –5 to –20‰ depending on the $\delta^{15}\text{N}$ of the source DIN pool (Hoch et al. 1994). Thus, if surface deposit-feeders ingested foods derived from bacteria that had assimilated DIN, they would show smaller enrichment in ^{15}N relative to sediments than would be expected if they fed on the bulk pool of sediment PON. Much of this bacterial production may be present as extracellular material or other microbial products that have replaced the algal detritus (Rice & Hanson 1984, Mayer & Rice 1992). This explanation is consistent with the patterns of $\delta^{15}\text{N}$ we observed.

Compared to the bivalves and *Pontoporeia*, the much greater increase in $\delta^{15}\text{N}$ of the polychaete *Pectinaria* over SPOM (6.0‰) and sediments (4.8‰) indicates feeding on reworked PON rather than bacteria that assimilated isotopically lighter DIN. This difference might reflect feeding deeper in the sediments on larger particles (including meiofauna and fecal pellets) by *Pectinaria*, as opposed to feeding nearer the surface by the bivalves and *Pontoporeia* (references in Table 2). Bioturbation can rapidly mix precipitating phytoplankton deeper into sediments where decay rates are much lower (Mayer & Rice 1992, Danovaro et al. 2001, Witte et al. 2003), so *Pectinaria's* diet may include more phytodetritus. Diatoms from spring blooms may survive for months after being buried in the sediments by bioturbation, providing food for deep burrowers over an extended period of the year (Kannevorff & Christensen 1986, Josefson et al. 2002).

Trophic buffering and need for specific nutrients

It has been proposed that a large pool of sediment organic matter, including bacterial products, may buffer benthic deposit-feeders from annual variations in magnitude of the spring bloom (Levinton 1972, Cammen 1982). Devol et al. (1997) noted the lack of seasonality in both denitrification rates and oxygen fluxes in nearshore sediments of the NE Chukchi Sea, despite the presumed extremes of pulsed carbon input to the seabed; however, primary production at that site is much lower than in our study area. A perpetual sediment 'food bank' was recently found near the Antarctic Peninsula: despite strong pulses of spring bloom deposition at 600 m depth, there was little seasonal variation in sediment chlorophyll *a*, or in assays of bacterial activity such as sediment ATP and oxygen consumption; sediment microbial biomass was high all year (S. L. Mincks, C. R. Smith & D. J. DeMaster unpubl. data). In our study area, sediment oxygen demand at the same stations varied substantially among seasons and years (Cooper et al. 2002), suggesting that any trophic buffering by long-term organic pools and associated bacteria was variable.

If deposit-feeding bivalves depend on a large perpetual pool of labile organic matter in the sediments, perhaps including a substantial bacterial component, then why do many bivalves typically spawn after the spring bloom (Davis & Wilson 1983, Christensen & Kannevorf 1985, Wenne 1985, Stead & Thompson 2003)? In the Baltic Sea, glycogen and lipid in *Macoma balthica* increased immediately after spring settling of fresh phytoplankton (Graf et al. 1982); however, such seasonal inputs also increased bacterial biomass and production (Graf et al. 1982, Meyer-Reil 1983). In the arctic Laptev Sea, microbial biomass was likewise correlated with the supply of labile organic matter (Boetius & Damm 1998). Thus, the correlation of bivalve spawning with the spring bloom does not necessarily imply direct dependence on newly settled, living phytoplankton.

Bivalves might also spawn after spring blooms because specific nutrients in fresh phytoplankton are important to pre-breeding conditioning (see Nichols & Garling 2000). C:N ratios are often lower for fresh phytoplankton than for SPOM at other times (Davies & Payne 1984). However, C:N ratios may not be good indicators of nutrient quality if pre-spawn conditioning is limited by lipids, which contain no nitrogen. Bivalves often increase their reserves of lipids, much of which are triacylglycerols, before spawning, with oocytes containing high levels of triacylglycerols (Davis & Wilson 1983, Pollero et al. 1983). Bacteria are notably lacking in some essential fatty acids that are abundant in fresh algae (Phillips 1984). Seasonal data on the tri-

acylglycerol content of SPOM, adults, and larvae are needed to assess whether triacylglycerols in the diet are important to pre-spawn conditioning (see Scott et al. 2002, Wacker & von Elert 2004).

Diets of zooplankton

We sampled copepods and the small euphausiid *Thysanoessa inermis* at the end of winter and the end of summer, which should ensure equilibration to winter or summer conditions. We found increases in $\delta^{13}\text{C}$ of 2.8‰ from SPOM to copepods, and 3.7‰ from SPOM to euphausiids. With a mean fractionation of $\leq 1\%$ $\delta^{13}\text{C}$ per trophic transfer, the labile carbon in SPOM appears highly reworked. Values of $\delta^{15}\text{N}$ increased by 0.8 to 2.8‰ from SPOM to copepods, and by 3.4‰ from SPOM to euphausiids. Assuming mean fractionation of 3.4‰ $\delta^{15}\text{N}$ per trophic transfer (Vander Zanden & Rasmussen 2001), the nitrogen assimilated was far less reworked than was the carbon. These patterns suggest 2 alternatives. First, nitrogen might have been limiting, so that copepods assimilated nitrogen with little isotopic discrimination (Hoch et al. 1994, Waser et al. 1999). However, nitrogen limitation seems unlikely, because during late winter 2001, when our zooplankton were collected, primary production was very low, inorganic nitrogen levels were high (Clement et al. 2004), and C:N ratios of SPOM in most of the water column were < 10.4 (Fig. 2). Thus, unless the zooplankton were starving, the algae or other microbes in their SPOM foods should have been, and appeared to be, replete with nitrogen. As a second alternative, the zooplankton diet might have included a substantial fraction of bacteria that were consuming reworked carbon while incorporating isotopically lighter DIN, rather than assimilating reworked, isotopically heavier PON (Wada 1980, Altabet 1988, Caraco et al. 1998).

Assimilation of DOC and DIN by flocculating bacteria (Biddanda 1985, Alber & Valiela 1994) is a possible explanation for observed isotope patterns between SPOM and zooplankton. DOC levels we measured in March 2001 ($\sim 65 \mu\text{mol l}^{-1}$) were appreciably lower than summer values in the northern Bering Sea and other arctic areas (82 to $105 \mu\text{mol l}^{-1}$, Hansell 1993, Børsheim & Mykkestad 1997, Daly et al. 1999); our low values probably reflect the long period since the previous spring bloom and perhaps high bacterial consumption. Under such conditions, DOC is expected to be highly reworked and isotopically heavy (Amon & Benner 1994). Furthermore, under such conditions, nitrogen required for bacterial growth is typically from DIN, with little turnover of DON (Kirchman et al. 1991, Amon & Benner 1994). In situations of limited substrate

availability, grazing protists excrete DIN and some DON that have lower $\delta^{15}\text{N}$ than the original substrate, and bacteria assimilate this lighter DIN and DON (Hoch et al. 1996). By these mechanisms, part of the very large pool of dissolved organic matter can be made available to macroinvertebrates via flocculation of bacteria or their exudates (Alber & Valiela 1995).

CONCLUSIONS

During winter ice cover in the north-central Bering Sea, limited light and minor contributions of ice algae led to very low concentrations of living algae in the water column. With the great majority of carbon in the dissolved pool (particulate carbon was below detection limits), much of SPOM may represent flocculated cells or exudates of bacteria that had assimilated DOC and DIN. Stable isotope values in SPOM versus zooplankton are consistent with this mechanism.

In late summer and late winter south of St. Lawrence Island, 4 to 11 mo after the spring bloom of phytoplankton, the diets of deposit-feeding macrobenthos appeared to be dominated by a reworked carbon source. There appeared to be little change in food quality for deposit-feeding bivalves between late summer and late winter, and between late winters with very different ice cover. Patterns of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ suggest that the labile fraction of sediment organic matter included material derived from bacteria assimilating isotopically heavy, reworked carbon and isotopically light DIN. If phytoplankton persisted alive in sediments for this long after the bloom, most of this material was apparently processed by bacteria before assimilation by the macrobenthos (cf. Hansen & Josefson 2004).

If seasonal pack ice in the Bering Sea were to decrease in extent or melt earlier, a shift from an ice-edge bloom to a later open-water bloom might cause long-term declines in the pool of sediment organic matter (see 'Introduction'). However, effects of shorter-term variations in ice-edge blooms might be buffered for bacteria consuming older organic matter, and for macrobenthos whose diets include a substantial fraction of bacterially derived material. The degree to which bacterially derived foods of macrobenthos depend on gradual decomposition of living phytoplankton persisting in the sediments needs further study. Moreover, material deposited over larger areas may be resuspended and advected into regions of persistently high secondary production, maintaining food resources despite short-term changes in bloom production (Lampitt 1985, Grebmeier & Cooper 1995, van der Loeff et al. 2002). Impacts may also depend on the unique nutritional importance of fresh phytoplankton

to breeding and early growth of macroinvertebrates. Our stable isotope data provide only indirect evidence, but indicate important directions for future research. In particular, studies combining different assays (gut contents, stable isotopes, fatty acids, triacylglycerols) are needed to determine the seasonal importance of direct consumption of sedimented algae versus bacterial products by pelagic and benthic macroinvertebrates (Kharlamenko et al. 2001, Scott et al. 2002, Bachok et al. 2003, Hart & Lovvorn 2003, Howell et al. 2003).

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