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FEATURE ARTICLE

Benthic community response to ice algae and phytoplankton in Ny Ålesund, Svalbard

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ABSTRACT: We assessed the digestibility and utilization of ice algae and phytoplankton by the shallow, subtidal benthos in Ny Ålesund (Kongsfjord) on Svalbard (79° N, 12° E) using chlorophyll *a* (chl *a*), essential fatty acids (EFAs) and stable isotopes as tracers of food consumption and assimilation. Intact benthic communities in sediment cores and individuals of dominant benthic taxa were given ice algae, phytoplankton, ^{13}C-enriched ice algae or a no food addition control for 19 to 32 d. Ice algae and phytoplankton had significantly different isotopic signatures and relative concentrations of fatty acids. In the food addition cores, sediment concentrations of chl *a* and the EFA C20:5(n-3) were elevated by 80 and 93%, respectively, compared to the control after 12 h, but decreased to background levels by 19 d, suggesting that both ice algae and phytoplankton were rapidly consumed. Whole core respiration rates in the ice algae treatments were 1.4 times greater than in the other treatments within 12 h of food addition. In the ice algae treatment, both suspension and deposit feeding taxa from 3 different phyla (Mollusca, Annelida and Sipuncula) exhibited significant enrichment in δ^{13}C values compared to the control. Deposit feeders (15% uptake), however, exhibited significantly greater uptake of the ^{13}C-enriched ice algae tracer than suspension feeders (3% uptake). Our study demonstrates that ice algae are readily consumed and assimilated by the Arctic benthos, and may be preferentially selected by some benthic species (i.e. deposit feeders) due to their elevated EFA content, thus serving as an important component of the Arctic benthic food web.

KEY WORDS: Ice algae · Phytoplankton · Food quality · Arctic benthos · Climate change · Stable isotopes · Essential fatty acids · Svalbard

Arctic warming will likely cause a decrease in ice algae and may cause an increase in phytoplankton reaching the seafloor. In our study, we found that ice algae may be preferentially selected by some benthic species, such as the bivalve *Macoma calcarea* (photo). Thus global warming may increase the quantity, but reduce the quality of food input to the Arctic benthic food web.

Photo: G. R. Lopez, Marine Sciences Research Center, SUNY Stony Brook

INTRODUCTION

In the Arctic, oceanic primary production is partitioned between ice algae and phytoplankton (Horner & Schrader 1989, McMinn & Hegseth 2004). Ice algae live both attached to the bottom of sea ice and within the ice column and bloom during spring, while phytoplankton live in the water column and bloom after the ice melts in early summer (Hsiao 1992). Accordingly, sea ice plays a crucial role in mediating many of the

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physical, chemical and biological processes that structure the composition of these dominant primary producers (Wassmann 1991). Sea ice is also profoundly affected by local, regional and global climate conditions (Weller & Lange 1999). Reductions in Arctic Ocean sea ice extent and thickness, as has been observed in recent decades (Johannessen et al. 1999), are projected to continue through this century (Cubasch & Meehl 2001), and will likely cause a decrease in ice algae and may cause an increase in phytoplankton (Horner & Schrader 1989, Hsiao 1992).

Pelagic–benthic coupling is particularly tight on the Arctic shelves (Hobson et al. 1995, Ambrose & Renaud 1997, Clough et al. 2005), and a large portion (48 to 96%) of the photosynthesized carbon in the water column falls to the seafloor each year (Wassmann 1991). Although the relative contributions of ice algae and phytoplankton to total marine primary production varies with ice cover and water column productivity, presumably some fraction of the carbon reaching the seafloor will be ice algae. Ice algae can comprise a large portion (up to 64%) of the total primary production in winter and early spring and in areas of extended ice cover (Wheeler et al. 1996). For example, Ambrose et al. (2001) observed intact strands of the ice alga *Melosira arctica* on the bottom of the Chukchi Sea (50 m depth). Therefore, a climate change-mediated shift in primary producers will affect the composition and quantity of food transported to the benthos. This shift could significantly impact the structure and function of the sea floor community, which is dependent upon the deposition of organic material from the overlying water column for its energetic requirements.

Seasonal sedimentation of primary production to the seafloor causes marked elevations in surface sediment chlorophyll *a* (chl *a*) concentrations (Bauerfeind et al. 1997, Stephens et al. 1997) and fatty acid content (Sun & Wakeham 1999). The benthos rapidly responds to this influx of organic matter, often mixing it to depths of 9 cm or more below the sediment–water interface (Graf 1989). As a result, benthic community respiration rates significantly increase shortly after spring and summer algal blooms (Graf 1989, Rysgaard et al. 1998, Gooday 2002, Moodley et al. 2005).

Fatty acids in marine fauna play an integral role in somatic growth and egg production, cold tolerance and a wide range of other physiological processes (Anderson & Pond 2000, Graeve et al. 2005). Herbivores and detritivores cannot synthesize all of the fatty acids that they require and must rely on their diet to supply some essential fatty acids (EFAs) (Olsen et al. 1991, Park et al. 2002, Howland et al. 2003). Ice algae have high concentrations of EFAs, such as C20:5(n-3) (Arrigo & Thomas 2004), and may be important for many coastal Arctic species that synchronize their reproductive efforts with the deposition of lipid-rich (high quality) food to the seafloor (Gooday 2002, Park et al. 2002). Ice algae may also be important as early season food sources for the benthos when reduced grazing pressure in the water column increases the amount of organic matter reaching the sea floor (Ambrose & Renaud 1995). For example, ice algae can be found in benthic sediment traps from late winter through June (Hsiao 1992), and influxes of ice algae to the sea floor have been shown to initiate benthic biological production prior to summer phytoplankton blooms (Arrigo & Thomas 2004).

Little is known about the relative food quality of ice algae versus phytoplankton for Arctic benthic fauna, and therefore, it has been difficult to predict how climate change will impact the Arctic benthic ecosystem via changes in food sources. Our study examined the digestibility and utilization of ice algae and phytoplankton by the Arctic benthos. We hypothesized that ice algae would be readily consumed and assimilated into biomass because of its elevated concentrations of EFAs, making ice algae an important food source for the Arctic benthic community. To test this hypothesis, a series of food addition experiments were conducted using intact sediment cores (entire community) and individual organisms collected from a soft-sediment cove in Ny Ålesund, Svalbard (79° N, 12° E).

MATERIALS AND METHODS

Site characteristics. The Svalbard archipelago, lying between 76 and 81° N and 10 to 35° E, is bounded by the Arctic Ocean basin to the north and the Barents and Norwegian Seas to the south. The coastline is surrounded by continental shelves broken by large fjord systems. Our research was conducted in Ny Ålesund (78° 56′ N, 11° 56′ E) on the west coast of Svalbard. This area experiences both seasonal ice cover and input from Atlantic-origin water carried by the West Spitsbergen current. During July and August of 2004, sediment cores and individuals organisms were collected from Thiisbukta, a fine sand cove on the west edge of town. During July and August, the mean tidal range in this area was 2 m, water temperatures varied from 4 to 6°C, and glacial runoff caused fluctuating salinities (10 to 33‰) and high sediment loads.

Feeding experiments were conducted with intact sediment cores and individual benthic invertebrates collected during July of 2004 from the study site, a 5 m^2 plot in the center of Thiisbukta. Prior to the start of the experiments, 3 short sediment cores (6 cm diameter and 6 cm long) were collected from the study site and sieved to determine graphic mean grain size and

graphic standard deviation using standard granulometric methods (Folk 1968). Five replicate surface sediment samples were also collected from the study site to determine the mean baseline chl *a* concentration at the site using standard fluorometric procedures (modified from Holm-Hansen et al. 1965). This concentration was used to calculate the amount of ice algae and phytoplankton to be added to the cores to increase surface sediment chl *a* concentrations by 70%, representing a large spring/summer bloom in primary production for this area (Hansen & Josefson 2003).

To determine macrofaunal density and biomass for Thiisbukta, 8 large sediment cores (10 cm diameter and 30 cm long made of acrylic with 5 mm thick walls with half sediment and half water) were collected from the study site during July 2004. Five of the replicate cores were sieved (500 µm) immediately to determine community composition. All samples were fixed in 4% formaldehyde and stained with Rose Bengal, then transferred to 70% isopropyl alcohol for preservation. Organisms from each core were identified to species when possible, and individuals were counted. Faunal biomass for each phylum (Annelida, Mollusca, Arthropoda, Sipuncula, and Foraminifera) was determined by drying samples at 60°C to constant weight and ashing at 500°C for 4.5 h to yield ash-free dry weight integrated to 9 cm depth. The remaining 3 large cores were sectioned into 1 cm intervals by depth and sorted to determine the vertical distribution of taxa within the sediment. Faunal densities were used to determine the species richness, Shannon Wiener diversity index (H') and Shannon Wiener evenness (J') at Thiisbukta.

Whole core incubations. Whole core incubation experiments were carried out to examine the response of the intact benthic community to additions of ice algae and phytoplankton. Twenty-two large sediment cores were collected at low tide (0.5 m above mean low water) from the 5 m^2 study site at the same time the surface sediment samples and the faunal density cores were collected. Low salinity water in the sediment cores (~12‰ at the time of collection) was exchanged for higher salinity water (~30‰) collected at high tide to minimize osmotic stress on the faunal communities in the cores. Sediment cores were incubated at ambient temperature (5°C) in the dark and aerated to maintain saturated oxygen concentrations throughout the 19 d experiment. Cores were divided into 4 treatment groups: (1) fresh-frozen ice algae addition (primarily *Nitzschia frigida*, which is the most abundant ice algal species around Svalbard; McMinn & Hegseth 2004), (2) fresh-frozen phytoplankton addition (a mix of *Phaeocystis pouchetii* and *Thalassiosira hyalina*, both of which are common spring bloom species in the Barents Sea and Svalbard area; McMinn & Hegseth 2004), (3) ^{13}C-enriched ice algae addition (fresh-frozen *N. frigida* enriched to $\delta^{13}C$ 684‰), and (4) a no food addition control. Approximately 11 ml $core^{-1}$ of ice algae (5.1 mg chl *a* l^{-1}, 0.2 mg phaeopigments l^{-1}), 9 ml $core^{-1}$ of phytoplankton (6.0 mg chl *a* l^{-1}, 0.3 mg phaeopigments l^{-1}) or 14 ml $core^{-1}$ of ^{13}C-enriched ice algae (4.0 mg chl *a* l^{-1}, 0.2 mg phaeopigments l^{-1}) were added to the respective treatments.

Material for both the ice algal and phytoplankton additions were collected during a May 2004 cruise to the Barents Sea aboard the RV 'Jan Mayen'. Ice algae were suctioned from the underside of sea ice and phytoplankton were collected using a vertical phytoplankton net haul (from 50 m depth). Samples were frozen (–30°C) immediately after concentration by settling. Ice algae for the ^{13}C-enriched treatment were labeled using 0.1 g ^{13}C bicarbonate (from Cambridge Isotope Laboratories) l^{-1} of culture media, and were allowed to incubate for 5 to 7 d before freezing.

At 3 time points during the incubation experiment: (T = 0.5, 5 and 19 d), 2 replicate cores from 3 treatments (ice algae, phytoplankton, and control) were sectioned into 8 depth intervals (0–0.5, 0.5–1, 1–2, 2–3, 3–4, 4–5, 5–7 and 7–9 cm). The ^{13}C-enriched ice algae treatments were only sectioned at T = 0.5 and 19 d. Changes in surface sediment chl *a* and C20:5(n-3) fatty acid concentrations (see below for methods) across treatments and time points were analyzed using a 2-way ANOVA with significance set at $p < 0.05$. A Bonferroni multiple comparison post-hoc test was used to compare concentrations among treatments at a given time. No data required transformation prior to statistical analyses.

Prior to each sectioning time point, whole core respiration rates were determined for 3 sediment cores per treatment (ice algae addition, phytoplankton addition, and no food addition control) and 2 water cores (to control for water-associated respiration). During the respiration experiments, bubbling of the cores was terminated and the cores were sealed with an air-tight top fitted with a motor that completely mixed the water column (40 rpm) to prevent oxygen gradient formation without disturbing the sediment. Dissolved oxygen in the water column was measured through a stoppered hole in the core top using a YSI oxygen meter (non-stirring BOD probe). Oxygen readings were taken every 4 to 6 h until oxygen concentrations decreased by 35% (usually 18 to 24 h). Average water depth was measured at 3 points around the core and coupled with the core area to calculate water volume. For each core, oxygen concentrations were corrected for water volume, and respiration rates (decrease in total oxygen per unit time) were determined by regression analysis ($R^2 > 0.9$). Differences among mean respiration rates across treatments and time points were analyzed with a 2-way ANOVA and Bonferroni multiple comparison post-hoc test.

At T = 0.5 and 19 d, *Liocyma fluctuosa* (suspension feeding bivalve), *Macoma calcarea* (surface deposit feeding bivalve), *Euchone analis* (suspension feeding, tube dwelling polychaete), *Onisimus littoralis* (scavenging amphipod) and *Phascolopsis gouldii* (deposit feeding sipunculid) were collected from the sectioned cores, frozen, and analyzed for bulk tissue and C20:5(n-3) isotope values to assess the assimilation of ice algae and phytoplankton into biomass (see below for methods). The relative abundance of C20:5 (n-3) in suspension and deposit feeders was determined using the ratio of C20:5(n-3) to the ubiquitous fatty acid C16:0 (by relative %) for each species. In addition, a 2-end member mixing model was used to determine the degree to which the isotopic signal of the sample was attributed to uptake of ^{13}C-enriched ice algae as follows (modified from Robinson 2001):

$$X(\%) = (\delta^{13}C_{sample} - \delta^{13}C_{control})/(\delta^{13}C_{tracer} - \delta^{13}C_{control}) \times 100$$

where X is the percent of ^{13}C-enriched ice algae taken up by the organism, $\delta^{13}C_{sample}$ is the organism fed ^{13}C-enriched ice algae, $\delta^{13}C_{tracer}$ is the ^{13}C-enriched ice algae (684‰) and $\delta^{13}C_{control}$ is the control organism.

The same species analyzed in the whole core incubation experiments were also collected directly from Thiisbukta (i.e. without experimental treatments) and analyzed for δ^{13}C and δ^{15}N compositions of bulk tissue and C20:5(n-3) fatty acids.

Individual feeding experiments. Individual feeding experiments were also established to examine the assimilation of ice algae and phytoplankton by individual benthic fauna. Individuals of 2 numerically abundant bivalve species, *Liocyma fluctuosa* and *Macoma calcarea*, were placed in separate cups with 100 ml of seawater (30‰), and fed phytoplankton (only *L. fluctuosa*), ice algae or ^{13}C-enriched ice algae. Food was added daily as needed such that a concentration of 10 µg chl *a* ml^{-1} was maintained, with complete water changes performed every other day. Cups were aerated continuously, and incubated in the dark at ambient temperature (5°C) for 32 d. At the termination of the experiment, bulk tissue and C20:5(n-3) stable isotope analyses were conducted on each species and compared to the whole core incubation experiment.

Stable isotope and fatty acid analyses. Sediment samples, ice algae, phytoplankton, and soft tissues from benthic invertebrates were freeze-dried and homogenized prior to fatty acid extraction and isotopic analysis. Samples of white Arctic mountain heather *Cassiope tetragona* and snow algae, both commonly found in the glacial runoff emptying into Thiisbukta, were also analyzed for stable isotope signatures to determine possible alternative food sources for benthic organisms at the study site. Approximately 0.05 g of animal/plant tissue and 1.5 g of surface sediment (0 to 0.5 cm) were Soxhlet extracted for ~24 h in methylene chloride:methanol (2:1 v/v) (Wakeham & Canuel 1988). Approximately 0.4 to 0.6 mg of solvent extracted animal/plant tissue and 15 mg of solvent extracted sediment were analyzed for stable carbon and nitrogen isotope signatures using a ThermoFinnigan Delta Plus Advantage stable isotope ratio mass spectrometer (IRMS) coupled to a Costech elemental analyzer (EA) via a Conflo III combustion interface in the Environmental Geochemistry Laboratory (EGL), Department of Geology, Bates College, Maine, USA. Stable isotope analyses were performed on 3 replicate individuals for each sample when possible. All samples in the ^{13}C-enriched ice algae treatment (2 replicates per sample) were analyzed for carbon and nitrogen isotope signatures using the aforementioned IRMS in the Analytical Chemistry Laboratory, Institute of Ecology, University of Georgia, USA. Stable isotope values were expressed in δ (‰) notation according to the following definition:

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

where X is ^{13}C or ^{15}N and R is ^{13}C:^{12}C or ^{15}N:^{14}N, and the standards were Vienna Pee Dee Belemnite (VPDB) for carbon and air for nitrogen. The accuracy and precision of the IRMS were determined by multiple analyses of a working standard (acetanilide: C_8H_9NO) run every 6th sample and were ±0.2‰ for both δ^{13}C and δ^{15}N. Significant differences in animal isotopic signatures across treatments for each species were determined with a 1-way ANOVA and Bonferroni multiple comparisons post-hoc test.

The total lipid extracts isolated from the Soxhlet extraction process were saponified in 0.5 N KOH-MeOH and separated into neutral and acid fractions (Wakeham & Canuel 1988). The acid fractions were methylated with 3% BF_3 in MeOH and the resultant fatty acid methyl esters (FAME) were quantified by GC-FID (Agilent 6890N) in the EGL, Bates College. Compound identification was determined using the GC-MS (Agilent 6890/MS 5973) in the Department of Chemistry, Bates College. The δ^{13}C signatures of the fatty acids were analyzed using the aforementioned IRMS interfaced to a Trace GC and GCIII combustion interface in the EGL, Bates College. The running conditions for both GCs were similar so results could be readily compared between instruments. Samples were injected isothermally at 250°C and compounds were separated on an HP-5MS column (30 m, 0.25 mm i.d., 0.25 µm film). The oven temperature program was as follows: T_1 = 60°C (with 5 min hold); T_2 = 160°C (15°C min^{-1} with 0 min hold); and T_3 = 310°C (4°C min^{-1} with 25 min hold). Significant differences in the isotopic signatures of C20:5(n-3) across treatments for each species were determined with a 1-way ANOVA and

Bonferroni multiple comparison post-hoc test. A 2-tailed *t*-test was used to examine differences in fatty acid composition between ice algae and phytoplankton.

RESULTS

Site characteristics

The study site at Thiisbukta was a poorly sorted (graphic standard deviation 375 µm), fine sand cove (graphic mean grain size: 179 µm). Thiisbukta had high total macrofaunal density (18 926 ± 7470 ind. m^{-2}) and biomass (59.8 ± 4 g m^{-2} ash-free dry weight) despite low species diversity (H' = 1.43) and evenness (J' = 0.54) (relative to findings from Wlodarska-Kowalczuk et al. 1998). Fourteen different taxa were found at the study site, not including multiple species of oligochaeta and possibly foraminifera (Table 1). Annelida was the dominant phylum at the study site, comprising 88% of the total macrofaunal abundance and 62% of the total macrofaunal biomass (Table 1). Nearly 84% of the benthic invertebrates in Thiisbukta occurred in the top 2 cm of the sediment and 96% of the organisms were in the top 4 cm. Annelids, however, were present at every depth sampled (to 9 cm below sediment surface). Although mollusks comprised only 7% of the total macrofaunal abundance at Thiisbukta, they accounted for 35% of the total macrofaunal biomass (Table 1). *Liocyma fluctuosa* comprised 80% of the mollusks found, followed by *Macoma calcarea* at 9%.

The ice algae (predominantly *Nitzschia frigida*) and phytoplankton (a mix of *Phaeocystis pouchetii* and *Thalassiosira hyalina*) used in the feeding experiments were significantly different from one another in several aspects, including their bulk tissue and C20:5(n-3) $\delta^{13}C$ signatures, fatty acid compositions, and relative C20:5(n-3) concentrations (Table 2). The fatty acid composition

Table 1. Mean abundance (number of individuals per 78.5 cm^2 core ± SD), biomass (mg ash-free dry weight per 78.5 cm^2 core ± SD) and feeding strategies of benthic invertebrates from Thiisbukta in July 2004. N = 5 replicate sediment cores

Taxon	Abundance	Biomass (mg)	Feeding strategy
Annelida	130.9 ± 56.4	290.0 ± 41.2	
Oligochaeta	92.6 ± 49.1		Deposit feeder
Scoloplos armiger	13.3 ± 9.1		Deposit feeder
Travisia forbesii	9.3 ± 7.2		Deposit feeder
Spio filicornis	9.3 ± 8.2		Deposit/suspension feeder
Euchone analis	5.6 ± 8.8		Suspension feeder
Eteone longa	0.9 ± 1.2		Predator
Mollusca	10.7 ± 2.6	162.3 ± 22.4	
Liocyma fluctuosa	8.6 ± 2.2		Suspension feeder
Macoma calcarea	1.0 ± 1.0		Deposit/suspension feeder
Buccinium sp.	0.9 ± 1.2		Predator
Astarte borealis	0.1 ± 0.4		Suspension feeder
Mytilus sp.	0.1 ± 0.4		Suspension feeder
Sipuncula	0.9 ± 0.9	15.9 ± 8.4	
Phascolopsis gouldii	0.9 ± 0.9		Deposit feeder
Arthropoda	0.9 ± 0.9	1.3 ± 1.1	
Onisimus littoralis	0.9 ± 0.9		Scavenger
Foraminifera	5.3 ± 2.1	<1.0	
Psammosphaeridae	5.3 ± 2.1		Detritivore

Table 2. Comparisons between ice algae (primarily *Nitzschia frigida*) and phytoplankton (a mix of *Thalassiosira hyaline* and *Phaeocystis pouchetii*) collected during a spring cruise in the Barents Sea and used in sediment core and individual feeding experiments. Differences between ice algae and phytoplankton were determined using a 2-tailed *t*-test where $^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, $^{ns}p > 0.05$. N = 3 samples for $\delta^{13}C$ and C:N comparisons and N = 2 samples for fatty acid comparisons. SFA: saturated fatty acids; MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids

Variable	Ice algae	Phytoplankton	*t*-statistic
$\delta^{13}C$ signatures (‰) of bulk tissue	−15.7 ± 0.5	−24.5 ± 0.5	18.0^{**}
$\delta^{13}C$ signatures (‰) of C20:5 (n-3)	−21.9 ± 0.4	−32.0 ± 0.3	28.7^{**}
C:N ratio	6.7 ± 0.3	6.5 ± 0.4	0.6^{ns}
Fatty acids (relative %)			
C14:0	6.5	6.1	0.9^{ns}
C15:0	3.4	3.5	0.2^{ns}
C16:0	13.6	27.9	20.2^{**}
C16:1(n-7/9)	24.1	13.5	15.0^{**}
C16:2(n-4)	–	0.8	
C16:3(n-4)	–	0.6	
C16:4(n-1)	1.2	0.6	1.4^{ns}
C18:0	3.3	8.9	5.7^{*}
C18:1(n-9)	5.1	9.8	4.7^{*}
C18:1(n-7)	1.0	–	
C18:2(n-6)	1.1	3.9	2.8^{ns}
C18:3(n-6)	1.4	2.1	1.0^{ns}
C20:1(n-9)	8.9	4.5	4.4^{*}
C20:2(n-8)	0.4	–	
C20:4(n-3)	0.9	–	
C20:5(n-3)	16.3	4.7	27.3^{**}
C22:1(n-9)	0.7	2.7	2.4^{ns}
C22:6(n-3)	1.9	3.7	2.1^{ns}
Unidentified	8.8	8.1	1.2^{ns}
Total SFA	26.8	46.4	34.6^{***}
Total MUFA	39.8	30.5	16.4^{**}
Total PUFA	23.2	16.4	6.9^{*}

of ice algae was dominated by monounsaturated fatty acids (39.8% of the fatty acids), such as C16:1(n-7/9), whereas saturated fatty acids (46.4%), such as C16:0, dominated the fatty acid composition of the phytoplankton (Table 2). Although polyunsaturated fatty acids (PUFAs) were the least abundant group for both ice algae (23.2%) and phytoplankton (16.4%), ice algae had significantly more PUFAs than phytoplankton (Table 2). Ice algae and phytoplankton were not significantly different in their C:N ratios (Table 2); however, ice algae and phytoplankton had significantly lower C:N ratios than the glacial runoff-derived food sources *Cassiope tetragona* (18.6 ± 0.9) and snow algae (13.7 ± 0.3) (1-way ANOVA, F = 394.8, $p < 0.001$). Similarly, ice algae (3.5‰) and phytoplankton (3.9‰) had significantly enriched $\delta^{15}N$ signatures compared to *C. tetragona* (1.1‰) and snow algae (0.8‰) (1-way ANOVA, F = 44.1, $p < 0.001$) (Fig. 1).

Whole core incubations

Surface sediment chl *a* concentrations were affected by both food addition and time, but the interaction between the two was not significant (Table 3A). Down-core profiles of sediment pigments in all treatments showed a general trend of decreasing chl *a* concentration until approximately 5 to 6 cm, where the concentrations remained at a constant minimum (Fig. 2). The average standard deviation of sediment chl *a* concentrations was ±0.3 µg chl *a* ml^{-1} in the control cores and ±0.4 µg chl *a* ml^{-1} in the food addition cores. At T = 0.5 d the surface sediment chl *a* concentrations were significantly higher in the sediment cores inoculated with ice algae (78% increase), ^{13}C-enriched ice algae (47%) and phytoplankton (82%) compared to the control (Fig. 2A, Table 3A). After 19 d of incubation, the mean surface chl *a* concentrations in the sediment cores inoculated with ice algae (57% decrease from T = 0.5 d), ^{13}C-enriched ice algae (59%) and phytoplankton (56%) were not significantly different from the control (Fig. 2C). Sediment chl *a* to phaeopigment ratios in the control cores (0.5) did not change significantly during the experiment (2-tailed *t*-test, t = 0.3, $p > 0.05$); however, chl *a* to phaeopigment ratios were significantly reduced after 19 d in the sediment cores inoculated with ice algae (from 0.6 to 0.4) (2-tailed *t*-test, t = 5.6, $p < 0.05$), ^{13}C-enriched ice algae (from 0.5 to 0.2) (2-tailed *t*-test, t = 6.0, $p < 0.05$) and phytoplankton (0.5 to 0.4) (2-tailed *t*-test, T = 6.3, $p < 0.05$).

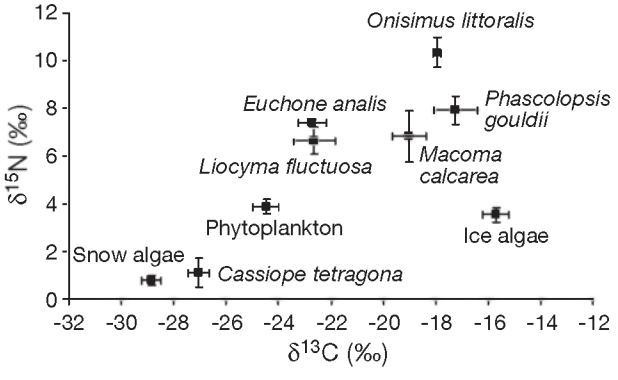

Fig. 1. Dual stable isotope plots of mean $\delta^{13}C$ and $\delta^{15}N$ signatures (±SD) for flora and fauna collected from Thiisbukta during July 2004. N = 3 samples

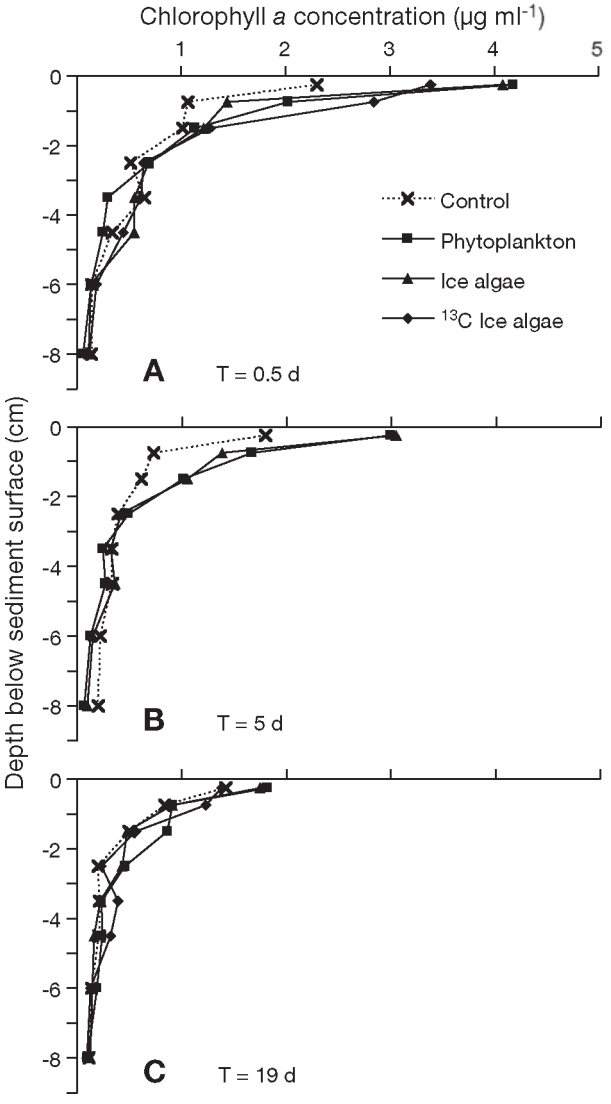

Fig. 2. Down-core profiles of mean sediment chlorophyll *a* concentrations in sediment cores inoculated with phytoplankton, ice algae, ^{13}C-enriched ice algae, or a no food addition control after (A) 0.5 d, (B) 5 d and (C) 19 d of incubation at 4 to 5°C. N = 2 replicate sediment cores

Table 3. Results of 2-way ANOVA (food addition and time) for (A) surface sediment chlorophyll *a* (chl *a*) concentrations (N = 2 cores), (B) surface sediment C20:5(n-3) concentrations (N = 2 cores) and (C) whole core respiration rates (N = 3 cores). Food addition treatments: phytoplankton, ice algae and no food addition control. Time treatments: T = 0.5, 5 and 19 d of incubation. $^{***}p < 0.001$, $^{**}p < 0.01$ $^{*}p < 0.05$, $^{ns}p > 0.05$

Effect	df	MS	*F*
(A) Chl *a*			
Time	2	5.18	33.84^{***}
Food addition	2	2.61	17.01^{***}
Time × Food addition	4	0.36	2.37^{ns}
Error	9	0.15	
(B) C20:5(n-3)			
Time	1	2.3×10^6	51.79^{***}
Food addition	2	3.0×10^5	6.57^{*}
Time × Food addition	2	1.8×10^5	4.07^{ns}
Error	6	4.5×10^4	
(C) Respiration rate			
Time	2	3.1×10^4	62.64^{***}
Food addition	2	2.7×10^4	55.27^{***}
Time × Food addition	4	2.6×10^3	5.25^{**}
Error	18	6.0×10^2	

In the control treatment, bulk sediment $\delta^{13}C$ signatures did not change down-core or through time ($\delta^{13}C$ –24‰). Bulk sediment $\delta^{13}C$ signatures in the ^{13}C-enriched ice algae treatment were more enriched than in the control in the top 1 cm of the sediment at T = 0.5 d and down to 4 cm below the sediment–water interface by 19 d (Fig. 3).

Surface sediment C20:5(n-3) concentrations were affected by both food addition and time, but the interaction between the two was not significant (Table 3B). The patterns in reduction of surface sediment C20:5 (n-3) concentrations over time were similar to those observed for the sediment chl *a* concentrations. There was a significant increase in surface sediment C20:5 (n-3) concentration over the control in the ice algae treatment (129%) and phytoplankton treatment (57%) at T = 0.5 d, followed by a rapid decrease to control levels by T = 19 d (Fig. 4).

There was no measurable oxygen consumption in any of the water controls, so values presented are for the cores without any corrections applied. At 12 h, the mean respiration rate in the ice algae treatment was 1.4 times faster than the control, but by the 19th day of incubation, respiration rates in the ice algae and control treatments were not significantly different from one another (Fig. 5). The mean respiration rate in the phytoplankton treatment was always significantly less than in the ice algae treatment (37% less at T = 0.5 d and 15% less at T = 19 d), but never significantly different from the control (Fig. 5).

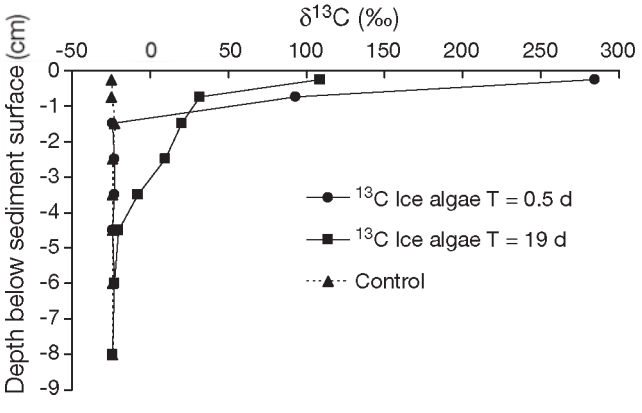

Fig. 3. Down-core profiles of mean sediment $\delta^{13}C$ signatures in sediment cores inoculated with ^{13}C-enriched ice algae and a no food addition control after 0.5 and 19 d of incubation at 4 to 5°C. N = 2 replicate sediment cores

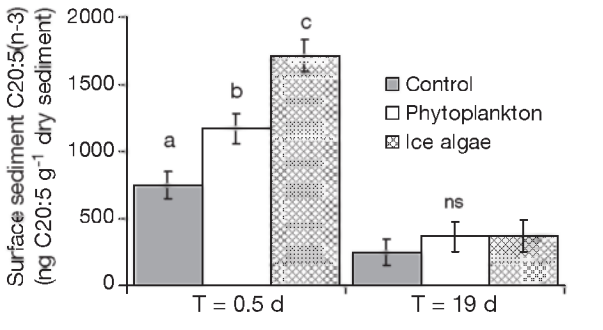

Fig. 4. Mean surface sediment C20:5(n-3) concentrations (±SD) from sediment cores inoculated with ice algae, phytoplankton, or a no food addition control after 0.5 and 19 d of incubation. Means with the same letter were not significantly different from each other based upon a 2-way ANOVA and Bonferroni multiple comparison post-hoc test with significance set at $p < 0.05$. N = 2 replicate sediment cores

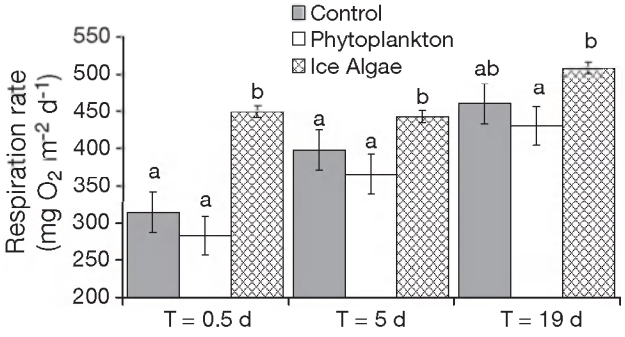

Fig. 5. Whole core respiration rates (±SD) in sediment cores inoculated with phytoplankton, ice algae, or a no food addition control after 0.5, 5 and 19 d of incubation at 4 to 5°C. Means with the same letter were not significantly different from each other based upon a 2-way ANOVA and Bonferroni multiple comparison post-hoc test with significance set at $p < 0.05$. N = 3 replicate sediment cores

Individual feeding experiments

In the ice algae treatment, both *Liocyma fluctuosa* and *Macoma calcarea* exhibited significant enrichment in bulk tissue $\delta^{13}C$ signatures compared to the control; however, only *L. fluctuosa* exhibited a significant depletion in $\delta^{13}C$ compared to the control when fed phytoplankton (Table 4). Although both *L. fluctuosa* (2-tailed *t*-test, $t = 13.1$, $p < 0.05$) and *M. calcarea* (2-tailed T-test, $t = 38.5$, $p < 0.0001$) exhibited significant enrichment in $\delta^{13}C$ signatures when fed $\delta^{13}C$-enriched ice algae compared to the control, *M. calcarea* exhibited a greater degree of assimilation (15% of the organism's signature coming from ^{13}C-enriched tracer) relative to *L. fluctuosa* (4%) (Fig. 6). It should be noted that there were no significant differences in the patterns of assimilation for species in the whole core experiments versus the individual feeding experiments (Table 4).

Stable isotope and fatty acid analyses

Liocyma fluctuosa and *Euchone analis* collected directly from Thiisbukta (Fig. 1) had similar isotopic signatures, which were more depleted in their $\delta^{13}C$ values than *Macoma calcarea* and *Phascolopsis gouldii*. *L. fluctuosa*, *M. calcarea*, *E. analis*, and *P. gouldii* appeared to be 1 trophic level above ice algae and phytoplankton, and *Onisimus littoralis* appeared to be 2 trophic levels above ice algae and phytoplankton, based upon a 3 to 4‰ isotopic fractionation in $\delta^{15}N$ values between trophic levels (Hobson et al. 1995) (Fig. 1). The C20:5(n-3) to C16:0 abundance ratios in the deposit feeders *M. calcarea* (0.54:1) and *P. gouldii* (0.55:1) were significantly higher than in the suspension feeders *L. fluctuosa* (0.45:1) and *E. analis* (0.42:1) (1-way ANOVA, $F = 14.2$, $p < 0.01$).

After incubation with ice algae, *Liocyma fluctuosa*, *Macoma calcarea*, *Euchone analis*, and *Phascolopsis gouldii* exhibited significant enrichment in bulk tissue and C20:5(n-3) $\delta^{13}C$ signatures compared to the control, while *Onisimus littoralis* showed no change in $\delta^{13}C$ signature among the treatments (Table 4). All benthic invertebrates fed phytoplankton appeared to

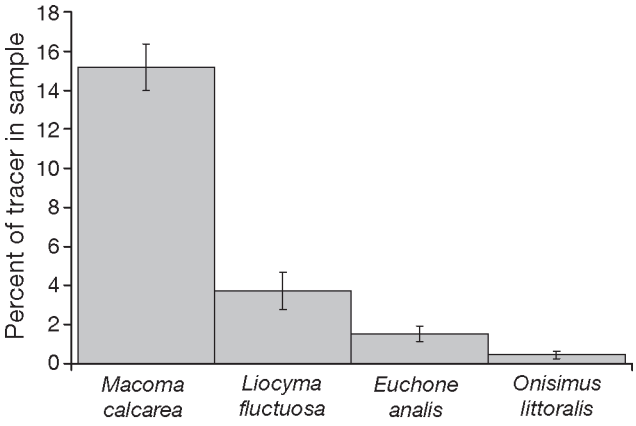

Fig. 6. Mean percent of ice algae and phytoplankton in the diet of benthic invertebrates collected from Thiisbukta during July 2004 determined by $\delta^{13}C$ values of C20:5(n-3). N = 2 individuals

Table 4. Comparisons of (A) bulk tissue and (B) C20:5(n-3) $\delta^{13}C$ signatures of benthic invertebrates fed ice algae (IA), phytoplankton (PP), or a no food addition control (C) for 19 to 32 d of incubation. WCI: whole core incubation (19 d of incubation); IFE: individual feeding experiment (32 d of incubation). Differences among treatments were determined using a 1-way ANOVA and Bonferroni multiple comparison post-hoc test where $^{***}p < 0.001$, $^{**}p < 0.01$ $^{*}p < 0.05$, $^{ns}p > 0.05$. N = 3 replicates for bulk tissue and N = 2 replicates for C20:5(n-3)

	Treatment			Comparison	*F*-ratio
	Control	Ice algae	Phytoplankton		
(A) Bulk tissue					
Liocyma fluctuosa (WCI)	−22.6 ± 0.3	−21.8 ± 0.4	−23.4 ± 0.3	IA > C > PP	16.7^{**}
Liocyma fluctuosa (IFE)	−22.3 ± 0.3	−21.5 ± 0.3	−23.4 ± 0.2	IA > C > PP	16.8^{**}
Macoma calcarea (WCI)	−19.6 ± 0.3	−18.4 ± 0.4		IA > C	4.9^{*}
Macoma calcarea (IFE)	−19.3 ± 0.3	−18.1 ± 0.3		IA > C	4.8^{*}
Onisimus littoralis	−17.9 ± 0.2	−17.8 ± 0.3	−18.1 ± 0.2	IA = C = PP	1.2^{ns}
Phascolopsis gouldii	−17.6 ± 0.3	−16.0 ± 0.3	−18.1 ± 0.3	IA > C = PP	39.1^{***}
Euchone analis	−22.8 ± 0.3	−22.2 ± 0.4	−23.2 ± 0.3	IA > C = PP	7.5^{*}
Food		−15.7 ± 0.5	−24.5 ± 0.5	IA > PP	18.0^{**}
(B) C20:5(n-3)					
Liocyma fluctuosa	−31.5 ± 0.3	−31.0 ± 0.3	−31.9 ± 0.3	IA > C > PP	8.8^{*}
Macoma calcarea	−27.5 ± 0.3	−26.5 ± 0.3		IA > C	3.9^{*}
Onisimus littoralis	−27.7 ± 0.4	−27.6 ± 0.4	−27.6 ± 0.4	IA = C = PP	0.1^{ns}
Phascolopsis gouldii	−25.4 ± 0.4	−24.1 ± 0.3	−25.6 ± 0.3	IA > C = PP	18.3^{**}
Euchone analis	−27.9 ± 0.2	−27.3 ± 0.2	−27.9 ± 0.2	IA > C = PP	8.6^{*}
Food		−21.9 ± 0.4	−32.0 ± 0.3	IA > PP	28.7^{**}

be depleted in their $\delta^{13}C$ signatures relative to the control; however, only *L. fluctuosa* exhibited a significant depletion in $\delta^{13}C$ (Table 4).

All the species fed ^{13}C-enriched ice algae exhibited significant enrichment in $\delta^{13}C$ signatures (1-way ANOVA, $F = 17.9$, $p < 0.05$). *Macoma calcarea* exhibited the greatest degree of assimilation (15% of the organism's signature coming from ^{13}C-enriched tracer), *Liocyma fluctuosa* and *Euchone analis* assimilated 4 and 2%, respectively, and *Onisimus littoralis* assimilated the least amount of the ^{13}C-enriched ice algae tracer (0.5%) (Fig. 6).

DISCUSSION

The decrease in sediment chl *a* and fatty acid concentrations, the increase in respiration rate and the incorporation of the ice algal stable isotope signature into the tissue of benthic invertebrates support the hypothesis that ice algae are readily consumed and assimilated into biomass. These results are the first to indicate that ice algae are high quality food sources for benthic organisms that must be considered when assessing the impact of climate change on the Arctic marine ecosystem.

In the whole core incubation experiment, addition of ice algae or phytoplankton increased the surface sediment chl *a* concentrations in treatments by approximately 80% relative to the control (Fig. 2A); this was similar to the 86% increase in sediment pigments observed by Hansen & Josefson (2003) following an early summer bloom in the North and Baltic Seas. After 19 d of incubation, surface sediment chl *a* concentrations in the food addition treatments decreased to control levels (Fig. 2), suggesting that both ice algae and phytoplankton were rapidly consumed. The sediment chl *a* to phaeopigment ratios in the food addition treatments decreased significantly during the 19 d experiment, while that ratio in the control treatment did not change. Although freezing and thawing ice algae and phytoplankton prior to use in the feeding experiments could have enhanced their rates of degradation, previous research has shown that diatoms buried in sediments without faunal grazing activity decay very slowly (half life of 120 d) (Stephens et al. 1997, Moodley et al. 2005). Therefore, the reduction in the chl *a* to phaeopigment ratios in the food addition cores was probably due to ingestion of chl *a* by consumers. Furthermore, in the sediment cores inoculated with ^{13}C-enriched ice algae, surface sediment $\delta^{13}C$ signatures became more depleted than the enrichment of the subsurface sediments (Fig. 3), which indicates that the ^{13}C-enriched ice algae were being consumed (Middelburg et al. 2000).

Food added to the sediment cores was mixed to depth prior to being completely consumed. This was evident by the enrichment of sediment $\delta^{13}C$ signatures in the ^{13}C-enriched ice algae treatment over the control down to 4 cm after 19 d of incubation (Fig. 3). This down-core movement of food indicates that Thiisbukta has an active benthic community making food available to subsurface organisms (Graf 1989, Jumars & Wheatcroft 1989, Middelburg et al. 2000). The rapid movement of food down to 4 cm below the sediment–water interface reflects the vertical distribution of fauna in the sediment, as 96% of the benthic invertebrates occur in the top 4 cm of the sediment. Evidence of active bioturbation and down-core movement of food at Thiisbukta was consistent with previous research by Clough et al. (1997), who found high degrees of bioturbation in the top 3 cm of the sediments from the Chukchi Sea to the Abyssal Plain of the central Arctic Ocean.

Changes in surface sediment C20:5(n-3) concentrations followed a pattern similar to that observed for sediment chl *a* concentrations. C20:5(n-3) concentrations in the surface sediments of both food addition treatments were significantly elevated above the control level at T = 0.5 d (Fig. 4, Table 3B); however, the increase in C20:5(n-3) concentration in the ice algae treatment (129%) was much higher than in the phytoplankton treatment (57%). This was probably because ice algae have approximately 3 times more C20:5(n-3) than phytoplankton (Table 2). By 19 d, C20:5(n-3) concentrations were reduced to the control level in both the ice algae and phytoplankton treatments (Fig. 4), which follows the pattern seen for the chl *a* analyses. These reductions indicate that the benthos in Thiisbukta rapidly responded to the fresh organic matter provided to them and efficiently digested the bioreactive components.

The overall benthic response to ice algae and phytoplankton was examined via changes in whole core respiration rates. Baseline respiration rates in the control cores of the whole core incubation experiment (Fig. 5) suggest that Thiisbukta was functioning similar to other Arctic soft-sediment systems. Respiration rates at Thiisbukta were on a par with Arctic sites, such as the Alaskan Coastal Waters (Devol et al. 1997) and the northern Bering and Chukchi Seas (Grebmeier & McRoy 1989), which were also shallow, subtidal and approximately 5°C (Table 5). Respiration rates at Thiisbukta were greater than at the deeper, colder Arctic sites in Greenland Sound (Glud et al. 2000) and Young Sound (Rysgaard et al. 1998), and much lower than at the temperate, intertidal areas of Puget Sound (Thom et al. 1994) and the River Thames Estuary (Trimmer et al. 2000) (Table 5).

Table 5. Mean respiration rates (range) of intertidal and subtidal benthic communities in Arctic and temperate climates. Data for the present study are shown in bold

Climate	Location	Depth (m)	Temp. (°C)	Respiration rate (mg O_2 m^{-2} d^{-1})	Source
Arctic	Greenland Sound	20–36	–1	172 (113–231)	Glud et al. (2000)
Arctic	Young Sound, Greenland	36	–1	288 (160–416)	Rysgaard et al. (1998)
Arctic	Norwegian Fjord	60–90	6–11	301 (276–326)	Wassmann (1984)
Arctic	Northern Bering Chukchi Seas	20–55	2	320 (19–621)	Grebmeier & McRoy (1989)
Arctic	**Ny Ålesund, Svalbard**	**1–3**	**4–6**	**387 (314–460)**	**Present study**
Arctic	Alaskan Coastal Waters	11–48	3–8	407 (237–576)	Devol et al. (1997)
Temperate	Puget Sound	Intertidal	9–18	1469 (904–2033)	Thom et al. (1994)
Temperate	River Thames Estuary	2–3	4–24	2494 (1023–3965)	Trimmer et al. (2000)

The whole core respiration rate in the ice algae treatment was significantly greater than in the phytoplankton treatment (Fig. 5). This pronounced difference in response to ice algae versus phytoplankton was probably not due to differences in biomass among the treatments because the variance in total faunal biomass for the study site was quite low (<7% of the total biomass). It is interesting to note the lack of respiration response to the addition of phytoplankton (Fig. 5). According to the sediment chl *a* and C20:5(n-3) concentrations, organic matter in the phytoplankton treatment was being consumed; however, this matter was probably the higher quality *Thalassiosira hyalina* in the phytoplankton mix. The presence of *Phaeocystis pouchetii* may have inhibited a response of the magnitude seen in the ice algae treatment, because although *P. pouchetii* is a common component of the phytoplankton community in the Barents Sea and Svalbard waters (Wassmann et al. 1990, Ratkova & Wassmann 2002), it has been shown to be low in food quality and cause arrested development in some benthic species (Tang et al. 2001, Klein Breteler & Koski 2003). Similarly, the presence of *P. pouchetti* in the phytoplankton treatment could have diluted the amount of accessible organic matter in that treatment relative to the ice algae treatment. Alternatively, anaerobic bacteria could also play a role in the reduction of sediment chl *a* and C20:5(n-3) concentrations without affecting short term whole core respiration rates measured by oxygen consumption (Capone & Kiene 1988). Although the benthic community exhibited an elevated respiration response to the addition of ice algae at T = 0.5 and 5 d, by 19 d the respiration rate in the ice algae treatment decreased to the control level. This return to background respiration rates tracks the decrease in chl *a* (Fig. 2C) and C20:5(n-3) (Fig. 4) concentrations to control levels in the ice algae treatment. The respiration rate in all treatments increased throughout the experiment despite a reduction in bioavailable organic matter, which may be due to the small, uncontrollable increase in incubation temperature from 4.5 to 5.5°C during the course of the experiment.

The data discussed thus far suggest that the benthic community responds differently to ice algae compared to phytoplankton; however, they did not show how food was utilized after consumption. Therefore we also examined the assimilation of ice algae and phytoplankton into biomass using stable isotope analyses. Both suspension and deposit feeding organisms from 3 phyla (Mollusca, Annelida, and Sipuncula) exhibited significant enrichment in bulk tissue and C20:5(n-3) $\delta^{13}C$ signatures over control (Table 4), suggesting that ice algae-derived carbon was digestible by multiple taxa with several different feeding strategies. Although all benthic invertebrates fed phytoplankton appeared to be depleted in their $\delta^{13}C$ signatures relative to the control, only *Liocyma fluctuosa* exhibited a significant assimilation of phytoplankton into biomass (Table 4). This result may be due to the low food quality of *Phaeocystis pouchetii* present in the phytoplankton treatment (Tang et al. 2001, Klein Breteler & Koski 2003). It should be noted that there were no significant differences in the isotopic signatures or patterns of assimilation for species in the whole core incubation experiments (with sediment) versus the individual feeding experiments (without sediment), suggesting that the lack of sediment in the individual feeding experiments did not bias the results (Table 4).

Onisimus littoralis was the only species to show no changes in $\delta^{13}C$ signatures across treatments (Table 4). *O. littoralis* is a scavenger and was probably feeding on dead or moribund organisms (Werner 1997) as opposed to directly on ice algae or phytoplankton according to the significantly enriched $\delta^{15}N$ signature of *O. littoralis* compared to the primary consumers (Fig. 1). *O. littoralis* did, however, have a $\delta^{13}C$ signature (–17.9‰), which suggests it was feeding on organisms that relied predominantly on ice algae, such as the deposit feeders (Table 1). Benthic amphipods like *O. littoralis* provide a link between higher trophic level consumers, such as bottom feeding fish and birds, and deposit feeding primary consumers, which rely on ice algae (Hop et al. 2002). Therefore, climate change-

mediated reductions in ice algae could have ecosystem wide ramifications that are amplified through a trophic cascade.

It is clear according to natural stable isotope analyses that ice algae were readily assimilated into biomass by a variety of benthic invertebrates. Unfortunately, the small differences between the $\delta^{13}C$ value of ice algae and the organisms' natural $\delta^{13}C$ signatures made it difficult to assess species-specific differences in the degree of ice algae assimilation. Therefore, ^{13}C-enriched ice algae (~684‰) were implemented as a more powerful tracer of ice algae assimilation. Although all of the species fed ^{13}C-enriched ice algae showed some degree of assimilation, the deposit feeder *Macoma calcarea* (15%) exhibited a greater degree of ice algae assimilation than the suspension feeders (2 to 4%) (Fig. 6). These data suggest that deposit feeders assimilate ice algae better than suspension feeders. *Onisimus litto-ralis* showed the least enrichment in $\delta^{13}C$ values (<1%) (Fig. 6). Although the natural isotope experiment indicated that *O. littoralis* was not consuming ice algae, the more sensitive ^{13}C-enrichment experiment showed that *O. littoralis* did consume a small amount of ice algae. Werner (1997) showed that *Onisimus* sp. consumed enough ice algae to maintain basal metabolic rate, but relied on dead or moribund animal matter to support an active lifestyle. Therefore, it appears that benthic organisms across several phyla and feeding strategies differentially consumed and assimilated ice algae.

Although the assimilation experiments showed that ice algae and phytoplankton could be assimilated into biomass by a variety of species, it is still unclear how these food sources were being used in the natural benthic setting. Therefore, we examined the stable isotope signatures of benthic fauna collected directly from Thiisbukta (i.e. without experimental manipulations). Thiisbukta supports an abundant but taxonomically simple faunal assemblage (Table 1), similar in biomass and community composition to other shallow soft-sediment systems on western Svalbard (Wlodarska-Kowalczuk et al. 1998, Hop et al. 2002). The $\delta^{13}C$ values of the suspension feeders *Liocyma fluctuosa* (–23‰) and *Euchone analis* (–23‰) suggest a diet consisting primarily of phytoplankton (Fig. 1). Although terrestrial organic matter transported into Thiisbukta with glacial runoff has a $\delta^{13}C$ signature (ca. –28‰) similar to phytoplankton (ca. –25‰), it was not a likely food source for the primary consumers in Thiisbukta. The primary consumers in the area (mean $\delta^{15}N$ 7‰) were too enriched in $\delta^{15}N$ to be feeding primarily on terrestrially derived phytodetritus (ca. 1‰) (Fig. 1).

The suspension feeders' phytoplankton signal reflects their food availability during the sampling season. The suspension feeders were only able to feed on organic matter sedimenting from the overlying water column, which during the summer was primarily phytoplankton. Although we do not have data from the spring, this theory could be tested by analyzing the isotopic signatures of benthic invertebrates collected during the spring when ice algae were the dominant food sources. Furthermore, phytoplankton is produced and can remain in the water column for a long time (1 to 2 mo) due to slow sedimentation rates and frequent resuspension (Van der Loeff et al. 2002). Ice algae, on the other hand, sink rapidly to the seafloor as a short pulse input after the spring ice melts (Haecky et al. 1998, Ambrose et al. 2005). For example, *Nitzschia frigida* has been shown to remain in the water column for less than a day (Haecky et al. 1998). Therefore, phytoplankton may be a more accessible food source for suspension feeders during the summer.

The deposit feeders and suspension feeders were feeding on a food sources in the same trophic level based upon their $\delta^{15}N$ values ($\delta^{15}N$ ~7‰). However, both of the deposit feeders *Macoma calcarea* ($\delta^{13}C$ –19‰) and *Phascolopsis gouldii* ($\delta^{13}C$ –17‰) were relying on food sources with a more enriched $\delta^{13}C$ value in addition to phytoplankton (Fig. 1). *M. calcarea* had a $\delta^{13}C$ signature between the suspension feeders *Liocyma fluctuosa* and *Euchone analis* and the deposit feeder *P. gouldii*, which may be indicative of *M. calcarea*'s ability to suspension feed as well as deposit feed. The enriched food source for *M. calcarea* and *P. gouldii* could be ice algae ($\delta^{13}C$ –16‰; Table 2) or benthic microalgae ($\delta^{13}C$ –15‰; Middelburg et al. 2000). Reductions in light reaching the benthos (Horner & Schrader 1982) and low salinity are major factors limiting the distribution and abundance of benthic microalgae (Kies 1997). Since Thiisbukta frequently experiences low salinity (10‰) and high turbidity due to glacial runoff, the presence of benthic microalgae in the sediment was probably negligible. Deposit feeders, however, were probably able to feed on ice algae in the sediment into the early summer months because ice algae are often buried deep in the sediment as a result of caching, or storage of high quality food items at depth by infauna (Jumars & Wheatcroft 1989, Mincks et al. 2005). As in many other glacial bays along the Svalbard coast (Wlodarska-Kowalczuk et al. 1998), the macrobenthos at Thiisbukta was dominated by deposit feeding polychaetes and bivalves (Table 1), which were distributed down to 9 cm below the sediment surface. This community composition and distribution allows for active reworking of a large volume of sediment. In our study, the sediment cores inoculated with ^{13}C-enriched ice algae showed significant enrichments in subsurface sediment $\delta^{13}C$ values down to 4 cm after 19 d (Fig. 3). Although stored food is sometimes lost from the system, it is common for large quantities of ice algae to resurface due to active

sediment mixing (Mincks et al. 2005). This supplies deposit feeders with ice algae long after the spring ice algal blooms.

The deposit feeders had significantly higher concentrations of C20:5(n-3) than suspension feeders according to their C20:5(n-3) to C16:0 ratios, which indicates that they were consuming a diet higher in C20:5(n-3) content. Since ice algae have significantly higher total concentrations of EFAs (C20:5(n-3), 18:2(n-6) and C22:6(n3)) than phytoplankton (Table 2), deposit feeders may be preferentially selecting ice algae for its EFA content (quality) rather than relying solely on phytoplankton (quantity). Many aquatic species are able to discriminate between and selectively feed on different components of seasonally deposited phytodetritus, such as EFAs, during the digestive processes (Müller-Navarra et al. 2000, Suhr et al. 2003). Ice algae and phytoplankton have similar C:N ratios (Table 2), and thus food quality was likely not based upon carbon or nitrogen limitations (Hessen 1992). In a study conducted on *Daphnia magna*, 69% of the variation in normalized growth was explained by the ω3-fatty acid content of the diet, while only 11% of the growth was explained by the elemental composition of the diet (Park et al. 2002).

Warming of the Arctic as a result of global climate change will likely have an impact on the relative quantities of ice algae and phytoplankton reaching the benthos. Previous studies have been limited in their evaluations of the importance of ice algae as carbon sources for the Arctic benthos (Grebmeier & Dunton 2000, Hansen & Josefson 2001, Poltermann 2001). Our results clearly demonstrate that ice algae are readily consumed and assimilated by the Arctic benthos, and may in fact be preferentially selected by some benthic species, such as deposit feeders. Deposit feeders often dominate Arctic soft-sediment systems (Denisenko et al. 2003), and thus a climate change-mediated reduction in their preferred food source could significantly affect their distribution and abundance. These alterations could, in turn, propagate through the food web to have wide reaching ramifications on the structure and function of the Arctic marine ecosystem. Therefore, ice algae are high quality food sources for benthic organisms that must be considered when assessing the impact of climate change on the Arctic marine ecosystem.

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