

# Small-scale spatial variability in benthic food webs in the northeastern Chukchi Sea

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**ABSTRACT:** Benthic food-web structure can differ over large scales across Arctic shelves in relation to hydrographic conditions, but little is known if such differences also occur on smaller scales (10s of km) in hydrographically complex areas. The length, food sources, trophic composition, and energy distribution of benthic food webs in 3 neighboring study areas in the northeastern Chukchi Sea (i.e. Klondike, Burger, and Statoil, 3000 km<sup>2</sup> each) were compared using stable isotope analysis and bomb calorimetry. Food-web length (4 trophic levels), food sources, and plots of  $\delta^{13}\text{C}$  versus  $\delta^{15}\text{N}$  were comparable among areas. Marked differences in food-web structure were observed when trophic levels in the 3 areas were quantified by benthic biomass and abundance. High proportions of biomass and abundance of trophic level (TL) 3 taxa at Burger were attributed to a large presence of refractory material. High proportions of TL 1 and TL 2 taxa at both Klondike and Statoil reflected higher availability of fresh material. Burger is a rich foraging ground for some benthic top predators due to high benthic prey energy densities. This study demonstrates that marine food webs can vary on small spatial scales with hydrographic conditions, particularly when quantitative trophic level distribution is considered.

**KEY WORDS:** Food web · Benthic · Stable isotope · Carbon isotopes · Nitrogen stable isotope · Calorimetry · Chukchi Sea · Arctic

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## INTRODUCTION

The abundant and biomass-rich benthic communities in the northeastern Chukchi Sea are an important link between seasonal pelagic and sea ice-associated production and higher trophic-level (TL) consumers (Bluhm & Gradinger 2008, Grebmeier 2012). The structure of the benthic food web (e.g. number of TLs, quantitative distribution of feeding guilds, and energy content of benthic food-web members) is influenced by the amount of energy passing through the TLs in benthic communities on the Arctic shelves (Iken et al. 2010). Benthic food-web characteristics are known to vary on large regional scales in the Chukchi Sea, due in part to different water mass characteristics and nutrient regimes (Dunton et al. 1989, Iken et al. 2010, Feder et

al. 2011, Wilt et al. 2014). In the southern Chukchi Sea, identical consumers fed directly on primary production in the nutrient-rich Anadyr Water (AW) compared to more recalcitrant material in the less nutrient-rich Alaskan Coastal Water (ACW), indicating more direct pelagic–benthic coupling under AW conditions (Iken et al. 2010). The generally stable spatial location of regional-scale water masses and their hydrographic characteristics likely maintain these benthic food-web differences. It is currently unknown if such large-scale patterns in benthic food-web characteristics (100s of km) may be downscaled to smaller spatial scales (10s of km) (Piepenburg 2005). Small-scale comparisons in this study are defined as spatial comparisons between 60 and 120 km (each study area has a total area of ~3000 km<sup>2</sup> and sampling locations are separated by a few to 10s

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of km). This range is smaller than that of comparisons made in previous studies in the Chukchi Sea (Iken et al. 2010, Feder et al. 2011), which we considered large- or regional-scale (total area sampled in those studies was up to ~70000 km<sup>2</sup> with sampling locations separated by 10s to 100s of km). Possibly, advective processes may prohibit the establishment of distinct benthic food webs or energy hotspots over small scales. Alternatively, such small-scale differences may exist due to geomorphological variations and persistent hydrodynamic processes, and may be of importance to higher trophic level consumers (Desrosiers et al. 2000, Dunton et al. 2005, Dubois et al. 2007).

Benthic food webs in the Chukchi Sea are characterized by tight pelagic–benthic coupling and are highly influenced by sea-ice dynamics (Dunton et al. 1989, Grebmeier & McRoy 1989, Grebmeier et al. 1989, Iken et al. 2010). Much of the sea-ice algae and seasonal pelagic production released early in the season in the Chukchi Sea sinks to the benthos before zooplankton communities develop after their winter diapause in the Bering Sea (Walsh & McRoy 1986, Grebmeier & Barry 1991, Ambrose et al. 2005). The high standing stock of benthic macrofauna on the northeastern Chukchi shelf (averaging 5–15 g carbon m<sup>-2</sup>, but with values as high as 100 g carbon m<sup>-2</sup> at the head of Barrow Canyon, Grebmeier et al. 2006) is attributed to the flux of ungrazed particulate organic matter (POM) to the bottom and advection of carbon from the highly productive northern Bering and southern Chukchi seas (Dunton et al. 2005, Feder et al. 2007, Woodgate et al. 2010). The energy from primary producers fuels the biomass-rich benthic communities of the northeastern Chukchi Sea, which then in turn support high densities of benthic predators such as bearded seals *Eriignathus barbatus*, Pacific walrus *Odobenus rosmarus divergens*, and gray whales *Eschrichtius robustus* (Lowry et al. 1980, Dehn et al. 2007, Sheffield & Grebmeier 2009). Consequently, changes to the supply of primary production can propagate up the food chain and affect large predator populations (Grebmeier et al. 2006).

The strength of pelagic–benthic coupling in the Chukchi Sea is reflected in trophic structure of the benthos, as determined by stable carbon and nitrogen isotopes. Benthic food webs in the southern offshore Chukchi Sea (AW) are fueled by mostly marine primary production in the water column, while greater proportions of terrestrial carbon reach the benthos inshore (ACW) (Grebmeier et al. 2006, Iken et al. 2010). High proportions of consumer species

within the first TL and high biomass at low TLs indicate tight pelagic–benthic coupling for the benthic community under AW (Iken et al. 2010). Tight pelagic–benthic coupling in the eastern Chukchi Sea food web between Cape Lisburne and Wainwright, Alaska is shown by the low stable carbon isotope variability among consumer feeding groups (~2‰, Dunton et al. 1989). Stable carbon isotope ranges of benthos from the southeastern Chukchi Sea below Cape Lisburne are, however, larger (6.3‰ on the southeastern Chukchi Shelf, and 5.2‰ in the Chukchi Bight) due to mixing of isotopically lighter carbon from terrestrial sources into the food webs of these areas (Feder et al. 2011). In the northeastern Chukchi Sea, the benthic system separates into a trophic guild that relies mostly on water-column production and a guild with looser pelagic–benthic coupling that assimilates a non-pelagic marine carbon source (McTigue & Dunton 2014).

While benthic stable isotope food-web investigations describe trophodynamics and pelagic–benthic coupling, benthic prey energy assessments can quantify the actual amount of energy within benthic communities that is available to top predators. The caloric content of a local benthic community is largely determined by the energy available through primary production delivered to the system, as well as the feeding-type composition of the community (Bagatini et al. 2010, Wilt et al. 2014). Currents and changes in water circulation due to topographic variations can cause increased availability of POM through advection processes, or increased deposition of POM where water movements are slow (Snelgrove & Butman 1994, Blanchard et al. 2013a,b). Such depositional areas are typically characterized by finer sediments and higher proportions of deposit-feeding organisms (Rhoads & Young 1970, Grebmeier 1993). In contrast, coarser sediments and greater proportions of suspension-feeding organisms are found where water currents are stronger (Feder et al. 1994, 2007, Bluhm et al. 2009). These differences in particle deposition and feeding types translate into variations in energy density within the benthic community (Bagatini et al. 2010).

Benthic energy assessments are useful for understanding potential influences of natural and anthropogenic stressors on benthic predators in the Arctic. Benthic energy density information (kJ m<sup>-2</sup>) can demonstrate the potential value of a particular area as a foraging ground for top-level predators, the capacity of predators it can support, and the specific energetic impact that predation has on a benthic community (Wesławski et al. 2006). Caloric data can

also provide insight on prey quality, which is spatially and temporally variable and affects reproduction and population dynamics of marine mammal predators and seabirds (Rosen & Trites 2000, Trites & Donnelly 2003, Österblom et al. 2008). Tracking changes of the benthic community food web and energy composition due to continued climatic warming or local anthropogenic influences may give insights into potential effects on marine mammal populations relying on the benthos, as well as direct effects of predators on the benthic prey populations (Darling et al. 1998, Piepenburg 2005, Bluhm & Gradinger 2008).

From an ecosystem standpoint, it is not known if large-scale trends in benthic food webs and energy distributions across the Chukchi Sea shelf (Dunton et al. 1989, Iken et al. 2010, Feder et al. 2011) are homogeneous, or if they exist as a mosaic of small-scale patches that differ in energy flow and benthic food-web and energy structure. Environmental variations in the northeastern Chukchi Sea may alter small-scale patterns in benthic community characteristics as well as food-web structure, energy flow, and energy density. The hypotheses tested in the present study were that the benthic food web will vary over small spatial scales (10s of km) in food source charac-

teristics, food-web length and trophic composition, and that these small-scale benthic communities will vary in energy density. In doing so, this study sought to determine if the small-scale spatial patterns, previously shown in benthic communities (Blanchard et al. 2013a,b), are matched by variations in food-web characteristics in a hydrographically and topographically diverse region of the northeastern Chukchi Sea.

## MATERIALS AND METHODS

### Study region and study areas

The study region is located off the northwestern coast of Alaska, southwest of Hanna Shoal, between Barrow Canyon and the Chukchi Sea Central Channel (Fig. 1). The study region is 100 to 200 km northwest of the coastal community of Wainwright, Alaska, and contains 3 focused study areas: Klondike, Burger, and Statoil. The 3 study areas were determined by the successful lease bids for oil and gas development made during the February 2008 Chukchi Sea Lease Sale 193. Each study area is about 3000 km<sup>2</sup> with Klondike approximately 14 km southwest of Burger, and Statoil adjacent to Burger, where they share a border to the northwest (Fig. 1).

One of the primary water masses affecting the northeastern Chukchi Sea (Bering Shelf Water, BSW) flows north through the Bering Strait, transporting nutrients, primary production, and biota into the Chukchi Sea (Weingartner et al. 1998, 2005). Topographical features, such as the Central Channel and Hanna Shoal (Fig. 1), play an important role in modifying water mass movement and influencing environmental and biological characteristics of each study area (Winsor & Chapman 2004, Blanchard et al. 2013a). Hanna Shoal is approximately 100 km in diameter and rises 10 to 20 m above its surroundings (Martin & Drucker 1997). Northward-flowing BSW from the Central Channel wraps around Hanna Shoal in an anticyclonic gyre (Martin & Drucker 1997, Winsor & Chapman 2004, Spall 2007). Circulation models indicate that the recirculating water converges over

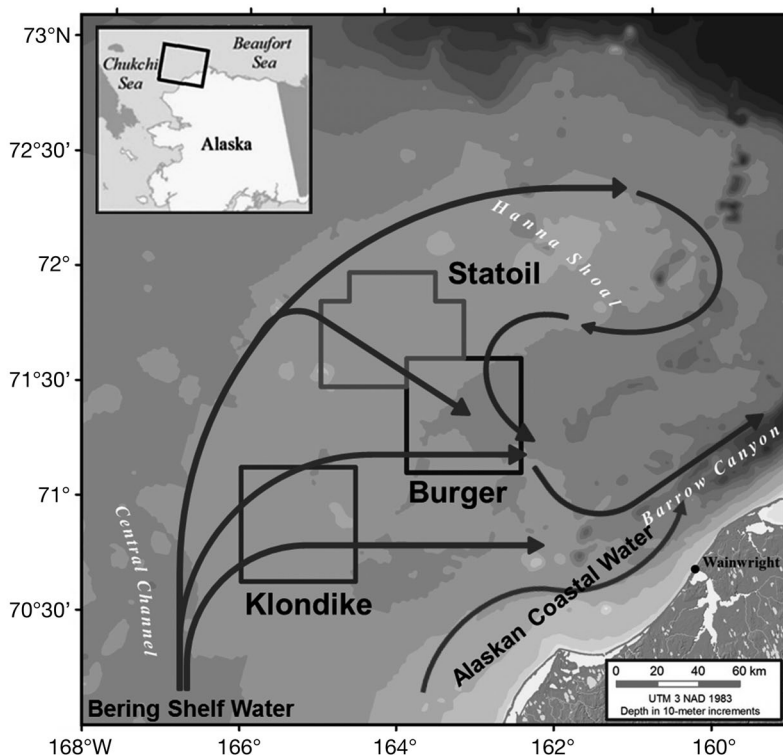


Fig. 1. Map of the study region. The 3 study areas (Klondike, Burger, and Statoil) are denoted by boxes; arrows indicate conceptual oceanographic circulation based on Spall (2007) and Weingartner et al. (2013)

Burger with eastward moving currents from Klondike, creating an area of reduced water movement ( $2 \text{ cm s}^{-1}$ , Weingartner et al. 2013), as also indicated by fine bottom sediments. Faster currents over Klondike ( $4 \text{ cm s}^{-1}$ , Weingartner et al. 2013) carry away finer bottom sediment fractions and leave coarser grain sizes, resulting in lower organic carbon (OC), mud content, and benthic biomass and abundance compared to Burger and Statoil (Blanchard et al. 2013a). Subtle differences in environmental characteristics also exist between Burger and Statoil, though these 2 areas are similar overall; Statoil is slightly shallower, with lower OC and coarser sediments, while increased water depths exist at Burger at the head of a submerged watershed draining towards Barrow Canyon (Blanchard et al. 2013a).

Water circulation patterns in the northeastern Chukchi Sea create an environmental gradient that spans from a more dynamic habitat in the south (Klondike) to a more depositional environment in the northern study areas (Burger and Statoil) over a relatively small spatial scale of  $\sim 100 \text{ km}$ . Despite similar

overall benthic faunal composition among all areas (Blanchard et al. 2013a), seabird and marine mammal observations suggest that Klondike is a more pelagic-driven system, while Burger is more of a benthic-driven system (Day et al. 2013). Densities of fishes and planktivorous seabirds are higher at Klondike than Burger, where benthic-feeding marine mammals occur in higher densities and benthic biomass and density are higher (Aerts et al. 2013, Blanchard et al. 2013a, Gall et al. 2013). Statoil shares biological characteristics with both of the other study areas.

### Sample collection and preparation

Sampling for this study occurred annually from 2009–2011 at Klondike, Burger, and Statoil (2010 and 2011 only) at a total of 76 stations. However, not all sample types were collected every year and at every station. Samples used in this study were collected from 17 August to 10 October 2009, 5 August to 20 September 2010, and 5 August to 20 September 2011.

Three sample types were collected: sediments, POM, and benthic invertebrates for food-web structure and/or benthic energy content (Fig. 2). All samples were kept frozen shipboard at  $-4^\circ\text{C}$ .

POM and surface sediments were sampled to characterize the food sources available to the benthic food web. POM from the chlorophyll maximum layer (5 to 43 m above the seafloor) was sampled using Niskin bottles on a Seabird SBE25/SBE55 CTD rosette from 1–20 September 2010, with 1 replicate per station. Fifty ml of water was filtered under low pressure onto a Whatman GF/F filter ( $0.7 \mu\text{m}$ ) and frozen for stable isotope analysis (Parsons et al. 1984a). POM sampling was logistically not possible during other sampling years. The top 5 cm of sediment from one side of a  $0.1 \text{ m}^2$  double van Veen grab was collected with 1 replicate per station and frozen for stable isotope analysis during the 2009–2010 cruises.

Epifauna were collected with a 3.05 m plumb staff beam trawl (4 mm codend liner, 7 mm mesh) during the 2009–2010 cruises from 8 stations at Klondike, 12 stations at Burger, and 1

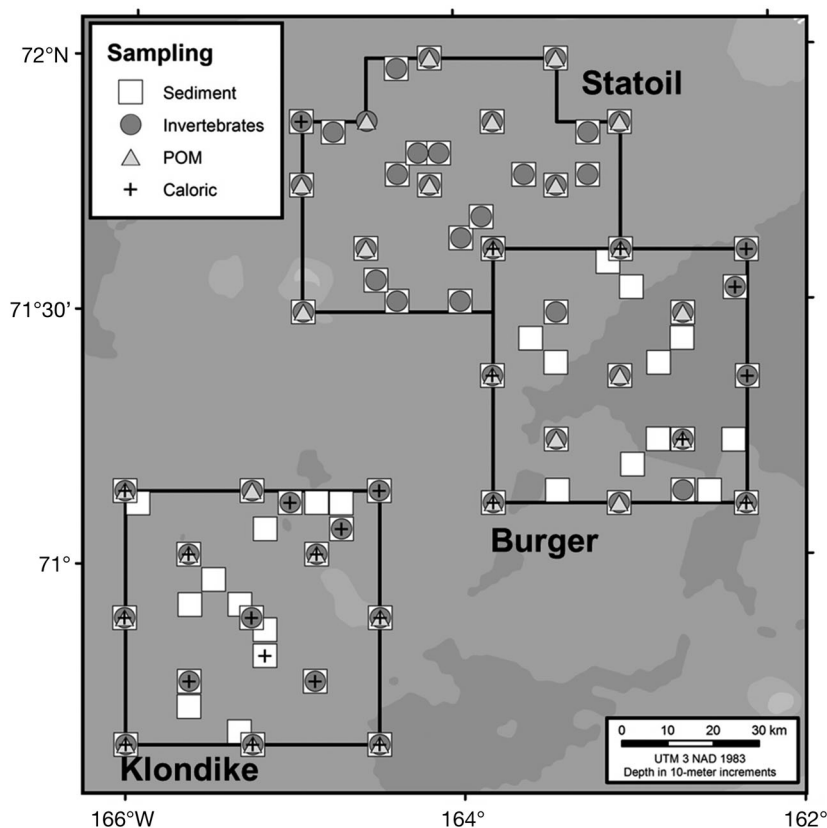


Fig. 2. Map of samples taken at stations within the Klondike, Burger, and Statoil study areas. The 3 sample types for stable carbon and nitrogen isotope analysis (sediments, infaunal and epifaunal invertebrates, particulate organic matter [POM]) are indicated by squares, circles, and triangles, respectively. Caloric samples (invertebrates) are indicated by crosses

station at Statoil. Epifauna were sorted, identified to the lowest taxonomic level possible, and all major epifaunal taxa were frozen in individual Whirlpak™ bags by taxon. Whole organisms were partially thawed in the laboratory, rinsed with deionized water to remove debris, and then freeze-dried for a minimum of 48 h in preparation for stable carbon and nitrogen isotope analysis and bomb calorimetry.

Infaunal samples were collected from one side of a 0.1 m<sup>2</sup> double van Veen grab during the 2009–2011 cruises from 14 stations each at Klondike and Burger, and 26 stations from Statoil. Grabs were rinsed through 1 mm mesh screens, invertebrate taxa collected and frozen for stable isotope analysis and bomb calorimetry. Whole organisms were partially thawed in the laboratory, identified to the lowest taxonomic level possible, rinsed with deionized water to remove debris, and then freeze-dried for a minimum of 48 h. Infaunal taxa representative of common fauna in the Chukchi Sea as found by other studies (Feder et al. 2005, 2011, Iken et al. 2010), were selected for stable carbon and nitrogen isotope analysis and bomb calorimetry. A total of 98 taxa were analyzed, consisting of 45 infaunal and 53 epifaunal taxa.

### Stable isotope analysis

POM filters were oven-dried at 60°C for 24 h and acid-fumed for 48 h with HCl vapors in a vacuum chamber for removal of carbonates (Iken et al. 2010). A fraction of each filter's top layer was scraped off into tin capsules for stable carbon and nitrogen isotope analysis. Sediments were rinsed in 1 N HCl until bubbling ceased, rinsed with deionized water, freeze-dried for a minimum of 24 h, and weighed (13–17 mg) into tin capsules for stable carbon and nitrogen isotope analysis.

Differences in tissue turnover rates can bias organism stable isotope measurements (Peterson & Fry 1987). Therefore, benthic invertebrate samples were prepared using whole body homogenates, including shells, to obtain an average stable isotope signature for the organism (McClelland et al. 1997, Anderson & Polis 1998, Michener & Kaufman 2007). Multiple individuals were composited when organisms were too small to provide at least 5 mg of material for stable isotope processing (to account for loss of material during processing). Samples large enough to yield sufficient mass were homogenized with mortar and pestle prior to processing, otherwise they were processed whole. Consumer homogenates were acid-

ified and lipid-extracted to remove bias of <sup>13</sup>C-depleted carbonates and lipids, respectively, on <sup>δ</sup><sup>13</sup>C measurements (DeNiro & Epstein 1978). Samples were soaked with 1 N HCl for removal of carbonates (Dunton et al. 1989, Iken et al. 2010). Samples were freeze-dried for a minimum of 48 h, and then lipid-extracted with a minimum of three 24 h soaks in 5 ml of 2:1 chloroform methanol (Folch et al. 1957, Post & Parkinson 2001, Hobson et al. 2002, Arrington et al. 2006). Lipid-extraction can affect stable nitrogen isotope signatures (Sotiropoulos et al. 2004, Logan et al. 2008), which will need to be considered when comparing <sup>δ</sup><sup>15</sup>N to results of other studies as there was no separate treatment for stable carbon and nitrogen isotope analysis. Samples were freeze-dried for a minimum of 24 h after solvent removal. A 0.1 to 0.5 mg subsample from each homogenized sample was weighed into a tin capsule for stable carbon and nitrogen isotope analysis.

Samples were analyzed for stable carbon and nitrogen isotopes at the Alaska Stable Isotope Facility (University of Alaska Fairbanks). All analyses were performed using a Thermo Finnigan Delta Isotope Ratio Mass-Spectrometer with Pee-Dee Belemnite (PDB) and atmospheric nitrogen (N<sub>2</sub>) as standards for stable carbon and nitrogen isotopes, respectively. Sample isotope ratios are expressed in standard  $\delta$  notation in parts per thousand (‰) using the equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000 \quad (1)$$

where  $X$  is <sup>13</sup>C or <sup>15</sup>N, and  $R$  is the corresponding isotopic ratio <sup>13</sup>C/<sup>12</sup>C or <sup>15</sup>N/<sup>14</sup>N. Instrument error was determined by a laboratory peptone standard (Ben-David & Flaherty 2012). Analytical instrument error was  $\pm 0.10\text{‰}$  for <sup>δ</sup><sup>13</sup>C and  $\pm 0.18\text{‰}$  for <sup>δ</sup><sup>15</sup>N ( $n = 144$  each). Trophic levels were calculated based on primary consumer <sup>δ</sup><sup>15</sup>N values using the following formula:

$$TL_{(\text{PC})} = (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{primary consumer}}) / 3.4 + 2 \quad (2)$$

where  $TL_{(\text{PC})}$  is the calculated trophic level based on a primary consumer (PC), and 3.4‰ is the average enrichment among trophic levels for aquatic consumers (Minagawa & Wada 1984, Vander Zanden & Rasmussen 2001, Post 2002, Iken et al. 2010). Trophic level calculations were based on a primary consumer (the amphipod *Ampelisca eschrichtii*) rather than POM, as the POM source is temporally and spatially highly variable and was only available for one sampling year, while primary consumers present a time-integrated measure of local primary production (Post 2002). *A. eschrichtii* was chosen over other primary

consumers due to its known suspension feeding habits (Highsmith & Coyle 1990, 1991), and because it was sampled at all study areas.

To quantify the community distribution within trophic levels, biomass (g wet mass [WM]  $m^{-2}$ ) and abundance (ind.  $m^{-2}$ ) data from 2009–2011 of the infaunal and epifaunal community (Blanchard et al. 2013a,b) were averaged for each of the 3 study areas by taxon and binned by trophic level. Although some interannual differences in biomass and abundance exist in each area, averaging across years was considered appropriate to answer the question of small-scale variability of this study. Nevertheless, averaging across years likely added a low to moderate amount of variation in average biomass and abundance values based on the standard deviations calculated for the benthic communities over the 3 yr (Table 1).

Molar C/N ratios were calculated for POM and sediments. These ratios were used to determine nutritional quality, with lower C/N ratios indicating higher nutritional quality due to microbial proteins and labile material (Gnaiger & Bitterlich 1984, Parsons et al. 1984b, Taylor & Roff 1984, Dorgelo & Leonards 2001). Animals were categorized by feeding type (see Table 2) based on known feeding methods (e.g. Fauchald & Jumars 1979, Holte & Gulliksen 1998, Feder et al. 2011).

### Bomb calorimetry

Infaunal and epifaunal taxa from the study region were selected for bomb calorimetry on the basis that they are known prey items of Arctic pinniped and cetacean top predators (e.g. Fay 1982, Darling et al. 1998, Sheffield et al. 2001, Dehn et al. 2007). The relatively large amount of material needed for calorimetry and prevalence of epibenthic prey items in many marine mammal diets restricted taxon selection mostly to those collected from trawls. Limited spatial coverage of trawls prohibited study area comparisons of caloric content within a taxon; therefore, mean caloric content for a taxon was extrapolated for all areas or averaged across study areas if several collections existed. Only taxa collected in 2009 were selected for bomb calorimetry to exclude temporal variability in caloric content. For caloric processing, shells were removed from gastropods and bivalves as soft body parts are extracted from shells during consumption by marine mammals (Fay 1982). Invertebrates with inorganic structures that were difficult to separate from tissue (e.g. echinoderms, decapods)

Table 1. Mean and SD of 2009–2011 biomass and abundance data for the macro- and megafaunal community at Klondike, Burger, and Statoil. Values are based on biomass and abundance data from Blanchard et al. (2013a,b). WM = wet mass

	Biomass (g WM $m^{-2}$ )		Abundance (ind. $m^{-2}$ )	
	Mean	SD	Mean	SD
Klondike	154.67	38.32	1355.33	592.41
Burger	310.10	59.92	3695.03	1133.03
Statoil	307.50	65.47	1205.00	219.20

were homogenized and analyzed whole. These types of prey are consumed whole by marine mammal predators; therefore, this method appropriately approximates energy ingested. Multiple specimens were pooled where single individuals did not provide sufficient mass for analysis. Pooled samples consisted of individuals collected from the same station.

Wet mass (shell-free) was recorded, and samples were frozen before freeze-drying for a minimum of 48 h. Dry mass (DM) was recorded following lyophilization (for wet weight to dry weight conversion factors) and samples were homogenized with mortar and pestle. Dried samples were formed into pellets (~0.5–1 g) and analyzed on a Parr model 6300 oxygen bomb calorimeter for gross energy content at the Marine Mammal Laboratory (University of Alaska Fairbanks). Samples that did not hold their form in a pellet were analyzed in gelatin capsules. Five empty gelatin capsules were weighed and analyzed to determine their average caloric value for correction of prey caloric content (2.06 kJ per capsule). Instrument error ( $\pm 0.04$  kJ  $g^{-1}$ ) was determined by analysis of 12 runs of a benzoic acid standard (Parr Instrument Co.). Replicates on pooled and individual taxa were run as many times as the amount of available sample would allow (2–10 times). Mean energy content of taxa is reported in kJ  $g^{-1}$  WM. Conversion factors for tissue dry mass to total wet mass were calculated or based on literature values (Stoker 1978, Ricciardi & Bourget 1998) when they could not be determined directly; for bivalves and gastropods these values included shell weight in reported WM values. Conversion factors were used to convert shell-free WM to shelled WM, as biomass data used for generating kriging plots included shells (see below).

### Statistical methods

Statistical analyses were performed using the software package R v.2.15.0 ([www.r-project.org](http://www.r-project.org)). Data

had equal variance and normality and no transformations were required. One-way ANOVA was used for regional comparisons of stable carbon and nitrogen isotope values for sediment (with Year as a blocking factor), POM, and energy densities. Tukey's post hoc test was used for multiple comparisons. A significance level of  $\alpha = 0.05$  was used for all tests. Simple linear regression has traditionally been used to model the correlation between stable carbon and nitrogen isotopes in marine food webs (Mincks et al. 2008, Fanelli et al. 2009, Feder et al. 2011, Kędra et al. 2012). The use of  $\delta^{13}\text{C}$  as a quantitative predictor, however, violates the assumption of a fixed predictor in simple linear regressions (Quinn & Keough 2002). Therefore, regressions of isotope data by area were performed using Model II regression (ranged major axis regression, RMA regression) for 2 random variables to account for the use of measured stable carbon isotope values in the regression models (Laws & Archie 1981, Quinn & Keough 2002). In this study, RMA regression considered  $\delta^{13}\text{C}$  as the quantitative predictor and  $\delta^{15}\text{N}$  as the response. RMA regression methods are defined for regression with 1 predictor variable; therefore, a 'study area effect' was determined by comparing confidence intervals of regression coefficients. Significant differences were determined by lack of overlap of 95% confidence intervals. Geospatial modeling of energy density was performed using the library *geoR* in R. Kriging plots modeling prey energy density ( $\text{kJ WM m}^{-2}$ ) in each study area were generated using caloric content ( $\text{kJ g}^{-1}\text{ WM}$ ) and biomass data (Blanchard et al. 2013a,b) of major marine mammal prey items known from stomach content analyses (e.g. Fay 1982, Sheffield et al. 2001, Dehn et al. 2007, Quakenbush et al. 2011a,b).

## RESULTS

### Stable isotope analysis

POM from Klondike stations was significantly more  $^{13}\text{C}$ -enriched compared with POM from Burger and Statoil ( $p < 0.001$ ) with the latter 2 showing no statistical difference ( $p = 0.891$ ). There was no significant difference among areas for POM  $\delta^{15}\text{N}$  (ANOVA,  $p = 0.332$ ) or C/N values (ANOVA,  $p = 0.150$ ). Average POM C/N ratios by study area ranged from 7.28 to 7.83.

Sediment  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were significantly different among study areas (ANOVA,  $p < 0.002$  and  $p < 0.001$ , respectively). Sediment  $\delta^{13}\text{C}$  was significantly lower at Klondike compared with Statoil

( $p < 0.001$ ), and  $\delta^{15}\text{N}$  was significantly lower at Klondike compared with Burger ( $p = 0.001$ ). Sediment C/N ratios differed significantly (ANOVA,  $p < 0.002$ ), with Klondike sediments having a higher C/N ratio than Statoil ( $p < 0.001$ ). All other area comparisons for sediment  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , or C/N were not significant (all  $p \geq 0.060$ ). Average sediment C/N ratios ranged from 8.59 to 9.74. POM from stations in Klondike was more  $^{13}\text{C}$ - and  $^{15}\text{N}$ -enriched than Klondike sediments, whereas POM from stations at Burger and Statoil was  $^{13}\text{C}$ -depleted and  $^{15}\text{N}$ -enriched compared with the sediments in their respective study area (Table 2).

A total of 91 taxa were analyzed for stable carbon and nitrogen isotopes with approx. 50 taxa from each study area (Table 2). The 95% confidence intervals for the intercepts and slopes from RMA regressions overlapped in range, indicating no difference in stable isotope regressions among study areas (Table 3). The fitted linear models of food webs were similar among areas, pointing to similar food-web structures (Fig. 3).

The food webs spanned 4 trophic levels in all study areas, from POM to higher-order benthic invertebrate predators such as predatory gastropods and polychaetes (Table 2). Proportional contributions of biomass and abundance to trophic levels by area showed the highest proportions of both quantitative measures within trophic level 3 at Burger (dominated in biomass by *Ophiura sarsi*, and by *Maldane sarsi* in abundance), while Klondike and Statoil exhibited higher proportions of biomass and abundance at trophic level 2 (mostly bivalves) (Fig. 4). Stable carbon and nitrogen isotope values were compared for 4 taxa collected in all 3 study areas to examine spatial variation within taxa. Stable carbon and nitrogen isotope ratios of these taxa showed no differences among the 3 study areas for the bivalve *Ennucula tenuis* and the polychaete family Maldanidae (Fig. 5). However, suspension-feeding Ampeliscidae from Klondike and scavenging *Anonyx* spp. from Statoil were more enriched in  $^{13}\text{C}$  than the same taxa at the other study areas.

### Benthic energy content

A total of 34 taxa collected in 2009 were analyzed for gross caloric content across the study region (Table 4). Mean energy density by study area was 477, 747, and 595  $\text{kJ WM m}^{-2}$  for Klondike, Burger, and Statoil, respectively. Burger had significantly higher gross energy density than Klondike ( $p =$

Table 2. Stable carbon and nitrogen isotope data of particulate organic matter (POM), sediments, and benthic invertebrates collected from Klondike, Burger, and Statoil. Values are reported as means with standard deviation (SD), number of replicates (n), trophic level (TL) based on a primary consumer (see 'Materials and methods: Stable isotope analysis' for details), and feeding type (BO: benthic omnivore, DF: deposit feeder [includes surface and subsurface], GR: grazer, P: predator, S: scavenger, SF: suspension feeder)

Sample type/ Taxon	Feeding type	Klondike			Burger			Statoil									
		$-\delta^{13}\text{C}$ (‰) Mean	$-\delta^{15}\text{N}$ (‰) SD	n	TL	$-\delta^{13}\text{C}$ (‰) Mean	$-\delta^{15}\text{N}$ (‰) SD	n	TL	$-\delta^{13}\text{C}$ (‰) Mean	$-\delta^{15}\text{N}$ (‰) SD	n	TL				
POM		-21.56	0.68	5.67	2.55	9	-23.23	0.71	6.39	2.43	10	-23.1	0.64	7.34	2.45	11	
Sediment		-22.75	0.39	4.99	1.04	26	-22.51	0.4	5.97	0.84	26	-22.28	0.32	5.6	0.95	24	
<b>CNIDARIA</b>																	
<b>Actinaria</b>																	
<i>Gersemia rubiformis</i>	P						-18.12		13.51		1	3.5					
<i>Stomphia</i> spp.	P	-19.3		14.6		1											
<b>Hydrozoa</b>	SF						-20.1		10.39		1	2.5					
<b>NEMERTEA</b>	P						-17.39		17.23		1	4.6					
<b>SIPUNCULA</b>																	
<i>Sipunculid</i>	DF	-18.44		10.89		1											
<i>Golfingia</i> spp.	DF																
<i>Golfingia margaritacea</i>	DF	-19.34	0.52	11.38	0.05	2	-18.68		11.27		1	2.8					
<i>Phascolion strombus</i>	DF						-18.82	0.84	13.66	0.4	2	3.5					
<b>PRIAPULA</b>																	
<i>Priapulus caudatus</i>	DF	-17.88		14.41		1	-18.18	0.28	15.52	0.11	2	4	-18.1	0.42	15.71	0.45	3
<b>ANNELIDA</b>																	
<b>Polychaeta</b>																	
Ampharetidae	DF	-20.76		11.16		1	-21.01		10.99		1	2.7	-18.73		12.95		
<i>Axiobella catenata</i>	DF	-19.37		12.22		1							-18.83		13.06		
<i>Axiobella</i> spp.	DF	-18.77	0.35	13.98	0.14	2											
<i>Brada</i> spp.	DF						-19.19		12.25		1	3.1					
Capitellidae	DF						-18.42		12.68		1	3.2	-18.83		11.71		
Flabelligeridae	DF	-23.34		8.61		1											
<i>Idanthyrus</i> spp.	SF	-20.11		11.17		1											
<i>Lumbrineris</i> spp.	P						-18.54	0.21	13.45	1.54	3	3.4	-18.72	0.75	13.64	0.54	3
<i>Maldane sarsi</i>	DF	-19.00	0.48	13.31	0.58	13	-19.35	0.70	13.75	0.95	6	3.5	-19.36	0.61	13.55	1.13	16
Maldanidae	DF	-19.56	1.00	12.56	1.99	15	-19.73	0.45	12.70	1.42	19	3.2	-19.39	0.38	13.00	1.11	31
<i>Nephtys</i> spp.	P	-17.85		16.11		1	-17.74		17.91		1	4.8	-18.15	0.57	15.36	0.49	6
<i>Ophelina</i> spp.	DF	-19.90	0.31	11.98	0.24	2											
<i>Paradiopatra parva</i>	P	-18.38		13.94		1											
Phyllocidae	P						-18.32	0.12	16.21	0.11	2	4.3	-17.79		16.37		
Polynoidae	P	-18.27		13.85		1	-19.00	0.40	12.08	1.00	2	3.0	-19.52	0.55	12.70	1.09	5
<i>Praxillella praetermissa</i>	DF	17.87		13.08		1											
<i>Praxillella</i> spp.	DF																
Sabellidae	SF	-20.98		11.20		1											
<i>Sternaspis fossor</i>	DF	-19.48		9.92		1											
Terebellidae	DF	-20.12	0.69	12.46	0.66	2	-19.17		12.42		1	3.1	-19.95		12.21		
<i>Terebellides stroemi</i>	DF																
<b>MOLLUSCA</b>																	
<b>Polyplacophora</b>	GR	-17.82		15.27		1											
<i>Ishnochiton albus</i>	GR	-16.71		14.57		1											

(Table continued on next 2 pages)



Table 2 (continued)

Sample type/ Taxon	Feeding type	Klondike			Burger			Statoil			
		$-\delta^{13}\text{C}$ (‰) Mean	$-\delta^{15}\text{N}$ (‰) SD	TL n	$-\delta^{13}\text{C}$ (‰) Mean	$-\delta^{15}\text{N}$ (‰) SD	TL n	$-\delta^{13}\text{C}$ (‰) Mean	$-\delta^{15}\text{N}$ (‰) SD	TL n	
<b>Gastropoda</b>											
<i>Boreotrophon</i> spp.	P				-18.18	12.27	1	-17.71	16.27	1	3.1
<i>Buccinum polare</i>	P				-18.14	15.00	1	-18.37		1	3.9
<i>Buccinum scalariforme</i>	P										
<i>Buccinum</i> spp.	P								16.34	1	3.9
<i>Colus</i> spp.	P	-15.24	17.13	1	-16.83	16.16	2	-18.04	12.78	1	2.9
<i>Cryptonatica affinis</i>	P			4.4	-18.21	14.02	1	-18.88	0.03	1	3.6
<i>Cyllichna alba</i>	P				-18.18	13.46	1	-18.57	14.42	2	3.4
<i>Euspira pallida</i>	P				-18.05	13.03	1	-18.48	12.72	5	2.9
<i>Margarites</i> spp.	P	-18.60	13.68	1	-18.70	11.10	1			1	2.7
<i>Solariella</i> spp.	P	-18.02	13.20	1	-19.10	11.81	1			1	3.0
<i>Tachytrichus reticulatus</i>	P			3.3							
<i>Tachytrichus</i> spp.	P	-19.61	10.32	1					11.35	1	2.5
<b>Bivalvia</b>											
<i>Astarte borealis</i>	SF				-20.13	11.93	1	-19.90	10.15	1	2.1
<i>Astarte montagui</i>	SF	-20.40	11.48	1	-19.54	11.56	1	-18.93	0.72	3	2.4
<i>Astarte</i> spp.	SF			2.6	-19.10	9.77	2	-18.28	10.57	1	2.2
<i>Cyclocardia crebricostata</i>	SF				-20.66	10.48	1	-18.57	0.65	73	2.0
<i>Ennucula tenuis</i>	DF	-18.73	0.54	24	-19.06	9.19	34	-19.79	0.04	2	1.6
<i>Liocyma fluctuosa</i>	SF			2.0	-20.55	9.87	2	-20.14	9.21	1	1.8
<i>Macoma calcaria</i>	DF							-19.57	0.26	4	1.7
<i>Macoma moesta</i>	DF	-19.41	8.37	1	-19.89	9.71	2				
<i>Macoma</i> spp.	DF			1.7	-18.49	9.76	1				
<i>Musculus niger</i>	SF				-20.07	9.23	1				
<i>Myssella planata</i>	DF										
<i>Nuculana pernula</i>	DF							-19.92	10.27	1	2.1
<i>Nuculana radiata</i>	DF	-19.43	10.21	1							
<i>Nuculana</i> spp.	DF	-18.57	7.95	1	-19.77	10.49	2	-20.22	10.05	1	2.1
<i>Serripes groenlandicus</i>	SF/DF			1.6				-20.30	10.48	1	2.2
<i>Thyasira flexuosa</i>	DF				-19.79	12.89	1	-19.37	0.27	5	1.7
<i>Yoldia</i> spp.	DF							-19.44	9.02	1	1.8
<i>Yoldia hyperborea</i>	DF				-19.03	9.88	1				
<b>CHELICERATA</b>											
Pycnogonidae	P	-20.24	11.30	1	-18.93	13.06	1				
<b>CRUSTACEA</b>											
<b>Amphipoda</b>											
<i>Ampelisca eschrichtii</i>	SF	-19.24	7.73	1	-22.33	8.56	1	-22.10	0.27	3	2.0
<i>Ampelisca</i> spp.	SF	-21.48	0.34	2.0	-22.77	7.51	1	-22.39	1.44	3	1.5
<i>Anonyx</i> spp.	S	-21.44	10.29	1	-19.23	14.37	2	-18.64	0.11	4	3.9
<i>Byblis</i> spp.	SF	-19.29	0.29	3.9				-22.24	0.65	3	1.6
<i>Haploops laevis</i>	SF	-21.63	0.05	2	-18.22	15.39	1	-22.17	0.52	5	1.4
<i>Paraphoxus</i> spp.	SF	-19.26	11.93	1	-19.27	12.54	1				
<i>Stegocephalus</i> spp.	S			2.8							

(Table continued on next page)

Table 2 (continued)

Sample type/ Taxon	Feeding type	Klondike			Burger			Statoil			
		— $\delta^{13}\text{C}$ (‰)— Mean SD	n	TL	— $\delta^{13}\text{C}$ (‰)— Mean SD	n	TL	— $\delta^{13}\text{C}$ (‰)— Mean SD	n	TL	
<b>Decapoda</b>											
<i>Chionoecetes opilio</i>	BO	-20.21	6.63	1	1.2	-19.57	0.08	10.29	4.11	2	2.5
Hippolytidae	BO	-18.51	15.24	1	3.8						
<i>Labidochirus splendescens</i>	BO	-19.11	0.35	2	2.4						
<i>Leucon nasica</i>	DF										
<b>Ostracoda</b>	P					-19.63		14.97		1	3.9
<b>Other crustaceans</b>											
<i>Synidotea</i> spp.	P					-20.37		9.77		1	2.4
<b>ECHINODERMATA</b>											
<b>Asteroidea</b>											
<i>Ctenodiscus crispatus</i>	DF	-17.74	12.72	1	3.0			12.51	0.24	2	3.2
<i>Leptasterias groenlandica</i>	P					-16.59	0.40				
<i>Leptasterias</i> spp.	P					-15.66		12.47		1	3.2
<i>Pteraster obscurus</i>	P	-18.01	13.25	1	3.2						
<b>Ophiuroidea</b>											
<i>Diamphiodia craterodonta</i>	DF					-18.54		12.52		1	3.2
<i>Ophiura sarsi</i>	BO	-15.83	14.66	1	3.6	-17.03		12.97		1	3.3
<i>Ophiura</i> spp.	BO										
Ophiuridae	BO					-17.80		15.13		1	3.9
<b>Holothuroidea</b>											
<i>Ocnus</i> spp.	DF					-22.00		11.56		1	2.9
<i>Psolus fabricii</i>	SF	-23.23	11.07	1	2.5						
<b>BRYOZOA</b>	SF	-20.13	10.36	1	2.3	-19.88		11.26		1	2.8

0.012), but was not statistically different from Statoil ( $p = 0.229$ ). Klondike and Statoil gross energy densities were not statistically different ( $p = 0.407$ ). Energy density had an increasing west–east gradient across each study area as shown by kriging plots (Fig. 6). This trend was particularly strong at Burger and Statoil, peaking in an area of highest energy density at the eastern edges of these areas. Projected west to east energy density gradients ranged from 640 to 760 kJ WM  $\text{m}^{-2}$  in Burger, and from 520 to 740 kJ WM  $\text{m}^{-2}$  in Statoil. Klondike energy density was relatively constant across the study area, ranging from 500 to 540 kJ WM  $\text{m}^{-2}$  (west to east).

## DISCUSSION

### Food sources

Sources of carbon for Arctic benthic marine food webs include water column, benthic, ice-edge, and sea-ice production, as well as export from terrestrial and nearshore sources to offshore sediments (Belicka et al. 2002, Ambrose et al. 2005, Glud et al. 2009). These POM carbon sources to the benthos are spatially and temporally heterogeneous materials resulting in use of multiple food sources by benthic organisms (Hill et al. 2005, Gradinger 2009, Iken et al. 2010). The stable carbon isotope signatures for POM and sediments in the northeastern Chukchi Sea in the present study suggest mainly marine carbon sources, which are isotopically heavier ( $-26$  to  $-21$ ‰, Gradinger 2009) than terrestrially derived sources ( $-27$ ‰, Naidu et al. 1993, 2000). The mean stable carbon isotope ratios of POM observed here were mostly between  $-21$  and  $-24$ ‰, indicating a food source composed of largely marine carbon with possibly some mixing of more  $^{13}\text{C}$ -depleted sources. There were some differences among study areas; Klondike POM  $\delta^{13}\text{C}$  ( $-21.56$ ‰) more closely reflected

Table 3. Ranged major axis (RMA) regression of benthic invertebrate stable carbon and nitrogen isotope ratios at Klondike, Burger, and Statoil

Site	Intercept	Slope ( $\beta_{RMA}$ )	p	95 % CI	
				Intercept	Slope
Klondike	44.55	1.69	0.01	(34.47, 61.07)	(1.17, 2.55)
Burger	47.29	1.83	0.01	(37.23, 62.82)	(1.30, 2.65)
Statoil	53.78	2.17	0.01	(42.08, 70.15)	(1.56, 3.01)

marine pelagic primary production (Bering Sea phytoplankton  $\delta^{13}C$ :  $-21.2 \pm 1\%$ , Naidu et al. 1993) than the other areas ( $\delta^{13}C = -23.23\%$  and  $-23.10\%$  for Burger and Statoil, respectively). The lower val-

ues at the latter study areas are indicative of isotopically depleted sources. Low C/N ratios (<6) and high  $\delta^{15}N$  values (8‰) are typical of marine POM (Naidu et al. 1993); C/N ratios in this study were ~7 and  $\delta^{15}N$  were near 8‰ at all study areas. Thus, terrestrial material was not present in high quantities in POM, and the  $^{13}C$ -depleted source at Burger and Statoil was of marine origin, discussed further below.

Multiple food sources and high degrees of omnivory in marine benthic food webs result in a continuum of trophic levels and complex trophic patterns (Shurin et al. 2006, Post & Takimoto 2007). Trophic-shift assumptions of 3.4‰ for nitrogen ( $\delta^{15}N$ , Vander

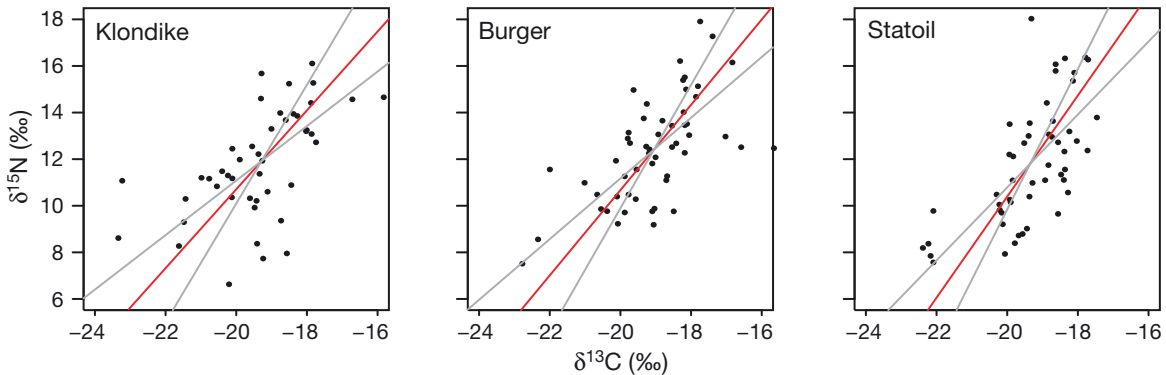


Fig. 3. Ranged major axis (RMA) regression of benthic invertebrate stable carbon and nitrogen isotope data from Klondike, Burger, and Statoil. Each point represents the mean stable carbon and nitrogen isotope signature of one taxon. The center line (red) is the fitted linear model, with slope 95% confidence interval lines (gray)

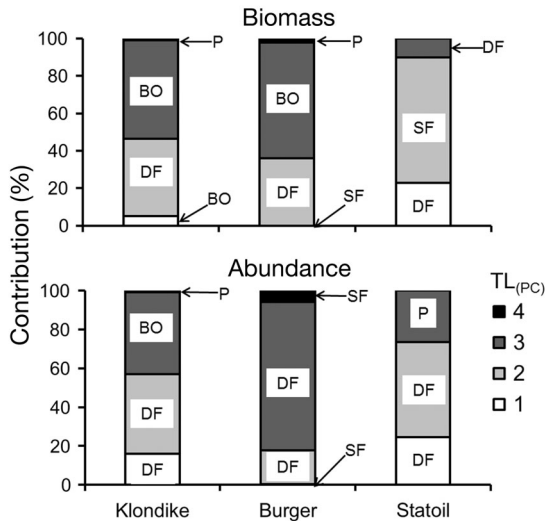


Fig. 4. Proportional contributions of benthic biomass and abundance of taxa to each trophic level at Klondike, Burger, and Statoil. Trophic level is based on the primary consumer *Ampelisca eschrichtii* ( $TL_{(PC)} = 2$ , see 'Materials and methods: Stable isotope analysis' for details). The feeding mode of the taxa with the highest biomass/abundance contributing to each trophic level is noted within each bar. Feeding mode—BO: benthic omnivore, DF: deposit feeder (includes surface and subsurface), SF: suspension feeder, P: predator

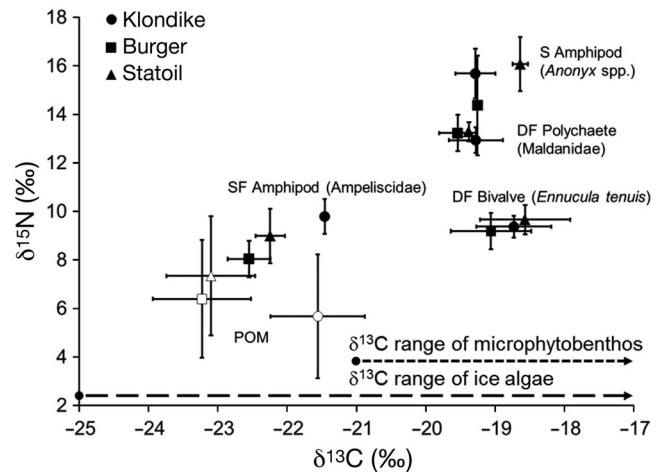


Fig. 5. Stable nitrogen vs. carbon isotope ratios of 4 benthic invertebrate taxa (closed symbols) and particulate organic matter (POM) (open symbols) at Klondike, Burger, and Statoil. Points are means; whiskers are SD. Feeding mode—DF: deposit feeder (includes surface and subsurface), S: scavenger, SF: suspension feeder. Ice algal and microphytobenthos  $\delta^{13}C$  range values from France (1995), Tremblay et al. (2006), and Gradinger (2009) for comparison of organism stable isotope ratios with those of potential food sources (see 'Discussion')

Table 4. Gross energy content ( $\text{kJ g}^{-1}$  WM) and tissue dry mass (DM) to total wet mass (WM) conversion (g tissue DM/g total WM), includes shell for bivalves, gastropods, and chitons) of selected benthic invertebrates. Values are reported as means with SD and number of replicates (n). Bivalve and gastropod conversion factors based on Stoker (1978) and Ricciardi & Bourget (1998)

Taxon	Gross energy content ( $\text{kJ g}^{-1}$ WM)		n	g tissue DM/g total WM
	Mean	SD		
<b>CNIDARIA</b>				
<i>Stomphia</i> spp.	2.16	0.23	2	0.13
<b>SIPUNCULA</b>				
Sipunculid	3.04	0.32	4	0.23
<i>Golfingia margaritacea</i>	2.33	0.55	4	0.23
<b>ANNELIDA</b>				
<b>Polychaeta</b>				
<i>Lumbrineris</i> spp.	5.42	0.07	4	0.29
Maldanidae	3.41	0.06	3	0.33
<i>Nephtys</i> spp.	4.49	–	1	0.25
<i>Paradiopatra parva</i>	3.34	–	1	0.17
<i>Paradiopatra</i> spp.	5.58	–	1	0.24
Polynoidae	2.84	0.01	3	0.15
Terebellidae	3.60	0.08	4	0.26
<b>MOLLUSCA</b>				
<b>Polyplacophora</b>				
<i>Ishnochiton albus</i>	2.15	0.26	7	0.27
<b>Gastropoda</b>				
<i>Buccinum polare</i>	2.15	0.03	4	0.11
<i>Buccinum scalariforme</i>	2.21	0.16	10	0.11
<i>Margarites</i> spp.	1.92	0.28	3	0.11
<b>Bivalvia</b>				
<i>Astarte borealis</i>	0.74	–	1	0.034
<i>Astarte montagui</i>	0.62	0.01	2	0.034
<i>Astarte</i> spp.	0.71	0.01	2	0.034
<i>Ennucula tenuis</i>	2.22	0.22	2	0.11
<i>Macoma</i> spp.	2.23	0.17	4	0.11
<i>Nuculana radiata</i>	0.98	0.47	2	0.06
<i>Yoldia hyperborea</i>	2.26	–	1	0.14
<b>CRUSTACEA</b>				
<b>Amphipoda</b>				
<i>Ampelisca</i> spp.	7.47	–	1	0.31
<i>Anonyx</i> spp.	11.41	–	1	0.41
<i>Stegocephalus</i> spp.	7.76	0.07	2	0.43
<i>Stegocephalus</i> spp.	5.19	0.15	3	0.30
<b>Decapoda</b>				
<i>Argis lar</i>	5.43	0.27	5	0.29
<i>Chionoecetes opilio</i>	4.97	0.32	3	0.36
<i>Hyas coarctatus</i>	2.58	0.13	2	0.32
<i>Pagurus</i> spp.	6.26	0.33	5	0.40
<b>ECHINODERMATA</b>				
<b>Asteroidea</b>				
<i>Leptasterias groenlandica</i>	3.06	1.26	3	0.38
<i>Leptasterias</i> spp.	4.55	0.41	3	0.36
<b>Ophiuroidea</b>				
<i>Gorgonocephalus</i> spp.	2.62	0.08	2	0.49
<i>Ophiura sarsi</i>	1.25	0.25	6	0.65
<b>Holothuroidea</b>				
<i>Psolus</i> spp.	2.24	0.04	2	0.37

Zanden & Rasmussen 2001, Post 2002, Iken et al. 2010) and 0.6‰ for carbon ( $\delta^{13}\text{C}$ , Søreide et al. 2006) provide a theoretical slope of approx. 5.67 ( $\delta^{15}\text{N}/$

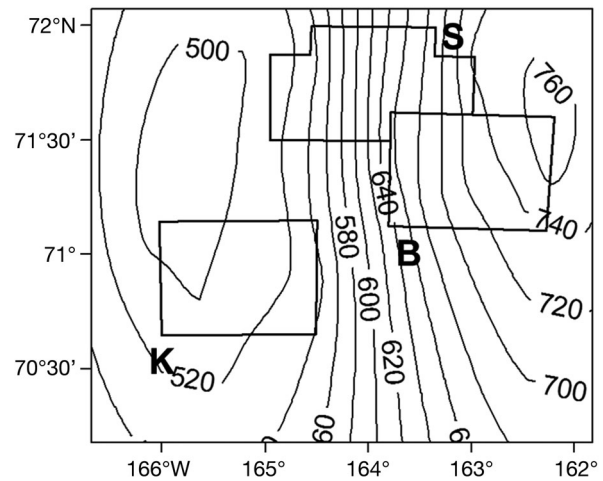


Fig. 6. Spatial model of potential prey gross energy density in  $\text{kJ wet mass m}^{-2}$ . B: Burger, K: Klondike, S: Statoil

$\delta^{13}\text{C}$ ) for a predatory food chain relying on a single food source (Mincks et al. 2008). When there are multiple food sources with different stable isotope signatures, the fitted model's slope will diverge from the theoretical value, or the model will become non-linear (Feder et al. 2011). Additionally, determination of trophic steps becomes more difficult with multiple food sources, as any individual animal may feed on several trophic levels, resulting in increased variability in the food-web model. This is even further complicated by the fact that the theoretical  $\delta^{15}\text{N}$  enrichment factor of 3.4 is likely not consistent among trophic levels; enrichment between marine mammals and their prey has been suggested to be approx. 2.4 (Newsome et al. 2010), and some predatory invertebrates such as *Nephtys* spp. and Phyllodocidae have comparable  $\delta^{15}\text{N}$  signatures to those of larger predators. Given that there appeared to be solely marine food sources in the study area, the large difference between RMA regression slope coefficients ( $\beta_{\text{RMA}} = 1.69\text{--}2.17$ ) and the theoretical slope was unexpected. The more depleted stable isotope signatures of the primary consumer *Ennucula tenuis*, as compared to Ampeliscidae (also a primary consumer) and relative to the linear increase from Ampeliscidae to Maldanidae, suggests the presence of an unmeasured marine food source. Despite the fact that POM and sediments in this study suggest primarily marine food sources, the stable isotope signatures of consumers as well as RMA regression slope coefficients indicate that there are multiple food sources, likely from different marine origins, assimilated into the benthic food webs in the study areas.

Seasonal ice and water movement patterns can affect phytoplankton composition in blooms and

POM  $\delta^{13}\text{C}$  values. Phytoplankton cell size, species composition, and growth rate during the bloom can affect POM stable carbon isotope signatures because larger, fast-growing cells in early stages of a bloom are typically more enriched in  $^{13}\text{C}$  compared with smaller, slower growing cells at late stages of a bloom (Fry & Wainright 1991, Burkhardt et al. 1999, Tamelander et al. 2009). Ice cover retreat and increasing stratification enable a spring phytoplankton bloom in the northeastern Chukchi Sea, which follows the retreating ice edge (Hill & Cota 2005, Wang et al. 2005). The seasonal ice retreat pattern in the study region is south to north with ice often persisting around Hanna Shoal (Weingartner et al. 2013); therefore, the spring bloom typically begins earlier in Klondike and reaches Statoil and Burger later. Similarly, cold winter water is ejected from the study areas in the same progression with delayed flushing of winter water at Burger and Statoil (Weingartner et al. 2013). As a result, Klondike is exposed to warmer BSW earlier than Burger or Statoil and planktonic communities can differ substantially (Questel et al. 2013). Different bloom stages at the time of sampling, due to hydrographic and ice-retreat differences among areas, could be a mechanism behind the observed differences in POM  $\delta^{13}\text{C}$  values.

Stable carbon isotope signatures of consumers can provide insight on the timescales of variability in food sources if tissue turnover rates are known. Primary consumers, such as suspension-feeding ampeliscids, are linked directly to available carbon sources in an area, and their  $\delta^{13}\text{C}$  signatures represent an average of local food source  $\delta^{13}\text{C}$  signatures (DeNiro & Epstein 1978, Fry 1988, Saupe et al. 1989). Benthic invertebrates integrate the stable isotope signature of their diet on the order of weeks to months (McMahon et al. 2006, Kaufman et al. 2008, Weems et al. 2012), as opposed to POM, which represents the immediately available material and its stable isotope signature can change in a matter of days (Tremblay et al. 2006). Therefore, the spatial differences in  $^{13}\text{C}$  enrichment observed in the Ampeliscidae indicate that the POM differences among areas may have been present for several weeks and allude to possible persistent small-scale spatial variation in food sources. However, the mean  $\delta^{13}\text{C}$  values of deposit-feeding consumers (*Ennucula tenuis* bivalves and Maldanidae polychaetes) only varied slightly among the 3 study areas, as values were within a 1‰ range. These taxa reflect spatial variation in deposited, time-integrated food sources instead of suspended matter due to their sedentary nature and feeding habits. Hence, although mean sediment  $\delta^{13}\text{C}$  values

were significantly different, observed differences were not ecologically significant as values were within 0.5‰ in all areas, but reflected temporal variability. Bacterial reworking is one of the main biological processes that affect sediment stable carbon and nitrogen isotope signatures due to deamination and decarboxylation processes (Macko & Estep 1984, Freudenthal et al. 2001). Therefore, despite variability in water column production, the detrital pool seems to be similar across all study areas, likely as a result of sediment microbial activity.

Microphytobenthos and sea-ice algae are 2 possible marine food sources to the benthos that were not examined in this study. Microphytobenthos are major contributors of primary production to communities in shallow seas (McMinn et al. 2005) and typically are enriched in  $\delta^{13}\text{C}$  by ~6‰ over phytoplankton (Herman et al. 2000, Kang et al. 2003). Substantial amounts of ice algae are released during ice melt in the Chukchi Sea and support benthic communities (McMahon et al. 2006), although the contributions of sea ice to the annual energy budget of the northeastern Chukchi Sea are still unknown (Gradinger 2009). Ice algal  $\delta^{13}\text{C}$  values in the Chukchi/Beaufort seas are highly variable (–25 to –14‰) and increase with ice algal biomass production during the growing season (Tremblay et al. 2006, Gradinger 2009), leaving them enriched in  $^{13}\text{C}$  over phytoplankton. Sediment  $\delta^{13}\text{C}$  from the study areas were  $^{13}\text{C}$ -depleted compared with expected ice algal and microphytobenthos stable carbon isotope signatures, and their presence in surface sediments during the time of collection is, therefore, unlikely. However, microphytobenthos and ice algal  $\delta^{13}\text{C}$  sources earlier in the season may have contributed to the higher  $\delta^{13}\text{C}$  signatures found in the deposit-feeding bivalve *Ennucula tenuis*. Microphytobenthos are an important food source for some benthos and may in part explain the observed variations among primary consumers and higher trophic levels in the present study (Oxtoby et al. 2013, McTigue & Dunton 2014).

Sampling methods in this study may contribute some bias to our results; POM was only sampled during 1 yr, sediment was sampled for 2 of the 3 sampling years, and benthic invertebrates were sampled for all 3 yr. POM sampling for this study was opportunistic, and therefore only 1 yr of data was collected. Consequently, any conclusions drawn from food source results should be regarded with some caution. Additionally, other possible food sources, as discussed above, were not sampled due to various constraints. Results here highlight the importance of POM measurements and make it difficult to deter-

mine the influence of other food sources. Although sampling of food-web endmembers was limited, it allowed us to include POM as a food source to the benthic community and stable isotope values were a general representation of typical POM signatures for the time of year sampled. Sediments collected for 2 yr of sampling give a better picture of deposited and reworked material, although not as complete as the 3 yr of consumers we sampled.

### Food-web structure

The quantitative representations of trophic levels (based on community biomass and abundance) in conjunction with feeding mode information can reflect the delivery processes and nature of primary production supplied to an area. For example, benthic communities in the southern Chukchi Sea under the influence of AW and ACW have the same number of trophic levels; however, communities under AW are quantitatively dominated by lower trophic level fauna (Iken et al. 2010). These animals feed directly on labile carbon, and their strong presence emphasizes the abundant supply of fresh material. This is in contrast to communities under ACW, which are dominated by higher trophic level deposit feeders utilizing more refractory material with enriched stable nitrogen isotope signatures. A similar pattern was observed in the present study, with communities at Klondike and Statoil showing higher abundance and biomass of trophic level 1 and 2 consumers of labile carbon, whereas Burger was dominated by trophic level 3 nonselective deposit feeders.

Spatial differences in quantitative representations of trophic levels may be attributed to indirect effects of topographic control of water movement on biological communities (Desrosiers et al. 2000, Blanchard et al. 2013a,b). The presence of Hanna Shoal north of the study region creates an anticyclonic gyre and causes currents to converge and slow over the Burger study area (Weingartner et al. 2013). The slowed water movement results in increased deposition of organic matter (Blanchard et al. 2013a, Weingartner et al. 2013). High amounts of organic matter are then subjected to microbial degradation and deposit-feeding bioturbation, which allows for reworking of matter through continual re-exposure. The resulting bacterial degradation of amino acids and deamination processes enrich sediments in  $^{15}\text{N}$  (Freudenthal et al. 2001, Granger et al. 2011). The  $^{15}\text{N}$  enrichment of the deposited food source propagates up the food chain when organic matter,

microbes, and meiofaunal degraders are assimilated by nonselective deposit-feeding organisms. For these reasons, depositional areas such as Burger are expected to show a strong presence of higher trophic level detritivores, e.g. the observed elevated trophic level of deposit-feeding Maldanidae. Conversely, stronger currents at Klondike and Statoil may create more favorable conditions for suspension feeders and other primary consumers by supplying fresh labile material from advection or re-suspension. The differences in flow processes and particle deposition vs. suspension appear to strongly influence the major energy pathways through the various trophic levels. These results suggest that water current regimes at Statoil are more similar to those at Klondike than those at Burger, despite the close proximity of Statoil and Burger.

High proportions of primary consumers at lower trophic levels are indicators of tight pelagic–benthic coupling where the labile material from primary production is delivered directly to the benthos (Iken et al. 2010). This condition was observed at Klondike and Statoil. The lower proportions of trophic level 1 organisms at Burger imply a more refractory energy pathway by nonselective deposit feeders, most likely due to a lack of fresh material. POM C/N ratios indicate that deposited material is primarily of marine origin. While marine carbon is considered highly labile, any recalcitrant components (e.g. components of bacterial cell walls) will remain and may decompose over a number of years (Burkhardt et al. 2014). The presence of a marine refractory carbon pool, or a long-term food bank in the sediments, may be what is continually reworked by deposit feeders at Burger, consequently elevating their trophic levels and skewing trophic level distribution. It is also possible that the large numbers of trophic level 3 Maldanidae polychaetes at Burger (thousands of individuals per  $\text{m}^2$ , Blanchard et al. 2013a) out-compete lower trophic level animals, such as bivalves, for space and food (Levin et al. 1997). The ability of Maldanidae to use refractory materials may provide them with a competitive advantage over suspension or surface-deposit feeding bivalves. Other explanations for the dominance of maldanids include sediment conditions favorable to tube-building, or the effects of patchy recruitment, i.e. the present community is the outcome of a good recruitment year. The small-scale differences in food-web structure were likely driven by differences in water flow and particle deposition in the different study areas, resulting in varying levels of pelagic–benthic coupling strength. Similar spatial variations associated with water circulation and parti-

cle deposition were observed in infaunal community structure as well (Blanchard et al. 2013a). The water circulation variations cause differences in the composition of benthic feeding types that are most apt at exploiting these particle flux differences (e.g. dominance in suspension-feeding vs. deposit-feeding).

### Energy density of benthic communities

Stable isotope analysis indicated that there were various strengths in pelagic–benthic coupling within the present study areas, and it was of interest whether this coupling was reflected in the spatial energy distribution of the benthic community. In an offshore environment, such as the present study, areas of strong pelagic–benthic coupling would be expected to have high benthic energy density values due to high biomass (Grebmeier & Barry 1991). The opposite was found here, where the areas of tightest coupling (Klondike and Statoil) had the lowest benthic energy densities. Burger, the site with the weakest pelagic–benthic coupling, exhibited the highest benthic energy densities. The discrepancy between expected and actual results suggests other processes are responsible for the energy-rich Burger study area. Landscape features such as canyons and shoals are areas of high benthic production due to focused deposition of sediments and organic matter (Rosenberg 1995, De Leo et al. 2010, Blanchard et al. 2013a,b). The presence of Hanna Shoal and its impact on water circulation results in greater delivery of organic material to the benthos in Burger. The resulting higher benthic biomass compared with Klondike and Statoil was a contributing factor to the higher energy density values at Burger (Blanchard et al. 2013a). While a high amount of organic material deposited at Burger is an indicator of strong pelagic–benthic coupling, the trophic distribution of the benthos suggests that there is less delivery of fresh, labile carbon and so the nature of the material being utilized differs among sites.

Taxonomic composition of the benthic community may have an effect on energy density values due to differences in caloric content of the individual taxa (Wacasey & Atkinson 1987, Lawson et al. 1998, Ball et al. 2007, Hondolero et al. 2012, Wilt et al. 2014). The small-scale spatial patterns of energy density observed here coincide with the distribution of bivalve and total benthic biomass, which peak in the eastern areas of Statoil and just to the east of Burger (Blanchard et al. 2013a). Although bivalves are low on this study's energy list due to inclusion of shell in

reported wet mass values, their high biomass is presumably a contributing factor to energy densities. On a larger spatial scale, the predicted benthic community energy densities in this study are comparable to or higher than other regions with similar benthic community composition. For example, the mean energy density of benthic and epibenthic invertebrates in St. Margaret's Bay, Nova Scotia, Canada is 318 kJ WM m<sup>-2</sup>, with a maximum station value of 728 kJ WM m<sup>-2</sup> (Brawn et al. 1968). Overall, it seems that the northeastern Chukchi Sea study region is comparatively rich in benthic invertebrate prey for higher trophic levels, provided that other foraging constraints are negligible (e.g. ice cover, depth).

Energy density information can be used to quantify the energetic impact of predation on a benthic community and determine the potential value of an area as foraging grounds. The benthic energy density values calculated here are only inclusive of benthic invertebrate prey for a select group of benthic-feeding marine mammals. Therefore, energy density estimates are an underestimate of total available prey energy density, which did not include other taxa (e.g. benthic fishes) that are important prey items but were not collected in this study. For example, a 550 kg adult female walrus summering in the Chukchi Sea may consume as much as 106 000 kJ per day (193 kJ per kg body mass, Fisher et al. 1992). Even in the highest density energy region of the study areas in eastern Burger (approx. 750 kJ WM m<sup>-2</sup>), a single adult female walrus would have to exploit roughly 140 m<sup>2</sup> of the bottom invertebrate community per day to satisfy daily energy needs. Therefore, the potential impact of just this one predator on the benthos is substantial and the eastern parts of Statoil and Burger are better benthic marine mammal feeding grounds compared with Klondike. This is supported by satellite tag (2008–2011, Jay et al. 2012) and observational data (2008, Aerts et al. 2013), indicating large aggregations of walruses (as many as 700 ind.) hauled out on ice in the Burger area. On the larger population-scale of bottom-feeding mammal predators, the benthic prey of the study region can likely only satisfy a small amount of their energy demands, although some high-energy prey taxa such as pelagic and benthic fishes were not considered here. Sampling artifacts contribute to a reduced understanding of true benthic energy distributions as some deeper-dwelling fauna (e.g. *Macoma* bivalves) occur with much greater biomass at deeper sediment depths (A. L. Blanchard unpubl. data) and others such as the bivalve *Mya* are present in the area, but not regularly sampled with the sampling gear employed here.

Data presented herein, however, are useful for area comparisons as well as an approximation of the mean caloric content/energy density values available for consumption by higher trophic levels during the late summer/early fall in the northeastern Chukchi Sea. These findings support the hypothesis that benthic food webs vary in energy density among study areas. This small-scale variability is most likely highly influenced by hydrographic conditions affecting particle deposition and benthic fauna (Blanchard et al. 2013a,b).

One possible scenario of continued climatic warming in the Chukchi Sea is a shift of ecosystems towards decreased primary production exports to the benthos through earlier delivery of and heavier feeding by zooplankton grazers, thereby directing more energy towards a pelagic food web. If the Chukchi Sea remains ice-covered in the winter, the annual arrival of zooplankton in the spring will be early enough to exploit the initial pulse of primary production. Additionally, potential large variations in water circulation through the Bering Strait and into the Chukchi Sea could force changes in water circulation around topographic features, thereby altering the processes that deliver particulate organic carbon to the benthos. These scenarios could have negative implications for the benthic communities in the study region, possibly to a higher degree in the energy-rich regions of Burger where high quantities of deposited food structure the benthic community.

The small-scale study here found food-web patterns similar to those described by Iken et al. (2010) in their regional-scale study, based on quantitative distribution of trophic levels. The distinct differences in food-web characteristics highlight the importance of focused food-web studies. It is shown here that comparable findings are possible from food-web comparisons at different spatial scales. Results from this study give insight on the scales appropriate for understanding and monitoring changes to the Arctic shelf benthic community, especially in areas of topographic and hydrographic complexity; small-scale variation as described here may be overlooked in larger regional studies, but such spatially focused investigations may be useful in the future as climatic and anthropogenic influences affect these complex ecosystems.

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#### LITERATURE CITED

- Aerts LAM, McFarland AE, Watts BH, Lomac-MacNair KS and others (2013) Marine mammal distribution and abundance in an offshore sub-region of the northeastern Chukchi Sea during the open-water season. *Cont Shelf Res* 67:116–126
- Ambrose WG Jr, von Quillfeldt C, Clough LM, Tilney PVR, Tucker T (2005) The sub-ice algal community in the Chukchi Sea: large- and small-scale patterns of abundance based on images from a remotely operated vehicle. *Polar Biol* 28:784–795
- Anderson WB, Polis GA (1998) Marine subsidies of island communities in the Gulf of California: evidence from stable carbon and nitrogen isotopes. *Oikos* 81:75–80
- Arrington DA, Davidson BK, Winemiller KO, Layman CA (2006) Influence of life history and seasonal hydrology on lipid storage in three neotropical fish species. *J Fish Biol* 68:1347–1361
- Bagatini YM, Benedito E, Higuti J (2010) Effect of the environmental factors on the caloric content of benthic and phytophilous invertebrates in neotropical reservoirs in the Paraná State, Brazil. *Int Rev Hydrobiol* 95:246–259
- Ball JR, Esler D, Schmutz JA (2007) Proximate composition, energetic value, and relative abundance of prey fish from the inshore eastern Bering Sea: implications for piscivorous predators. *Polar Biol* 30:699–708
- Belicka LL, Macdonald RW, Harvey HR (2002) Sources and transport of organic carbon to shelf, slope, and basin surface sediments of the Arctic Ocean. *Deep-Sea Res I* 49:1463–1483
- Ben-David M, Flaherty EA (2012) Stable isotopes in mammalian research: a beginner's guide. *J Mammal* 93:312–328
- Blanchard AL, Parris CL, Knowlton AL, Wade NR (2013a) Benthic ecology of the northeastern Chukchi Sea. Part I. Environmental characteristics and macrofaunal community structure, 2008–2010. *Cont Shelf Res* 67:52–66
- Blanchard AL, Parris CL, Knowlton AL, Wade NR (2013b) Benthic ecology of the northeastern Chukchi Sea. Part II. Spatial variation of megafaunal community structure, 2009–2010. *Cont Shelf Res* 67:67–76
- Bluhm BA, Gradinger R (2008) Regional variability in food availability for arctic marine mammals. *Ecol Appl* 18:S77–S96
- Bluhm BA, Iken K, Mincks-Hardy S, Sirenko BI, Holladay BA (2009) Community structure of epibenthic megafauna in the Chukchi Sea. *Aquat Biol* 7:269–293
- Brawn VM, Peer DL, Bentley RJ (1968) Caloric content of the standing crop of benthic and epibenthic invertebrates of St. Margaret's Bay, Nova Scotia. *J Fish Res Board Can* 25:1803–1811
- Burkhardt S, Riebesell U, Zondervan I (1999) Effects of



- growth rate, CO<sub>2</sub> concentration, and cell size on the stable carbon isotope fractionation in marine phytoplankton. *Geochim Cosmochim Acta* 63:3729–3741
- Burkhardt BG, Watkins-Brandt KS, Defforey D, Paytan A, White AE (2014) Remineralization of phytoplankton-derived organic matter by natural populations of heterotrophic bacteria. *Mar Chem* 163:1–9
- Darling JD, Keogh KE, Steeves TE (1998) Gray whale (*Eschrichtius robustus*) habitat utilization and prey species off Vancouver Island, B. C. *Mar Mamm Sci* 14: 692–720
- Day RH, Weingartner TJ, Hopcroft RR, Aerts LAM and others (2013) The offshore northeastern Chukchi Sea: a complex high-latitude ecosystem. *Cont Shelf Res* 67: 147–165
- De Leo FC, Smith CR, Rowden AA, Bowden DA, Clark MR (2010) Submarine canyons: hotspots of benthic biomass and productivity in the deep sea. *Proc R Soc B* 277: 2783–2792
- Dehn LA, Sheffield GG, Follmann EH, Duffy LK, Thomas DL, O'Hara TM (2007) Feeding ecology of phocid seals and some walrus in the Alaskan and Canadian Arctic as determined by stomach contents and stable isotope analysis. *Polar Biol* 30:167–181
- DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochim Cosmochim Acta* 42:495–506
- Desrosiers G, Savenkoff C, Olivier M, Stora G and others (2000) Trophic structure of macrobenthos in the Gulf of St. Lawrence and on the Scotian Shelf. *Deep-Sea Res II* 47:663–697
- Dorgelo J, Leonards PEG (2001) Relationship between C/N ratio of food types and growth rate in the snail *Potamopyrgus jenkinsi* (E. A. Smith). *J N Am Benthol Soc* 20: 60–67
- Dubois S, Orvain F, Marin-Léal JC, Ropert M, Lefebvre S (2007) Small-scale spatial variability of food partitioning between cultivated oysters and associated suspension-feeding species, as revealed by stable isotopes. *Mar Ecol Prog Ser* 336:151–160
- Dunton KH, Saupe SM, Golikov AN, Schell DM, Schonberg SV (1989) Trophic relationships and isotopic gradients among arctic and subarctic marine fauna. *Mar Ecol Prog Ser* 56:89–97
- Dunton KH, Goodall JL, Schonberg SV, Grebmeier JM, Maidment DR (2005) Multi-decadal synthesis of benthic-pelagic coupling in the western arctic: role of cross-shelf advective processes. *Deep-Sea Res II* 52:3462–3477
- Fanelli E, Cartes JE, Badalamenti F, Rumolo P, Sprovieri M (2009) Trophodynamics of suprabenthic fauna on coastal muddy bottoms of the southern Tyrrhenian Sea (western Mediterranean). *J Sea Res* 61:174–187
- Fauchald K, Jumars P (1979) The diet of worms: a study of polychaete feeding guilds. *Oceanogr Mar Biol Annu Rev* 17:193–284
- Fay FH (1982) Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. United States Department of Interior Fish and Wildlife Service, North American Fauna 74, Washington, DC
- Feder HM, Naidu AS, Jewett SC, Hameedi JM, Johnson WR, Whitley TE (1994) The northeastern Chukchi Sea: Benthos–environmental interactions. *Mar Ecol Prog Ser* 111:171–190
- Feder HM, Jewett SC, Blanchard A (2005) Southeastern Chukchi Sea (Alaska) epibenthos. *Polar Biol* 28:402–421
- Feder HM, Jewett SC, Blanchard AL (2007) Southeastern Chukchi Sea (Alaska) macrobenthos. *Polar Biol* 30: 261–275
- Feder HM, Iken K, Blanchard AL, Jewett SC, Schonberg S (2011) Benthic food web structure in the southeastern Chukchi Sea: an assessment using  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analyses. *Polar Biol* 34:521–532
- Fisher K, Stewart R, Kastelein R, Campbell L (1992) Apparent digestive efficiency in walrus (*Odobenus rosmarus*) fed herring (*Clupea harengus*) and clams (*Spisula* sp.). *Can J Zool* 70:30–36
- Folch J, Lees M, Sloane-Stanley GH (1957) A simple method for the isolation and purification of total lipids from animal tissues. *J Biol Chem* 226:497–509
- France RL (1995) Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. *Mar Ecol Prog Ser* 124:307–312
- Freudenthal T, Wagner T, Wenzhöfer F, Zabel M, Wefer G (2001) Early diagenesis of organic matter from sediments of the eastern subtropical Atlantic: evidence from stable nitrogen and carbon isotopes. *Geochim Cosmochim Acta* 65:1795–1808
- Fry B (1988) Food web structure on Georges Bank from stable C, N, and S isotopic compositions. *Limnol Oceanogr* 33:1182–1190
- Fry B, Wainright SC (1991) Diatom sources of super  $^{13}\text{C}$ -rich carbon in marine food webs. *Mar Ecol Prog Ser* 76: 149–157
- Gall AE, Day RH, Weingartner TJ (2013) Structure and variability of the marine-bird community in the northeastern Chukchi Sea. *Cont Shelf Res* 67:96–115
- Glud RN, Woelfel J, Karsten U, Kühl M, Rysgaard S (2009) Benthic microalgal production in the Arctic: applied methods and status of the current database. *Bot Mar* 52: 559–571
- Gnaiger E, Bitterlich G (1984) Proximate biochemical composition and caloric content calculated from elemental CHN analysis: a stoichiometric concept. *Oecologia* 62: 289–298
- Gradinger R (2009) Sea-ice algae: Major contributors to primary production and algal biomass in the Chukchi and Beaufort Seas during May/June 2002. *Deep-Sea Res II* 56:1201–1212
- Granger J, Prokopenko MG, Sigman DM, Mordy CW and others (2011) Coupled nitrification denitrification in sediment of the eastern Bering Sea shelf leads to  $^{15}\text{N}$  enrichment of fixed N in shelf waters. *J Geophys Res* 116: C11006, doi:10.1029/2010JC006751
- Grebmeier JM (1993) Studies of pelagic–benthic coupling extended onto the Soviet continental shelf in the northern Bering and Chukchi seas. *Cont Shelf Res* 13:653–668
- Grebmeier JM (2012) Shifting patterns of life in the Pacific Arctic and sub-Arctic Seas. *Annu Rev Mar Sci* 4:63–78
- Grebmeier JM, Barry JP (1991) The influence of oceanographic processes on pelagic–benthic coupling in polar regions: a benthic perspective. *J Mar Syst* 2:495–518
- Grebmeier JM, McRoy CP (1989) Pelagic–benthic coupling on the shelf of the northern Bering and Chukchi Seas. III. Benthic food supply and carbon cycling. *Mar Ecol Prog Ser* 53:79–91
- Grebmeier JM, Feder HM, McRoy CP (1989) Pelagic–benthic coupling on the shelf of the northern Bering and Chukchi Seas. II. Benthic community structure. *Mar Ecol Prog Ser* 51:253–268
- Grebmeier JM, Cooper LW, Feder HM, Sirenko BI (2006)

- Ecosystem dynamics of the Pacific-influenced Northern Bering and Chukchi Seas in the Amerasian Arctic. *Prog Oceanogr* 71:331–361
- Herman PMJ, Middelburg JJ, Widdows J, Lucas CHR, Heip CH (2000) Stable isotopes as trophic tracers: combining field sampling and manipulative labelling of food resources for macrobenthos. *Mar Ecol Prog Ser* 204:79–92
- Highsmith RC, Coyle KO (1990) High productivity of northern Bering Sea benthic amphipods. *Nature* 344:862–863
- Highsmith RC, Coyle KO (1991) Amphipod life histories: Community structure, impact of temperature on decoupled growth and maturation rates, productivity, and P:B ratios. *Am Zool* 31:861–873
- Hill V, Cota G (2005) Spatial patterns of primary production in the Chukchi Sea in the spring and summer of 2002. *Deep-Sea Res II* 52:3344–3354
- Hill V, Cota G, Stockwell D (2005) Spring and summer phytoplankton communities in the Chukchi and Eastern Beaufort Seas. *Deep-Sea Res II* 52:3369–3385
- Hobson KA, Fisk A, Karnovsky N, Holst M, Gagnon JM, Fortier M (2002) A stable isotope ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) model for the North Water food web: implications for evaluating trophodynamics and the flow of energy and contaminants. *Deep-Sea Res II* 49:5131–5150
- Holte B, Gulliksen B (1998) Common macrofaunal dominant species in the sediments of some north Norwegian and Svalbard glacial fjords. *Polar Biol* 19:375–382
- Hondolero D, Bluhm BA, Iken K (2012) Caloric content of dominant benthic species from the northern Bering and Chukchi Seas: historical comparisons and the effects of preservation. *Polar Biol* 35:637–644
- Iken K, Bluhm B, Dunton K (2010) Benthic food-web structure under differing water mass properties in the southern Chukchi Sea. *Deep-Sea Res II* 57:71–85
- Jay CV, Fischbach AS, Kochnev AA (2012) Walrus areas of use in the Chukchi Sea during sparse sea ice cover. *Mar Ecol Prog Ser* 468:1–13
- Kang CK, Kim JB, Lee KS, Kim JB, Lee PY, Hong JS (2003) Trophic importance of benthic microalgae to macrozoobenthos in coastal bay systems in Korea: dual stable C and N isotope analyses. *Mar Ecol Prog Ser* 259:79–92
- Kaufman MR, Gradinger RR, Bluhm BA, O'Brien DM (2008) Using stable isotopes to assess carbon and nitrogen turnover in the Arctic sympagic amphipod *Onisimus litoralis*. *Oecologia* 158:11–22
- Kędra M, Kuliński K, Walkusz W, Legeżyńska J (2012) The shallow benthic food web structure in the high Arctic does not follow seasonal changes in the surrounding environment. *Estuar Coast Shelf Sci* 114:183–191
- Laws EA, Archie JW (1981) Appropriate use of regression analysis in marine biology. *Mar Biol* 65:13–16
- Lawson JW, Magalhaes AM, Miller EH (1998) Important prey species of marine vertebrate predators in the northwest Atlantic: proximate composition and energy density. *Mar Ecol Prog Ser* 164:13–20
- Levin L, Blair N, DeMaster D, Plaia G, Fornes W, Martin C, Thomas C (1997) Rapid subduction of organic matter by maldanid polychaetes on the North Carolina slope. *J Mar Res* 55:595–611
- Logan JM, Jardine TD, Miller TJ, Bunn SE, Cunjak RA, Lutcavage ME (2008) Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. *J Anim Ecol* 77: 838–846
- Lowry LF, Frost KJ, Burns JJ (1980) Feeding of bearded seals in the Bering and Chukchi Seas and trophic interaction with Pacific walrus. *Arctic* 33:330–342
- Macko SA, Estep MLF (1984) Microbial alteration of stable nitrogen and carbon isotopic compositions of organic matter. *Org Geochem* 6:787–790
- Martin S, Drucker R (1997) The effect of possible Taylor columns on the summer ice retreat in the Chukchi Sea. *J Geophys Res* 102:10473–10482
- McClelland JW, Valiela I, Michener RH (1997) Nitrogen-stable isotope signatures in estuarine food webs: a record of increasing urbanization in coastal watersheds. *Limnol Oceanogr* 42:930–937
- McMahon KW, Ambrose WG Jr, Johnson BJ, Sun MY, Lopez GR, Clough LM, Carroll ML (2006) Benthic community response to ice algae and phytoplankton in Ny Ålesund, Svalbard. *Mar Ecol Prog Ser* 310:1–14
- McMinn A, Hirawake T, Hamaoka T, Hattori H, Fukuchi M (2005) Contribution of benthic microalgae to ice covered coastal ecosystems in northern Hokkaido, Japan. *J Mar Biol Assoc UK* 85:283–289
- McTigue ND, Dunton KH (2014) Trophodynamics and organic matter assimilation pathways in the northeast Chukchi Sea, Alaska. *Deep-Sea Res II* 102:84–96
- Michener RH, Kaufman L (2007) Stable isotope ratios as tracers in marine food webs: an update. In: Michener R, Lajtha K (eds) *Stable isotopes in ecology and environmental sciences*. Blackwell Publishing, Malden, MA, p 238–282
- Minagawa M, Wada E (1984) Stepwise enrichment of  $^{15}\text{N}$  along food chains: Further evidence and the relation between  $\delta^{15}\text{N}$  and animal age. *Geochim Cosmochim Acta* 48:1135–1140
- Mincks SL, Smith CR, Jeffreys RM, Sumida PYG (2008) Trophic structure on the West Antarctic Peninsula shelf: detritivory and benthic inertia revealed by  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analysis. *Deep-Sea Res II* 55:2502–2514
- Naidu AS, Scalan RS, Feder HM, Goering JJ and others (1993) Stable organic carbon isotopes in sediments of the north Bering-south Chukchi seas, Alaskan-Soviet Arctic Shelf. *Cont Shelf Res* 13:669–691
- Naidu AS, Cooper LW, Finney BP, Macdonald RW, Alexander C, Semiletov IP (2000) Organic carbon isotope ratios ( $\delta^{13}\text{C}$ ) of Arctic Amerasian continental shelf sediments. *Int J Earth Sci* 89:522–532
- Newsome SD, Clementz MT, Koch PL (2010) Using stable isotope biogeochemistry to study marine mammal ecology. *Mar Mamm Sci* 26:509–572
- Österblom H, Olsson O, Blenckner T, Furness RW (2008) Junk-food in marine ecosystems. *Oikos* 117:967–977
- Oxtoby LE, Mathis JT, Juraneck LW, Wooller MJ (2013) Technical note: Constraining stable carbon isotope values of microphytobenthos ( $\text{C}_3$  photosynthesis) in the Arctic for application to food web studies. *Biogeosciences Discuss* 10:18151–18174
- Parsons TR, Maita Y, Lalli CM (1984a) *A manual for chemical and biological methods in seawater analysis*. Pergamon Press, Toronto
- Parsons TR, Takahashi M, Hargrave B (1984b) *Biological oceanographic processes*. Pergamon Press, New York, NY
- Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. *Annu Rev Ecol Syst* 18:293–320
- Piepenburg D (2005) Recent research on Arctic benthos: common notions need to be revised. *Polar Biol* 28:733–755
- Post DM (2002) Using stable isotopes to estimate trophic

- position: models, methods, and assumptions. *Ecology* 83: 703–718
- Post JR, Parkinson EA (2001) Energy allocation strategy in young fish: allometry and survival. *Ecology* 82: 1040–1051
  - Post DM, Takimoto G (2007) Proximate structural mechanisms for variation in food-chain length. *Oikos* 116: 775–782
  - Quakenbush L, Citta J, Crawford J (2011a) Biology of the bearded seal (*Erignathus barbatus*) in Alaska, 1961–2009. Final Report to National Marine Fisheries Service. Alaska Department of Fish and Game, Fairbanks, AK
  - Quakenbush L, Citta J, Crawford J (2011b) Biology of the ringed seal (*Phoca hispida*) in Alaska, 1960–2010. Final Report to National Marine Fisheries Service. Alaska Department of Fish and Game, Fairbanks, AK
  - Questel JM, Clarke C, Hopcroft RR (2013) Seasonal and interannual variation in the planktonic communities of the northeastern Chukchi Sea during the summer and early fall. *Cont Shelf Res* 67:23–41
  - Quinn GP, Keough MJ (2002) Correlation and regression. In: Experimental design and data analysis for biologists. Cambridge University Press, New York, NY, p 72–110
  - Rhoads DC, Young DK (1970) The influence of deposit-feeding organisms on sediment stability and community trophic structure. *J Mar Res* 28:150–178
  - Ricciardi A, Bourget E (1998) Weight-to-weight conversion factors for marine benthic macroinvertebrates. *Mar Ecol Prog Ser* 163:245–251
  - Rosen DAS, Trites AW (2000) Pollock and the decline of Steller sea lions: testing the junk-food hypothesis. *Can J Zool* 78:1243–1250
  - Rosenberg R (1995) Benthic marine fauna structured by hydrodynamic processes and food availability. *Neth J Sea Res* 34:303–317
  - Saupe SM, Schell DM, Griffiths WB (1989) Carbon-isotope ratio gradients in western arctic zooplankton. *Mar Biol* 103:427–432
  - Sheffield G, Grebmeier JM (2009) Pacific walrus (*Odobenus rosmarus divergens*): differential prey digestion and diet. *Mar Mamm Sci* 25:761–777
  - Sheffield G, Fay FH, Feder H, Kelly BP (2001) Laboratory digestion of prey and interpretation of walrus stomach contents. *Mar Mamm Sci* 17:310–330
  - Shurin JB, Gruner DS, Hillebrand H (2006) All wet or dried up? Real differences between aquatic and terrestrial food webs. *Proc R Soc B* 273:1–9
  - Snelgrove PVR, Butman CA (1994) Animal-sediment relationships revisited: cause versus effect. *Oceanogr Mar Biol Annu Rev* 32:111–177
  - Søreide JE, Hop H, Carroll ML, Falk-Petersen S, Hegseth EN (2006) Seasonal food web structures and sympagic-pelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model. *Prog Oceanogr* 71:59–87
  - Sotiropoulos MA, Tonn WM, Wassenaar LI (2004) Effects of lipid extraction on stable carbon and nitrogen isotope analyses of fish tissues: potential consequences for food web studies. *Ecol Freshw Fish* 13:155–160
  - Spall MA (2007) Circulation and water mass transformation in a model of the Chukchi Sea. *J Geophys Res* 112: C05025, doi:10.1029/2005JC003364
  - Stoker S (1978) Benthic invertebrate macrofauna on the eastern continental shelf of Bering and Chukchi Seas. PhD dissertation, Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, AK
  - Tamelander T, Kivimäe C, Bellerby RGJ, Renaud PE, Kristiansen S (2009) Base-line variations in stable isotope values in an Arctic marine ecosystem: effects of carbon and nitrogen uptake by phytoplankton. *Hydrobiologia* 630:63–73
  - Taylor BR, Roff JC (1984) Use of ATP and carbon: nitrogen ratio as indicators of food quality of stream detritus. *Freshw Biol* 14:195–201
  - Tremblay JÉ, Michel C, Hobson KA, Gosselin M, Price NM (2006) Bloom dynamics in early opening waters of the Arctic Ocean. *Limnol Oceanogr* 51:900–912
  - Trites AW, Donnelly CP (2003) The decline of Steller sea lions *Eumetopias jubatus* in Alaska: a review of the nutritional stress hypothesis. *Mammal Rev* 33:3–28
  - Vander Zanden MJ, Rasmussen JB (2001) Variation in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  trophic fractionation: implications for aquatic food web studies. *Limnol Oceanogr* 46:2061–2066
  - Wacasey JW, Atkinson EG (1987) Energy values of marine benthic invertebrates from the Canadian Arctic. *Mar Ecol Prog Ser* 39:243–250
  - Walsh JJ, McRoy CP (1986) Ecosystem analysis in the southeastern Bering Sea. *Cont Shelf Res* 5:259–288
  - Wang J, Cota GF, Comiso JC (2005) Phytoplankton in the Beaufort and Chukchi Seas: distribution, dynamics, and environmental forcing. *Deep-Sea Res II* 52:3355–3368
  - Weems J, Iken K, Gradinger R, Wooller MJ (2012) Carbon and nitrogen assimilation in the Bering Sea clams *Nucula radiata* and *Macoma moesta*. *J Exp Mar Biol Ecol* 430:32–42
  - Weingartner TJ, Cavalieri DJ, Aagaard K, Sasaki Y (1998) Circulation, dense water formation, and outflow on the northeast Chukchi shelf. *J Geophys Res* 103:7647–7661
  - Weingartner T, Aagaard K, Woodgate R, Danielson S, Sasaki Y, Cavalieri D (2005) Circulation on the north central Chukchi Sea shelf. *Deep-Sea Res II* 52:3150–3174
  - Weingartner T, Dobbins E, Danielson S, Winsor P, Potter R, Statscewich H (2013) Hydrographic variability over the northeastern Chukchi Sea shelf in summer-fall 2008–2010. *Cont Shelf Res* 67:5–22
  - Wesławski JM, Kwa niewski S, Stempniewicz L, Błachowiak-Samołyk K (2006) Biodiversity and energy transfer to top trophic levels in two contrasting Arctic fjords. *Pol Polar Res* 27:259–278
  - Wilt L, Grebmeier JM, Miller TJ, Cooper LW (2014) Caloric content of Chukchi Sea invertebrates: modeling spatial and environmental variation. *Deep-Sea Res II* 102: 97–106
  - Winsor P, Chapman DC (2004) Pathways of Pacific water across the Chukchi Sea: a numerical model study. *J Geophys Res* 109:C03002, doi:10.1029/2003JC001962
  - Woodgate RA, Weingartner T, Lindsay R (2010) The 2007 Bering Strait oceanic heat flux and anomalous Arctic sea-ice retreat. *Geophys Res Lett* 37:L01602, doi:10.1029/2009GL041621