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Feeding ecologies of key bivalve and polychaete species in the Bering Sea as elucidated by fatty acid and compound-specific stable isotope analyses

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ABSTRACT: We characterized the feeding ecologies of common bivalves *Macoma calcarea*, *Nuculana radiata*, and *Ennucula tenuis*, and polychaetes *Leitoscoloplos pugettensis* and *Nephtys* spp. from the Bering Sea using relative proportions of fatty acids (FA profiles), FAs indicative of distinct organic matter sources (FA markers), and stable carbon isotope values of FA markers. We measured FAs from these invertebrates and from surface sediment scrapes collected during March to July in 2009 and 2010. The bivalve species had indistinguishable trophic signatures, as inferred by overlapping FA profiles and $\delta^{13}C$ values for algal marker FAs, and similar proportions of FA markers. FA $\delta^{13}C$ values from bivalve taxa were most similar to FA $\delta^{13}C$ values from particulate organic matter (POM) from surface sediments. In contrast, $\delta^{13}C$ values for the algal marker eicosapentaenoic acid in the polychaetes were higher relative to those from the bivalves and sediment from the same locations (mean difference of 3.6‰), suggesting low direct dietary contributions of benthic POM from surface sediments. *L. pugettensis*, a head-down deposit-feeding polychaete, had a higher contribution from bacterial sources to its total FA pool relative to the bivalves and to *Nephtys* spp., a predatory polychaete, based on a bacterial FA marker. Distinct FA profiles between the polychaetes imply different proportional contributions of dietary FA sources, including greater contribution of microbially altered FAs to *L. pugettensis* and greater contribution of ice algal FAs to *Nephtys* spp. Our findings revealed resource partitioning among select benthic invertebrates and suggest that responses to climate-induced changes in sub-Arctic production may be species specific.

KEY WORDS: Arctic benthos · Trophic markers · Bacteria · Sea ice algae · Phytoplankton · Microphytobenthos

INTRODUCTION

The Bering Sea is characterized by high benthic biomass (Grebmeier & Cooper 1995, Carmack & Wassmann 2006), which sustains populations of high trophic level benthic consumers, such as Pacific walruses, gray whales, bearded seals, and diving ducks (e.g. spectacled eiders) (Lovvorn et al. 2003, Moore et al. 2003, Blanchard et al. 2013), as well as the human communities that rely on these predators (Krupnik & Jolly 2002). Sources of organic matter (OM) in the Arctic marine ecosystem are diverse and can include pelagic, sympagic, and benthic production, along with terrestrial sources (Carmack et al. 2006). How-

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ever, the degree to which these different sources of OM contribute to the diets of consumers in the Bering Sea benthos is not fully understood. OM pathways in the sub-Arctic are strongly influenced by the presence of sea ice and its seasonal retreat, which is shifting as a result of climate change (e.g. Grebmeier et al. 2006, Brown & Arrigo 2013). An investigation of the sources of nutrients to consumers is critical in order to anticipate how ongoing changes at the base of the food web may propagate to higher trophic levels.

Annual primary production in seasonally sea ice-covered seas consists largely of pelagic and under-ice production (Gosselin et al. 1997, Sakshaug 2004, Arrigo et al. 2012). A smaller amount of total annual production is sympagic, originating within the sea ice matrix and on the underside of sea ice (Gradinger 2009). The contribution of *in situ* benthic production (including algal and microbial sources) to total annual production is unknown. In the sub-Arctic, spatial and temporal differences in light availability, sea ice cover, and nutrient supply influence the development of pelagic and sympagic algal blooms (Grebmeier & McRoy 1989, Gradinger 2002, Carroll et al. 2008). Physical and biological factors, such as wind mixing, the timing of ice melt, stratification, and pelagic grazing, subsequently affect the extent to which this material is deposited on the seafloor (Grebmeier & Barry 1991 and references therein, Renaud et al. 2007b, Cooper et al. 2009). Seasonal deployment of sediment traps under varying sea ice conditions have shown a wide range of vertical flux rates for a given geographical area, with peak carbon flux observed in spring (Grant et al. 2002, Moran et al. 2005, Morata & Renaud 2008).

At the seafloor, benthic invertebrate communities in high-latitude marine environments metabolize OM, causing sediment oxygen demand to increase and concentration of algal pigments (chlorophyll *a* and phaeopigments) to decline (e.g. Grebmeier & McRoy 1989, Ambrose & Renaud 1995, Renaud et al. 2007b). Sympagic and pelagic particulate OM (defined here as i-POM and p-POM, respectively) are generally considered high-quality food sources for benthic consumers (Kanneworff & Christensen 1986, Grebmeier & McRoy 1989, Renaud et al. 2007a), as they contain large amounts of polyunsaturated fatty acids (PUFAs) (Leu et al. 2010, Søreide et al. 2010) that cannot be synthesized de novo by consumer organisms (Parrish 2013). In addition to fresh i-POM and p-POM, benthic consumers have access to a heterogeneous mixture of OM within the sediment (benthic OM or b-POM). B-POM can comprise *in situ* production by microbes (Graf et al. 1982, Meyer-Reil 1983, Boetius & Damm 1998) and microphytobenthos (Matheke & Horner 1974, Karsten et al. 2006, Glud et al. 2009), as well as degraded phytodetritus originating from marine, terrestrial, and freshwater environments (Naidu et al. 1993, Naidu et al. 2000, Pirtle-Levy et al. 2009). Physical and biological processes, including resuspension and burial, bioturbation, and microbial degradation in the water column and sediment, influence the distribution and chemical composition of b-POM (e.g. Clough et al. 1997, Arnosti & Jørgensen 2006, Morata et al. 2011).

Dietary overlap and the relative importance of OM sources to benthic invertebrate diets in the Arctic and sub-Arctic have been investigated using stable isotope analysis (e.g. McConnaughey & McRoy 1979, Iken et al. 2005, McTigue & Dunton 2014). Pelagic algae (p-POM), ice-associated algae (i-POM) and b-POM can differ in their stable carbon isotope ratios (expressed as $\delta^{13}C$ values) (e.g. Hobson & Welch 1992, Lovvorn et al. 2005, Søreide et al. 2006). However, stable isotope analyses of benthic consumers have generated a wide range of values that cannot be attributed to anticipated sources (Iken et al. 2005). For example, Lovvorn et al. (2005) and McTigue & Dunton (2014) observed $\delta^{13}C$ values for invertebrate consumers that were consistently higher than $\delta^{13}C$ values from OM sources originating in the water column and in surface sediments. Values were similar to those of i-POM, but i-POM was not available to consumers during (and weeks prior to) sample collection in the aforementioned studies. Consequently, it has been suggested that benthic consumers may rely on phytodetrital POM that remains after microbial degradation (Lovvorn et al. 2005, McTigue & Dunton 2014). The phytodetrital POM that remains could be higher in ^{13}C relative to the OM sources analyzed due to fractionation associated with microbial degradation (Sun et al. 2004). Complementary analytical methods such as fatty acid (FA) analyses can further elucidate contributions of uncharacterized isotopic sources, such as microbially altered OM, to consumer diets.

FA profiles and markers are important ecological tools because they can reveal differences in diet and resource partitioning within a food web (e.g. Graham et al. 2014, Wang et al. 2015). FA analyses typically include the relative proportions (% of total) of all FAs in a sample (a FA profile) and a relative proportion or sum of individual FAs of particular interest (FA markers) that may be characteristic of diatoms, dinoflagellates, and bacteria, for example (e.g. Viso & Marty 1993, Dalsgaard et al. 2003, Parrish 2013). Individual FAs can also be analyzed for their $\delta^{13}C$ values, which can differ depending on the source from which the FA was derived. As such, they provide an independ-

ent and complementary line of evidence to determine particular source contributions to a consumer or sample. Compound-specific stable carbon isotope analysis confers a considerable advantage over stable isotope analysis of total organic carbon (TOC) because it provides multiple lines of evidence (i.e. FAs) from which to link consumers to their OM sources (Budge et al. 2008, Wang et al. 2015).

We investigated dietary overlap among bivalve and polychaete taxa that are abundant in the Bering Sea benthos. We examined the sources of FAs to these benthic invertebrates to determine whether organisms assimilate different POM sources. We selected species that are examples of several feeding types, including suspension/surface deposit-feeding bivalves (*Macoma calcarea* (Gmelin, 1791) and *Ennucula tenuis* (Montague 1808)), a subsurface deposit-feeding bivalve (*Nuculana radiata*), a head-down deposit-feeding polychaete (*Leitoscoloplos pugettensis* (Pettibone, 1957)), and a predatory scavenging polychaete (*Nephtys* spp.). We used stable isotope analyses of algal marker FAs in concert with FA profiles and various metrics (relative proportions and sums of individual FAs) (e.g. Budge et al. 2007, Sun et al. 2007, Wang et al. 2015) to test the hypothesis that resource partitioning among benthic invertebrates reflects differences in feeding strategy.

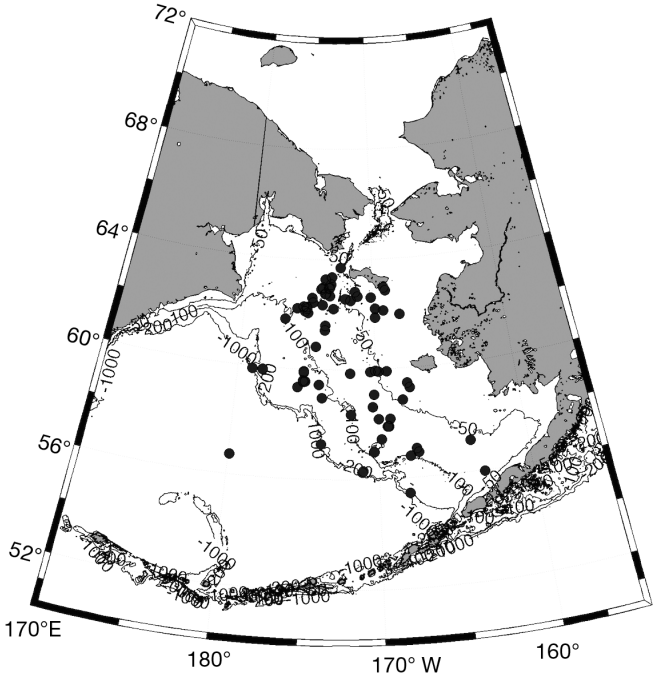

Fig. 1. Sampling locations for surface sediment scrapes and benthic invertebrate taxa in the Bering Sea. Numbers indicate isobath depth (m). Information on sampling stations is given in Table S1 in the Supplement at www.int-res.com/articles/suppl/m557p161_supp.pdf

MATERIALS AND METHODS

Study area

The Bering Sea acts as a sub-Arctic transition zone between the temperate North Pacific Ocean and Arctic marine ecosystems of the Chukchi Sea. It consists of a deep basin (>2000 m) to the west and a shallow continental shelf (<200 m) to the east (Fig. 1). The eastern shelf is separated by oceanographic fronts that subdivide the region into 3 domains. These regions are delineated by the 50, 100, and 200 m isobaths, which separate the inner (<50 m), middle (50–100 m), and outer (>100–200 m) shelf domains. Each domain is characterized by distinct physical (Coachman 1986) and biogeochemical (Mathis et al. 2010) features, and annual primary production, which ranges from 17 (inner domain) to 33 mmol C m^{-2} d^{-1} (outer domain) (Springer et al. 1996).

The Bering Sea is characterized by the most dramatic seasonal advance and retreat of sea ice of any region in the Arctic or sub-Arctic (Niebauer 1983, Bluhm & Gradinger 2008). Ice formation in the Bering Sea begins as prevailing winds drive ice southward to the shelf break, where the storage of deep basin heat prevents further advancement (Niebauer et al. 1999). On average, ~37% of the Bering Sea is seasonally ice-covered (Niebauer 1983). Sea ice minima and maxima in the Arctic generally occur in September and February, respectively. However, sea ice extent is subject to interannual variation due to large-scale ocean–atmosphere interactions, such as the El Niño–Southern Oscillation (ENSO) and the Pacific–North American pattern (PNA) (Niebauer 1988, Stabeno et al. 1999). Additionally, the Aleutian Low pressure system, created by the occurrence of winter storms, drives cooling or warming in the Bering Sea, depending on its strength and position (Niebauer et al. 1999, Stabeno et al. 2001). Observations of September sea ice minima in the Arctic between 1953 and 2006 show a 7.8 to 10.7% reduction in sea ice extent per decade (Stroeve et al. 2007, 2008). Observational data indicate that sea ice extent may continue to decline at a rate faster than predicted by present modeling efforts (Stroeve et al. 2007).

Sample acquisition

Sediment (n = 82), i-POM (n = 21), p-POM (n = 55), and invertebrate samples (n = 62) were collected opportunistically from the Bering Sea during 3 research cruises in 2009 and 3 in 2010 as part of the Bering Sea

Ecosystem Study–Bering Sea Integrated Ecosystem Research Program (BEST–BSIERP). In 2009, samples were collected during March and April (cruises HLY0901 and HLY0902, US Coast Guard Cutter [USCGC] 'Healy'), followed by sampling during June to July (cruise KNORR195, R/V 'Knorr'). In 2010, samples were collected during March (cruise PSEA10-01, USCGC 'Polar Sea'), May to June, and June to July (cruises TN249 and TN250, R/V 'Thomas G. Thompson'). Data and sample collection occurred each year during times ranging from maximum ice extent to ice-free conditions. A detailed analysis of sea ice cover in the study region is presented by Sullivan et al. (2014). Measurements from satellite data, ice cores, and moorings on the eastern Bering Sea shelf were used to describe the presence of sea ice, its movements, and its composition in 2009 (and 3 yr prior) (Sullivan et al. 2014). Ice extent reached a maximum on 28 February 2009 and persisted through March 2009 (NSIDC 2009). In 2010, maximum ice extent occurred 1 month later on 31 March (Richter-Menge & Overland 2010). All sampling stations were located south of St. Lawrence Island; most sites were located in the middle shelf domain (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m557p161_supp.pdf) (Fig. 1). Water column depth across all stations was 87 ± 57 m (mean ± SD).

At each station, a CTD (Seabird 911plus system using dual temperature, conductivity, and oxygen sensors) was used to measure temperature and salinity. Additional information describing sampling stations is provided in Table S1. A van Veen grab was deployed to collect surface sediment scrapes and benthic invertebrate specimens. Benthic invertebrate specimens were not present at all stations where surface sediment scrapes were collected (Table S1), but were evenly distributed in the study area. The invertebrate species investigated in this study co-occurred at many, but not all, sampling stations. When available, invertebrate specimens were identified to species with the exception of *Nephtys* spp., which we were unable to reliably identify to species level on the ship. All samples, including surface sediment scrapes, were frozen at –20°C until being freeze-dried for further analyses (described below). i-POM and p-POM sample collection and processing in 2009 and 2010 are described by Wang et al. (2015) and Wang et al. (2014), respectively.

Table 1. Mean lipid content (mg mg^{-1} wet wt × 100) of benthic invertebrate taxa. Values are means ± SD; *n*: sample size; individuals pooled by taxon. Polychaete taxa include *Leitoscoloplos pugettensis* and *Nephtys* spp., and bivalve taxa include *Macoma calcarea*, *Ennucula tenuis*, and *Nuculana radiata*

Taxon	*n*	Lipid content (%)
L. pugettensis	6	13.6 ± 7.8
Nephtys spp.	8	2.3 ± 1.2
M. calcarea	4	1.7 ± 1.1
E. tenuis	10	7.2 ± 8.9
N. radiata	5	3.9 ± 2.2

FA methyl ester transesterification and analysis

Lipids were extracted from sediments and invertebrate specimens using a modified Folch procedure (Folch 1957, Budge et al. 2006). All visible macroinfaunal material was removed from sediment samples prior to sediment lipid extraction. Between 3 and 25 g of freeze-dried sediment was acidified to remove inorganic carbon by soaking overnight in 1 N HCl until bubbling ceased. Sediments were rinsed 10 to 12 times with 30 ml of nanopure water for each rinsing, or until the pH of the supernatant became equal to the pH of nanopure water (>5.5). Multiple specimens from invertebrate taxa (<5 individuals) were pooled when necessary to obtain sufficient lipid content for FA analyses. Mean lipid content varied among taxa (Table 1). Shells were removed and invertebrate tissues were homogenized to reduce particle size. Gut contents were not removed prior to lipid extraction.

Lipids were extracted using a solvent mixture of HPLC-grade chloroform, methanol, and de-ionized water in a ratio of 8:4:3. This solvent mixture was added to sediments and invertebrates, and left to soak overnight at 4°C. Samples in solvent were then rinsed, centrifuged, and the lipid extract was evaporated under nitrogen in a water bath at 25 to 30°C. Extracted acyl lipids were then transesterified into their constituent FA methyl esters (FAMEs) using sulfuric acid (H_2SO_4) as a catalyst.

Relative proportions of individual FAs were determined using gas chromatography as described by Budge et al. (2006). FAMEs in hexane (1 µl) were introduced via splitless injection into a Perkin Elmer Autosystem II gas chromatograph (GC) with a flame ionization detector (FID) fitted with a 30 m long, 0.25 mm inner diameter column coated with 50% cyanopropyl polysiloxane (0.25 µm film thickness; J&W DB-23). GC-MS (Thermo Finnigan Polaris Q) was used, applying the same conditions as GC-FID, to characterize constituent FAs in an Atlantic menhaden (*Brevoortia tyrannus* (Latrobe, 1802)) oil sample containing FAs common to sediment and invertebrate samples. Retention times for sediment

and invertebrate samples were then cross-referenced with those from the menhaden oil profile to identify individual FAs. FAs are described by the nomenclature A:Bn-X, wherein A indicates the number of carbon atoms, B the number of double bonds, and X the position of the double bond closest to the terminal methyl group of a FA. Iso- and antiso-methyl branched FAs are further identified by lowercase italicized letters (e.g. *i*-15:0, a FA with 15 carbon atoms, 0 double bonds and a methyl branch on the second to last carbon atom in the chain).

We report relative proportions and sums of individual FAs that have been used as markers to identify OM sources (reviewed in Parrish 2013) in benthic invertebrate taxa (Table 2; complete FA datasets are available on request). We removed FAs present at relative proportions less than 0.01% total and renormalized FA data prior to statistical analysis. We then excluded non-methylene interrupted (NMI) FAs, which are synthesized by a diverse set of benthic invertebrate taxa, including bivalves (e.g. Paradis & Ackman 1977, Joseph 1982, Kawashima 2005). As a 'benthic' marker, NMI FAs do not provide information on dietary carbon sources for organisms that produce them, and may obscure differences among FA profiles of bivalve and non-bivalve taxa in our study. The sum of FAs with branched chains and odd numbers of carbon atoms (*ai*-15:0, *i*-15:0, *ai*-17:0, and *i*-17:0) is considered to be a composite bacterial marker (reviewed in Parrish 2013). Pelagic calanoid copepods produce high levels of the monounsaturated FAs 20:1n-9, 20:1n-11, and 22:1n-11, which

Table 2. Select FA proportions (% total) and sums from benthic invertebrate taxa (n = sample size pooled by taxon). Values are means ± SD. Polychaete taxa include *Leitoscoloplos pugettensis* and *Nephtys* spp., and bivalve taxa include *Macoma calcarea*, *Ennucula tenuis*, and *Nuculana radiata*. PUFAs: polyunsaturated FAs; MUFAs: monounsaturated FAs; SFAs: saturated FAs; Bac: odd branched chain FAs. Letters a to d indicate significant differences among taxa (Kruskal-Wallis 1-factor ANOVA, $p < 0.0001$, Mann-Whitney U-test with Bonferroni adjustment for pairwise comparisons, $\alpha = 0.01$)

	L. pugettensis (n = 12)	*Nephtys* spp. (n = 16)	*M. calcarea* (n = 9)	*E. tenuis* (n = 15)	*N. radiata* (n = 10)
12:0	0.8 ± 0.6	0.6 ± 0.8	1.5 ± 1.7	1.6 ± 1.7	1.4 ± 1.5
14:0	1.7 ± 0.8	0.6 ± 0.3	2.4 ± 1.0	1.7 ± 1.6	1.8 ± 0.5
i-15:0	0.4 ± 0.2	0.0 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
ai-15:0	0.8 ± 1.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.0
16:0	10.5 ± 2.0	11.2 ± 2.5	12.8 ± 0.8	15.1 ± 3.1	11.2 ± 0.8
16:1n-7	24.2 ± 10.7	3.6 ± 2.2	15.2 ± 11.3	14.8 ± 12.1	8.0 ± 6.6
i-17:0	0.6 ± 0.2	0.2 ± 0.1	0.3 ± 0.1	0.4 ± 0.3	0.5 ± 0.2
ai-17:0	0.4 ± 0.5	0.2 ± 0.3	0.4 ± 0.5	0.2 ± 0.4	0.3 ± 0.4
16:4n-1	0.2 ± 0.1	0.1 ± 0.2	0.2 ± 0.2	0.4 ± 0.4	0.2 ± 0.3
18:0	5.5 ± 1.4	5.7 ± 1.5	5.6 ± 2.8	5.3 ± 3.0	5.8 ± 1.7
18:1n-9	2.2 ± 1.9	4.9 ± 5.4	2.7 ± 1.2	2.8 ± 1.5	1.9 ± 1.1
18:1n-7	7.2 ± 2.1	6.0 ± 1.2	2.8 ± 1.4	6.5 ± 3.3	6.7 ± 3.1
18:2n-6	1.2 ± 1.4	1.1 ± 1.4	0.9 ± 0.7	1.2 ± 0.7	1.0 ± 0.8
18:2n-4	0.2 ± 0.0	0.1 ± 0.0	0.2 ± 0.1	0.3 ± 0.2	0.3 ± 0.1
18:3n-3	0.4 ± 0.2	0.3 ± 0.4	0.1 ± 0.1	0.3 ± 0.2	0.2 ± 0.1
18:4n-3	0.4 ± 0.2	0.2 ± 0.1	0.8 ± 0.4	0.8 ± 0.4	0.7 ± 0.2
20:1n-11	4.0 ± 1.4	4.5 ± 1.5	4.4 ± 2.6	6.0 ± 3.4	6.4 ± 1.4
20:1n-9	0.6 ± 0.3	1.5 ± 0.4	0.9 ± 0.4	0.5 ± 0.3	0.5 ± 0.2
20:1n-7	2.2 ± 0.7	3.3 ± 0.8	4.7 ± 0.5	4.6 ± 1.6	2.4 ± 0.6
20:2n-9	0.2 ± 0.1	0.5 ± 0.3	0.5 ± 0.3	0.3 ± 0.3	0.1 ± 0.1
20:2n-6	0.2 ± 0.1	0.7 ± 0.3	0.2 ± 0.0	0.1 ± 0.1	0.0 ± 0.0
20:4n-6	1.9 ± 0.7	2.5 ± 0.9	3.0 ± 1.5	3.7 ± 2.2	2.3 ± 0.6
20:5n-3	15.8 ± 6.5	23.5 ± 4.5	21.2 ± 3.1	15.6 ± 3.8	17.5 ± 1.5
22:1n-11	0.9 ± 0.3	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
22:1n-9	0.3 ± 0.1	0.2 ± 0.3	0.5 ± 0.4	0.6 ± 0.4	0.6 ± 0.4
21:5n-3	0.2 ± 0.1	0.4 ± 0.1	1.2 ± 0.8	0.5 ± 0.3	1.2 ± 0.4
22:4n-6	0.8 ± 0.5	1.5 ± 0.5	0.2 ± 0.1	0.2 ± 0.2	0.3 ± 0.4
22:5n-6	0.2 ± 0.1	0.5 ± 0.2	0.5 ± 0.3	0.7 ± 0.5	1.0 ± 0.3
22:5n-3	1.8 ± 0.8	3.1 ± 0.9	2.7 ± 1.7	1.4 ± 1.0	3.3 ± 1.1
22:6n-3	1.2 ± 0.6	11.4 ± 3.1	6.2 ± 2.9	4.4 ± 2.3	13.5 ± 4.4
ΣPUFAs	26.7 ± 8.7^{a}	47.3 ± 7.0^{bd}	39.6 ± 5.5^{abc}	31.6 ± 8.1^{a}	43.2 ± 6.0^{cd}
ΣMUFAs	45.2 ± 9.0^{a}	28.0 ± 6.3^{b}	34.2 ± 8.9^{ab}	38.9 ± 11.2^{ab}	29.8 ± 8.5^{b}
ΣSFAs	21.1 ± 3.2^{ab}	20.8 ± 4.2^{a}	24.1 ± 4.1^{ab}	25.6 ± 4.1^{b}	22.1 ± 3.5^{ab}
ΣBac	2.2 ± 1.5^{a}	0.5 ± 0.3^{b}	0.8 ± 0.5^{b}	0.7 ± 0.6^{b}	0.9 ± 0.6^{b}

makes them indicators of organic material derived from *Calanus* spp. (Falk-Petersen et al. 1987, Søreide et al. 2013). Relative proportions of 16:4n-1, 16:1n-7, 20:5n-3, and 22:6n-3 are considered to be algal indicators (e.g. Dalsgaard et al. 2003, Kelly & Scheibling 2012). Ice algal POM can be differentiated from pelagic POM by higher relative proportions of 16:4n-1, 16:1n-7, and 20:5n-3 (diatom FA markers), and lower proportions of C_{18} and C_{22} PUFAs, including 22:6n-3 (dinoflagellate FA markers) (e.g. Søreide et al. 2008). Accordingly, the sum of PUFAs can be indicative of high algal contributions.

Although additional FA markers have been reported in dietary investigations (e.g. Graeve et al. 1997, Dalsgaard et al. 2003, Kelly & Scheibling 2012), we relied on FA profiles and conservative FA markers of source to elucidate differences in feeding ecology. Conservative FA markers are those that originate from a unique source and are less likely to be modified by consumers through chain elongation, desaturation, or oxidation (e.g. the composite bacterial marker containing *ai*-15:0, *i*-15:0, *ai*-17:0, and *i*-17:0). There is evidence to suggest that relative proportions of FAs can be influenced by modification or catabolism prior to incorporation into tissues in the bivalve *Mya truncata* (Birkely et al. 2003). Given that the consumers we investigated are associated with different feeding types (including bivalve spp., which may or may not modify FAs in similar ways to *M. truncata*), application of individual biomarkers could be of limited utility. For instance, although the FAs 16:4n-1, 20:5n-3, and 22:6n-3 vary consistently with POM source (e.g. Søreide et al. 2008), these long chain PUFAs have high oxidative yield, and utility in cell membranes and as hormone precursors (e.g. Ackman & Cunnane 1992). This could make them less reliable proxies for determining proportional contributions of POM sources to diets, given the potential for storage or catabolism. Consequently, we relied on compound-specific stable isotope analysis of FAs as a very useful complementary approach to apportioning source contributions, such as i-POM, p-POM, and b-POM, to consumers.

Stable carbon isotope analysis of individual FAMEs

To measure the $\delta^{13}C$ values of individual FAs, 1 µl of FAMEs from each sample in hexane was injected on to a GC column connected to an isotope ratio mass spectrometer (Thermo Finnigan Delta V) via a combustion interface (IsoLink; www.isolink.com) at the Alaska Stable Isotope Facility. Sample concentration of FAMEs in hexane was optimized to produce a voltage of 500 to 3000 mV for 20:5n-3. The GC column, temperature program, and mode of injection were the same as the GC-FID analyses (described above). A FAME standard consisting of 16:0 and 18:0 (Nu-Chek Prep) was run between every 8 samples (n = 20) to track analytical error, which was <0.1 and <0.2‰, respectively (expressed as 1 SD of 16:0 and 18:0). Although we measured $\delta^{13}C$ values for algal marker and non-marker FAs, we only report values for FAs for which there was sufficient signal and no coelution. 16:4*n*-1, though a reliable algal marker, was present at 0.1% in consumer samples, which is below the detectable limit. $\delta^{13}C$ values of non-marker FAs for invertebrate taxa are included in Table S2 in the Supplement.

Stable carbon isotope ratios of samples are expressed relative to the ratios of the international standard Vienna PeeDee Belemnite (VPDB) using conventional delta (δ) notation in parts per thousand (‰) according to the following equation: $\delta X = [(R_{standard}/R_{sample}) - 1] \times 1000$, where $\delta X = \delta^{13}C$ value and R is the $^{13}C:^{12}C$ ratio. To calibrate the $\delta^{13}C$ values, we used a standard mixture containing 8 calibrated n-alkanoic acid esters (Mixture F8, Indiana University Stable Isotope Reference Materials), where r^2 of the known versus expected relationship was >0.99. To account for the carbon added during transesterification, we corrected $\delta^{13}C_{FA}$ values using the following equation: $\delta^{13}C_{FA} = [(n + 1)(\delta^{13}C_{FAME}) - (\delta^{13}C_{methanol})]/n$, where $\delta^{13}C_{FA}$ is the adjusted value of the FA of interest, n is the number of its carbon atoms, $\delta^{13}C_{FAME}$ is the F8 mixture calibrated value of the FAME, and $\delta^{13}C_{methanol}$ is the stable isotope composition of the carbon contributed by the methanol (Abrajano et al. 1994). $\delta^{13}C_{methanol}$ ($\delta^{13}C_{methanol} = -49$‰) was calculated by subtracting the $\delta^{13}C$ value of esterified C_{16} and C_{18} standards from the corresponding $\delta^{13}C$ values of their free FAs (Wang et al. 2014).

Data analysis

Owing to the opportunistic nature of sample collection, we did not have sufficient sample replicates to test variability associated with year, geography, or season (sample sizes included in Table 2). Therefore, we pooled data by taxon and performed univariate and multivariate statistical techniques to determine differences among invertebrate species. Because we pooled the invertebrate dataset across years, regions, and ice conditions, and had similarly low sample replicates available for i-POM and p-POM (Table S1),

we also pooled data to generate mean signatures for each POM source. Seasonal differences and variation between i-POM and p-POM samples included in this study are described in Wang et al. (2014). Preliminary analyses of b-POM data (FA profiles, individual FA markers, select $\delta^{13}C$ values) revealed no discernible patterns associated with shelf domain (a proxy for depth), ice condition, or year. FA data were standardized to 100% and transformed using a $\log(1 + X)$ function prior to multivariate analyses (Budge et al. 2006) because proportional data are rarely normally distributed. Bray-Curtis similarity matrices were constructed on FA data for those FAs present at proportions >0.1% (n = 71 FAs). Permutational multivariate analysis of variance (1-factor PERMANOVA with pairwise comparison) (Anderson 2001) was performed using PRIMER-6 (Primer-E) to describe variation among FA profiles of individual species (Table 3). Statistical significance of pairwise differences among FA profiles was determined based on a 99% confidence level (α = 0.01) adjusted to maintain a familywise error rate using a Bonferroni correction (Primer-E) (Table 3). Nonmetric multi-dimensional scaling (nMDS) plots were generated to visualize differences among FA profiles among species (Fig. 2). Similarity percentage routines (SIMPER) were run to identify the FAs that contributed most to differences in the relative proportions of FAs among samples.

Most FA markers (relative proportions and sums) and $\delta^{13}C$ values of FAs violated assumptions for parametric statistics so we used a Kruskal-Wallis 1-factor analysis of variance (ANOVA) (R version 3.2.0) and a Mann-Whitney *U*-test to test for pairwise differences among benthic invertebrate species (Tables 2 & 4) and among POM sources (Tables S3 & S4 in the Supplement). Statistical significance was determined based on a 99% confidence level (α = 0.01) corrected for the number of comparisons made using a Bonferroni correction (R version 3.2.0). $\delta^{13}C$ values (mean ± SD) of non-marker FAs common to the 5 invertebrate taxa (16:0, 18:0, 18:1n-9, 18:1n-7, and 20:1n-7) are provided in Table S2.

We performed a series of Bayesian multi-source stable isotope mixing models (Stable Isotope Analysis in R [SIAR]; Parnell et al. 2010) using 16:1n-7, 20:5n-3, and 22:6n-3 to estimate the proportional contributions of i-POM, p-POM, and b-POM (specifically, the fraction of b-POM in surface sediment scrapes) to bivalve taxa and to *Nephtys* spp. (Table 5). We did not include *Leitoscoloplos pugettensis* because its distinct isotopic composition in combination with FA analyses indicated that it likely sources FAs from a fraction of b-POM that we did not sample (specifically, microbially altered phytodetrital POM that may be abundant in sediment located below the top centimeter) (see 'Discussion'). $\delta^{13}C$ values for 16:1n-7, 20:5n-3, and 22:6n-3 from surface sediment b-POM fell between values from i-POM and p-POM (Table S4), which could imply that b-POM consists of an equal mixture of FAs from i-POM and p-POM. However, we selected a 3-source mixing model that includes b-POM as a unique source based on statistically significant differences in the relative proportions of individual FAs and marker FAs (Table S5 in the Supplement), FA profiles (Table S3), and $\delta^{13}C$ values of FA algal markers (Table S4). We further discuss the implications of including b-POM as a unique FA source to our mixing model results in the 'Discussion'.

We ran each Bayesian mixing model with and without concentra-

Table 3. p-values from pairwise comparisons of FA profiles of benthic invertebrate taxa. **Bold**: statistically significant differences among polychaete taxa (*Leitoscoloplos pugettensis* and *Nephtys* spp.) and bivalve taxa (*Macoma calcarea*, *Ennucula tenuis*, and *Nuculana radiata*) are based on 1-factor PERMANOVAs (taxon as factor) and a Bonferroni adjustment for pairwise comparisons (α = 0.01)

Taxon	p	Permutations
L. pugettensis × *Nephtys* spp.	**<0.01**	998
M. calcarea × *E. tenuis*	>0.01	997
E. tenuis × *N. radiata*	>0.01	998
M. calcarea × *N. radiata*	>0.01	992
Nephtys spp. × *M. calcarea*	**<0.01**	998
Nephtys spp. × *N. radiata*	**<0.01**	999
Nephtys spp. × *E. tenuis*	**<0.01**	997
L. pugettensis × *M. calcarea*	**<0.01**	994
L. pugettensis × *E. tenuis*	**<0.01**	999
L. pugettensis × *N. radiata*	**<0.01**	998

Table 4. Mean $\delta^{13}C$ values (‰) of algal marker FAs from benthic invertebrate taxa. Algal marker FAs are 16:1*n*-7, 20:5*n*-3, and 22:6*n*-3 (mean ± SD); individuals pooled by taxon; nd: no data. Polychaete taxa include *Leitoscoloplos pugettensis* and *Nephtys* spp., and bivalve taxa include *Macoma calcarea*, *Ennucula tenuis*, and *Nuculana radiata*. Letters a to d indicate significant differences among taxa (Kruskal-Wallis 1-factor ANOVA, p < 0.0001, Mann-Whitney *U*-test with Bonferroni adjustment for pairwise comparisons, α = 0.01)

	L. pugettensis	*Nephtys* spp.	*M. calcarea*	*E. tenuis*	*N. radiata*
16:1n-7	-26.7 ± 2.6^{bc}	-23.6 ± 2.5^{ab}	-26.9 ± 0.7^{c}	-26.7 ± 1.1^{c}	-27.3 ± 1.3^{c}
20:5n-3	-24.9 ± 1.4^{a}	-23.8 ± 1.6^{a}	-27.5 ± 0.5^{b}	-26.8 ± 0.9^{b}	-27.2 ± 1.0^{b}
22:6n-3	nd	-23.0 ± 1.5^{a}	-25.7 ± 0.7^{b}	-25.6 ± 1.0^{b}	-25.9 ± 0.6^{b}

Table 5. Estimates of the proportional contributions (%) of ice particulate organic matter (i-POM), pelagic POM (p-POM) and benthic POM (b-POM) to benthic invertebrate diets. Values are based on 4 SIAR stable isotope mixing models, showing means (95% credibility intervals), run with concentration dependencies (see Table S4 in the Supplement at www.int-res.com/articles/suppl/m557p161_supp.pdf) and a FA trophic isotope enrichment factor of zero. POM includes sympagic (ice; i-POM), pelagic (p-POM), and benthic (b-POM) sources. Polychaete taxa include *Nephtys* spp. and bivalve taxa include *Macoma calcarea*, *Ennucula tenuis*, and *Nuculana radiata*. *Leitoscoloplos pugettensis* was excluded from the mixing models because our evidence indicated that it likely sources FAs from a fraction of b-POM that we did not sample (specifically, sediment located below the top centimeter)

	Nephtys spp.	*M. calcarea*	*E. tenuis*	*N. radiata*
i-POM				
16:1n-7, 20:5n-3, 22:6n-3	79 (62–96)	18 (3–34)	28 (9–45)	24 (7–40)
16:1n-7, 20:5n-3	74 (47–97)	12 (0–26)	18 (1–36)	21 (2–38)
16:1n-7, 22:6n-3	78 (60–95)	25 (7–42)	32 (13–50)	28 (11–46)
20:5n-3, 22:6n-3	74 (51–96)	26 (4–47)	32 (10–54)	26 (7–47)
p-POM				
16:1n-7, 20:5n-3, 22:6n-3	4 (0–10)	23 (5–42)	19 (1–38)	26 (6–45)
16:1n-7, 20:5n-3	5 (0–16)	26 (8–44)	16 (0–35)	32 (9–52)
16:1n-7, 22:6n-3	5 (0–12)	21 (2–40)	19 (1–39)	26 (5–46)
20:5n-3, 22:6n-3	4 (0–11)	29 (5–52)	25 (2–48)	24 (4–46)
b-POM				
16:1n-7, 20:5n-3, 22:6n-3	17 (0–34)	59 (32–85)	53 (24–84)	50 (22–81)
16:1n-7, 20:5n-3	20 (0–46)	62 (35–87)	66 (33–95)	47 (17–83)
16:1n-7, 22:6n-3	17 (0–35)	54 (27–83)	49 (20–80)	45 (18–76)
20:5n-3, 22:6n-3	22 (0–45)	45 (10–81)	42 (5–78)	49 (14–84)

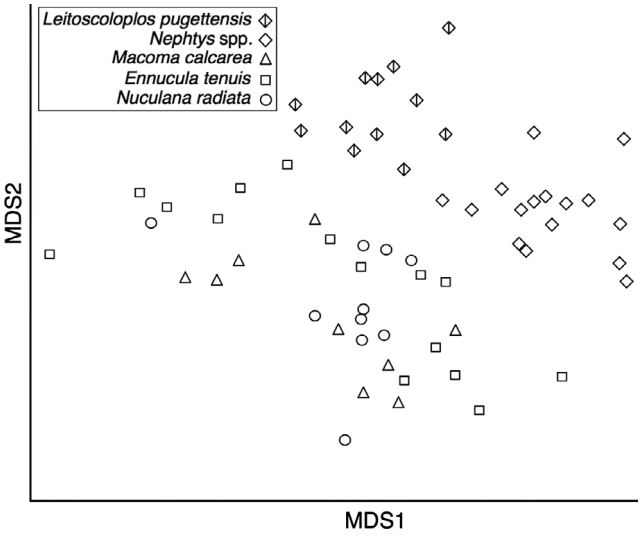

Fig. 2. Non-metric multidimensional scaling plot of benthic invertebrate taxa. Polychaete taxa include *Leitoscoloplos pugettensis* and *Nephtys* spp., and bivalve taxa include *Macoma calcarea*, *Ennucula tenuis*, and *Nuculana radiata*. Distances are based on Bray-Curtis similarity matrices using 71 FAs occurring in relative proportions >0.1%. Two-dimensional stress = 0.16

tion dependences (e.g. Wang et al. 2015), which adjust model estimates to account for the relative proportions of FAs (% total) in each source (Table 5). However, we report only the results from the concentration-dependent model, because our findings were the same for both models. We assumed a FA trophic isotope enrichment factor of zero in all models as in Wang et al. (2015) (see also Discussion). There have been no studies on trophic enrichment at the molecular level in marine bivalves or polychaetes to provide FA trophic enrichment factor estimates. However, research on FA trophic enrichment factors for Steller's eiders and spectacled eiders (Budge et al. 2011) showed no isotopic differences in 20:5n-3 and 22:6n-3 from dietary sources and those from adipose tissue (Budge et al. 2011). Futhermore, many marine organisms are incapable of FA biosynthesis of 20:5n-3 and 22:6n-3 from precursor FAs (i.e. 18:2n-6 and 18:3n-3) (Tocher 2010), a potential mechanism by which FA trophic fractionation can occur (e.g. Fujibayashi et al. 2016). The mean discrimination factor for 16:1 for the eiders was ~+1‰, suggesting that trophic enrichment factors may vary minimally for individual FAs in marine organisms (Budge et al. 2011).

RESULTS

FA profiles and markers

FA profiles significantly differed between *Leitoscoloplos pugettensis* and *Nephtys* spp., and among all polychaete–bivalve species pairings, but not among bivalve species (1-factor PERMANOVA with pairwise comparison) (Fig. 2; see Table 3 for p-values). FA profiles between *L. pugettensis* and *Nephtys* spp. were 32% dissimilar, with elevated relative proportions of bacterial markers (*ai*-15:0, *i*-15:0) in *L. pugettensis* contributing most to the dissimilarity (SIMPER) (Table 2). Higher relative proportions of 22:1n-11 and 16:1n-7, and a lower average relative proportion of 22:6n-3 in *L. pugettensis* relative to *Nephtys* spp., also differentiated the FA profiles of the polychaete taxa (SIMPER) (Table 2). These FAs (*i*-15:0, *i*-15:0, 22:6n-3, and 22:1n-11) also contributed most to the

dissimilarities among *L. pugettensis* and the bivalve taxa. FAs that contributed most to differences in FA profiles among *Nephtys* spp. and the bivalve taxa were 20:2n-6, 20:3n-3, 22:4n-6, and 18:1n-13, all of which were higher in *Nephtys* spp. (SIMPER).

L. pugettensis had the highest mean proportion of the composite bacterial marker (sum of the relative proportions of iso- and anteiso- 15:0 and 17:0; 2.2 ± 1.5%) (Kruskal-Wallis 1-factor ANOVA, $p < 0.001$, Mann-Whitney *U*-test pairwise comparison) (Table 2). Lipid content was variable among taxa (Table 1). The relative proportion of PUFAs was highest in *Nephtys* spp. (47.3 ± 7.0%) and lowest in *L. pugettensis* (26.7 ± 8.7%); bivalves had intermediate levels, ranging from 31.6 ± 8.1% (*Ennucula tenuis*) to 43.2 ± 6.0% (*Nuculana radiata*) (Mann-Whitney *U*-test pairwise comparison, $p < 0.01$) (Table 2). The proportion of 20:5n-3 was high in all taxa (ranging from 15.8% total in *L. pugettensis* to 23.5% in *Nephtys* spp.) (Table 2). Relative proportions of 22:6n-3 were lower in all taxa (1.2% in *L. pugettensis* to 13.5% in *N. radiata*), as were C_{18} PUFAs (<1% in all species) (Table 2). The proportion of 20:1n-11 was high in all taxa, but especially in *N. radiata* (6.4 ± 1.4%).

Stable carbon isotope values of FAs

$\delta^{13}C$ values for algal marker FAs differed among the benthic invertebrate taxa investigated (16:1n-7, 20:5n-3, and 22:6n-3) (Kruskal-Wallis 1-factor ANOVA, $p < 0.01$) (Table 4, Fig. 3). *Nephtys* spp. had the highest $\delta^{13}C$ values for algal marker FAs, which ranged from –23.8 ± 1.6‰ for 20:5n-3 to –23.0 ± 1.5‰ for 22:6n-3 (Table 4, Fig. 3). $\delta^{13}C$ values for FAs from *L. pugettensis* were similarly high (e.g. –24.9 ± 1.4‰ for 20:5n-3). $\delta^{13}C$ values of individual FAs from the 3 bivalve species were not significantly different (Mann-Whitney *U*-test pairwise comparison, $p > 0.01$) (Table 4, Fig. 3).

Mean $\delta^{13}C$ values for 16:1n-7 and 20:5n-3 from b-POM (–26.7 ± 1.0 and –26.9 ± 1.7‰, respectively) fell between values for i-POM and p-POM (Kruskal-Wallis 1-factor ANOVA, $p < 0.001$, Mann-Whitney *U*-test pairwise comparison, $\alpha = 0.01$) (Fig. 3). The mean $\delta^{13}C$ value for 22:6n-3 from b-POM (–27.2 ± 2.1‰) was not significantly different from p-POM (–27.9 ± 2.4‰) or i-POM (–24.2 ± 3.2‰) (Mann-Whitney *U*-test pairwise comparison, $p > 0.01$), though they were significantly different from each other (Mann-Whitney *U*-test pairwise comparison, $p < 0.01$). $\delta^{13}C$ values of 20:5n-3, an algal indicator, from samples of invertebrates and b-POM (surface sediment) collected concurrently overlapped for all bivalve taxa (Fig. 4). In contrast, the offset between $\delta^{13}C$ values of 20:5n-3 from polychaete tissue samples and surface sediment b-POM was significantly greater (~3.6‰ higher than b-POM on average) relative to the bivalves (Kruskal-Wallis 1-factor ANOVA, $p < 0.0001$, Mann-Whitney *U*-test pairwise comparison) (Fig. 4).

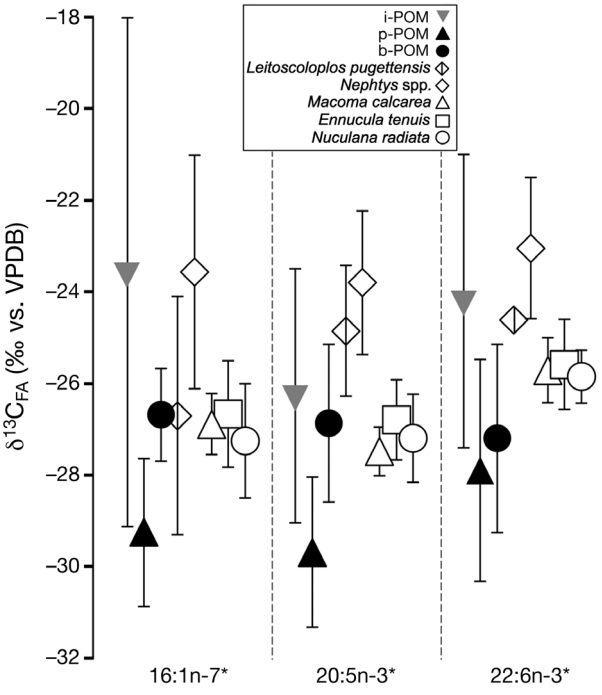

Fig. 3. $\delta^{13}C$ values (‰) of algal marker FAs from sympagic (ice; i-POM), pelagic (p-POM), and benthic particulate organic matter (b-POM) and benthic invertebrate taxa. Algal marker FAs are 16:1n-7, 20:5n-3, and 22:6n-3 (mean ± SD; individuals pooled by taxon). Sympagic and pelagic POM values are taken from Wang et al. (2014) and Wang et al. (2015). Polychaete taxa include *Leitoscoloplos pugettensis* and *Nephtys* spp., and bivalve taxa include *Macoma calcarea*, *Ennucula tenuis*, and *Nuculana radiata*. VPDB: Vienna PeeDee Belemnite. *Significant differences among taxa (POM excluded) (Kruskal-Wallis 1-factor ANOVA; see Table 4 for Mann-Whitney *U*-test for pairwise comparisons, $\alpha = 0.01$)

Based on different combinations of indicator FAs (16:1n-7, 20:5n-3, and 22:6n-3) and their $\delta^{13}C$ values in SIAR, we produced a range of estimates for b-POM, p-POM, and i-POM FA proportional contributions (mean [95% credibility interval] %) to the diets of 4 invertebrate taxa (*L. pugettensis* excluded) (Table 5). FAs from b-POM contributed most to bivalve FA pools, with mean estimates ranging from 59 (32–85)% for *Macoma calcarea*, 53 (24–84)% for *E. tenuis*, and 50 (22–81)% for *N. radiata*, based on the model with 3 FAs (Table 5). i-POM was the largest contributor of FAs to *Nephtys* spp., with mean contributions ranging from 79 (62–96)%.

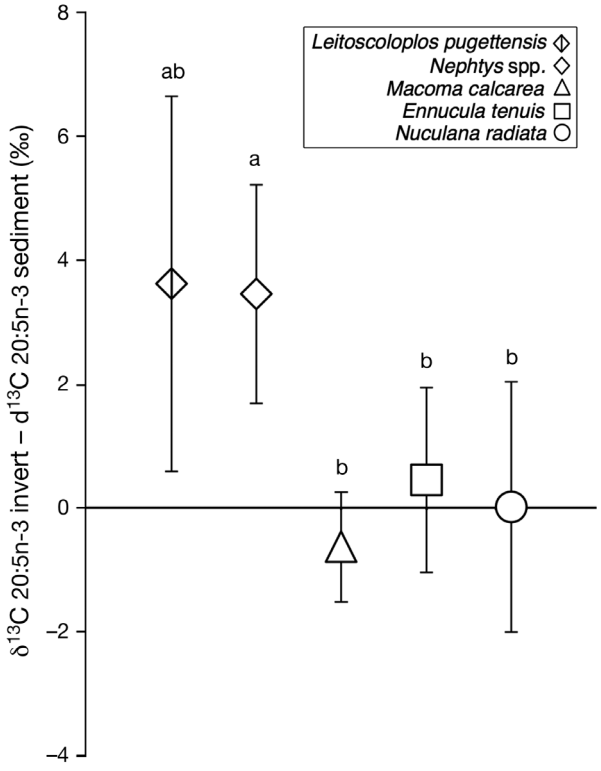

Fig. 4. $\delta^{13}C$ values (‰) of the algal marker 20:5*n*-3 from benthic invertebrate taxa relative to those from surface sediments from the same location. Values are mean ± SD, individuals pooled by taxon. Polychaete taxa include *Leitoscoloplos pugettensis* (n = 6) and *Nephtys* spp. (n = 13), and bivalve taxa include *Macoma calcarea* (n = 9), *Ennucula tenuis* (n = 13), and *Nuculana radiata* (n = 8). Letters a and b indicate significant differences among taxa (Kruskal-Wallis 1-factor ANOVA, $p < 0.0001$, Mann-Whitney *U*-test with Bonferroni adjustment for pairwise comparisons, $\alpha = 0.01$)

DISCUSSION

FA analyses indicated differences in diet for the bivalves compared with the polychaete taxa and between the 2 polychaete taxa examined, implying unique FA sourcing likely as a result of distinct feeding strategies. The 3 bivalve species had overlapping FA profiles, indicating that they obtained FAs from the same source or mixture of sources. The $\delta^{13}C$ values of marker FAs from bivalves were indistinguishable from sediment (b-POM) and exhibited little variability, despite pooling samples by taxon across varying sampling conditions. $\delta^{13}C$ values of algal FA markers (16:1n-7, 20:5n-3, and 22:6n-3) in both polychaete taxa were high relative to those in bivalves, indicating reliance on OM sources other than surface sediment b-POM and p-POM. In *Leitoscoloplos pugettensis*, an elevated bacterial marker suggests that the relatively high $\delta^{13}C$ values may be attributed to a microbially altered phytodetrital FA pool. In contrast, *Nephtys* spp. does not show an elevated bacterial marker; therefore, we posit that high $\delta^{13}C$ values for algal marker FAs in *Nephtys* spp. are derived from i-POM.

Elevated proportions of the calanoid FA marker 20:1n-11 in all taxa suggest that all species, irrespective of feeding strategy, rely on OM derived from *Calanus* spp. Low relative proportions of dinoflagellate markers (C_{18} PUFA and 22:6n-3) in all species compared to diatom markers (16:1n-7, 20:5n-3) indicate a general reliance on the ice-associated spring algal bloom and may suggest that the Bering Sea benthos is a diatom-dominated system. Overall, our findings support our initial hypothesis that FA sources vary with feeding strategy. The one exception was *Nuculana radiata*, a subsurface deposit-feeding bivalve, whose FAs were indistinguishable from the suspension/surface deposit-feeding bivalves we examined.

Sources of FAs to sediments and bivalve taxa

Based on the $\delta^{13}C$ values of algal markers, *Macoma calcarea*, *Ennucula tenuis*, and *N. radiata* appear to consistently assimilate algal FAs from a mixture of sources, including b-POM (from surface sediment), i-POM, and p-POM. Estimates of FA contributions to bivalve diets indicated that a majority of FAs originated from b-POM (>40%), relative to i-POM (<30%) and p-POM (<30%). When individual bivalves from each species were paired with surface sediment scrapes collected concurrently at the same location, there were no differences between $\delta^{13}C$ values for 20:5n-3, indicating that these bivalve species likely sourced OM from the surface sediments they inhabited. However, we note that the $\delta^{13}C$ values for marker FAs (16:1n-7, 20:5n-3, and 22:6n-3) from b-POM from surface sediments fell between those from i-POM and p-POM, allowing for the possibility that b-POM could be a mix of these 2 sources. If marker FAs from b-POM are a mixture of diagenetically unaltered FAs originating from i-POM and p-POM sources, then our mixing model results would be an underestimation of the relative importance of pelagic and sympagic FAs to bivalve diets. While we cannot conclusively determine the fractions of b-POM that originate from fresh or diagenetically altered i-POM and p-POM, or from *in situ* production (e.g. microphytobenthos), evidence from our supporting FA data (FA profiles and relative proportions of individ-

ual FAs) indicates that i-POM, p-POM, and b-POM FA sources are unique. Furthermore, a distinct advantage of treating these 3 POM sources separately is that we can account for indirect assimilation of p-POM and i-POM sources via the benthos (b-POM).

Previous research on bivalves, including *M. calcarea*, *E. tenuis*, and *N. radiata*, indicates that bivalves consume i-POM, p-POM, and b-POM, based on compound-specific stable isotope analyses (Sun et al. 2007, 2009) and stable isotope analyses of TOC (Weems et al. 2012, Tu et al. 2015). Additional controlled feeding studies are necessary to resolve the question of whether bivalves preferentially forage for or selectively assimilate particular sources, such as i-POM, because there is evidence both to support (McMahon et al. 2006, Sun et al. 2007) and refute (Sun et al. 2009) that claim. Our findings indicate that *N. radiata*, *M. calcarea*, and *E. tenuis* consume FAs that are available in surface sediment irrespective of source and feeding strategy.

Sources of FAs to polychaete taxa

We attribute the relatively high $\delta^{13}C$ values for 20:5n-3 in *L. pugettensis* to a fraction of b-POM located below surface sediments that was not sampled in this study (and thus was not included in our SIAR model) containing microbially altered phytodetrital FAs. Feeding behavior documented in *L. pugettensis* at lower latitudes describes the genus as conveyor-belt feeders that rely on OM sources near the redoxocline, a zone of microbial productivity and diversity located below surface sediments (Bianchi 1988). We observed a significantly higher proportion of a bacterial marker in *L. pugettensis* relative to all other invertebrate consumers. Additionally, *L. pugettensis* (and also *Nephtys* spp.) had $\delta^{13}C$ values for 20:5n-3 that were much higher than those from surface sediment scrapes collected at the same location.

Based on FA markers, we are confident that the diet of *L. pugettensis* includes contributions of microbial biomass, but we can only speculate as to why FAs from a microbial pool may have a distinct isotopic composition. Although research on isotopic fractionation of FAs in marine sediments is lacking, there are studies documenting increases in $\delta^{13}C$ values for FAs from algae as microbial degradation progresses in seawater (Sun et al. 2004, Pan et al. 2014). The degree to which a FA pool becomes enriched in ^{13}C over time is dependent on the stage of decomposition, the FAs in question, and whether the environment is oxic or anoxic (Sun et al. 2004). The proposed mechanism by which FA pools become isotopically enriched in ^{13}C relative to the source as a result of microbial degradation is based on a kinetic isotope effect associated with acetyl coenzyme A during FA biosynthesis (DeNiro & Epstein 1977, Monson & Hayes 1982). Assuming there is a kinetic isotope effect associated with the reverse reaction, FAs within a given pool that have isotopically light carbon in the carboxyl group will selectively be subject to decarboxylation first (Sun et al. 2004). As a result, the FA pool that remains would theoretically consist of FAs with elevated ^{13}C in the carboxyl group, and would become isotopically enriched in ^{13}C. We hypothesize that microbes present in deeper sediment layers catabolize 20:5n-3 from phytodetritus and preferentially catabolize 20:5n-3 that contains a higher ratio of ^{12}C. When microbes catabolize isotopically lighter 20:5n-3, they leave behind a pool of 20:5n-3 that is isotopically heavier relative to the original source. *L. pugettensis* would then theoretically consume the microbes and the 20:5n-3 remaining after microbial degradation of phytodetritus as it is feeding, and incorporate this signature into its tissues.

In recent decades, researchers have isolated a wide range of bacteria capable of producing long chain PUFAs, such as 20:5n-3 and 22:6n-3 (e.g. Nichols et al. 1992, Gentile et al. 2003, Shulse & Allen 2011). In contrast to microbial degradation of algal PUFAs, isotopic fractionation during bacterial synthesis of long chain PUFAs tends to result in lower $\delta^{13}C$ values for PUFAs relative to the carbon source (Teece et al. 1999, Fang et al. 2006). The level of long chain PUFA production and the degree to which fractionation occurs can vary depending on environmental conditions such as increases in pressure (Fang et al. 2006). We posit that microbial synthesis of long chain PUFAs is negligible due to the abundance of 20:5n-3 and 22:6n-3 originating from algal blooms in the water column (p-POM), sea ice (i-POM), and potentially microphytobenthos (b-POM). As a result, we hypothesize that fractionation associated with microbial synthesis of PUFAs has little influence on the diets of *L. pugettensis* or other benthic invertebrates living in a shallow and productive shelf environment.

In contrast to *L. pugettensis*, the bacterial FA contributions to *Nephtys* spp. were low, which makes it unlikely that the relatively high $\delta^{13}C$ values for 20:5n-3 in this organism came from a microbially altered phytodetrital 20:5n-3 pool. *Nephtys* spp. is a mobile predator-scavenger (Fauchald & Jumars

1979, Jumars et al. 2015). As such, it would integrate FAs from a diverse set of organisms living in a broader geographic range relative to the other consumers in this study. Based on stable isotope analyses of TOC and nitrogen, *Nephtys* spp. is known to feed at high trophic levels (up to 3.5) (Iken et al. 2010). As we have no evidence to assume trophic fractionation to be >0, we attribute the relatively high $\delta^{13}C$ values in *Nephtys* spp. to i-POM, a FA source in the environment with relatively high $\delta^{13}C$ values compared with other sources (e.g. p-POM and microphytobenthos) (Wang et al. 2014, Oxtoby et al. 2016). Our multisource mixing model estimates for *Nephtys* spp. indicate that the highest FA contributions originated from i-POM (>70%). We hypothesize that *Nephtys* spp. obtains i-POM-derived FAs indirectly via 2 possible mechanisms: it may be feeding most actively after ice algal bloom material is deposited and consumed by its prey; alternatively, it may favor consumption of organisms that selectively assimilate i-POM (Sun et al. 2007).

Marked differences in lipid content between *L. pugettensis* and *Nephtys* spp. may provide further evidence of differences in overall feeding strategy between these taxa. *L. pugettensis* had higher and more variable lipid content relative to *Nephtys* spp.. If we assume that higher lipid content is indicative of lipid accumulation, higher lipid content in the subsurface deposit feeder *L. pugettensis* suggests a response or adaptation to an unpredictable and limited food supply located below surface sediments. Lower lipid content (less reliance on lipid accumulation) in the predator-scavenger *Nephtys* spp. suggests improved access to a more abundant food supply. Analysis of additional replicates and of other benthic invertebrate taxa is necessary to further explore relationships between lipid accumulation, food availability, and feeding strategy in the Arctic benthos.

Future research should aim to advance our understanding of the importance of microbially altered and ice algal derived OM to benthic organisms through more comprehensive sampling and analyses of additional proxies of diet. For example, measurements of IP_{25}, a low-lability branched isoprenoid that is unique to ice algae (Belt & Müller 2013) would help constrain contributions from i-POM (Brown & Belt 2012). Analyses of ATP concentrations could be used to quantify microbial biomass (Mincks et al. 2005) in stratified sediment samples. This may be a source of OM to infaunal organisms, such as *L. pugettensis*, that feed and reside deeper in the sediment.

CONCLUSIONS

In conclusion, assimilation routes for FAs from pelagic, sympagic, and benthic production differ among the common benthic invertebrate taxa from several feeding groups we investigated from the Bering Sea. Evidence from FA profiles, $\delta^{13}C$ values for algal marker FAs, and relative proportions of individual FAs indicated that bivalve taxa were consuming a similar mixture of FAs available in surface sediment irrespective of POM source and feeding strategy. In contrast, *Nephtys* spp. and *L. pugettensis* did not appear to rely on surface sediment b-POM, even indirectly. Our evidence indicated that *Nephtys* spp. consumed a high proportion of biomass deriving from ice algae, whereas *L. pugettensis* appeared to consume microbially altered phytodetrital sources within subsurface sediment horizons, based on high bacterial FA biomarkers and $\delta^{13}C$ values that were outside the range of measured sources. It appears that benthic invertebrates occupy distinct dietary niches that likely result from unique feeding strategies and may mitigate interspecific competition among benthic consumers.

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