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Variation and Assimilation of Arctic Riverine Seston in the Pelagic Food Web of the Mackenzie River Delta and Beaufort Sea Transition Zone

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Abstract On-going shifts in the arctic climate and landscape have the potential to increase terrestrial particulate organic matter (POM) transported to the Mackenzie delta and coastal Beaufort shelf. If increased terrestrial/freshwater material exports to the coastal zone can be assimilated by the pelagic food web, then this represents a new pool of carbon for the regional food web and could result in a shift in the nature of carbon supporting pelagic productivity. Analysis of the $\delta^{13}C$ of POM from the riverine, estuarine, and marine (shelf) zones of the Mackenzie delta shows that the signatures of terrestrial/freshwater carbon does extend onto the shelf, although it diminishes with distance from the Mackenzie River. $\delta^{13}C$ values of calanoid copepods, mysid shrimp, and two species of Amphipods varied depending on their environment (river, estuary, or marine) and local POM $\delta^{13}C$ signature. From this, we conclude that exported terrestrial POM can be a subsidy for portions of both the estuarine and marine pelagic food web. However because the response of consumer $\delta^{13}C$ depended on both species and location, we also conclude that the response to increased riverine POM will be different for estuarine versus marine biota. The implication is that increases in exported terrestrial carbon represent a significant potential shift in coastal pelagic ecosystem structure and function.

Keywords Stable isotopes · River plume dynamics · Coastal food webs · Plankton · Estuary

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Introduction

Large river delta systems are conduits through which large amounts of riverine particulate organic matter (POM) are exported to the coastal marine environment (Walker 1998; Raymond and Bauer 2001a, b). Estimates of bulk carbon flux across the freshwater–marine transition show that only a small portion of POM is lost to sedimentation processes implying that the majority is either respired (Smith and Hollingbaugh 1993) or assimilated by the metazoan food web (Schlunz and Schneider 2000; Dagg et al. 2004; Goni et al. 2005). Thus, any changes in exported riverine POM may represent an important subsidy to metazoan productivity in freshwater–marine ecotones (Schell 1983; Schell et al. 1998; Opsahl et al. 1999; Mitra et al. 2000; Raymond and Bauer 2001a, b).

In river-influenced shelf zones of the Arctic, the composition of riverine POM found in shelf sediments and benthos is a mixture of freshwater bacteria, phytoplankton, and peaty detrital material (Macdonald et al. 1998; Walker 1998; Carmack et al. 2004; Macdonald and Yu 2006; O'Brien et al. 2006). This riverine signature, dominated by terrestrial organic matter, is particularly pronounced in the Mackenzie–Beaufort system where the river transports carbon and nutrients derived from the 1,787,000-km^2 Mackenzie River basin and 12,170 km of river and delta (Rosenberg and Barton 1986; Culp et al. 2005; Goni et al. 2005). Although it is well established that POM exports from river sources are seen in Beaufort shelf sediments and metazoans (Rachold et al. 2000;

Goni et al. 2005; O'Brien et al. 2006), it is less well demonstrated that riverine POM directly influences pelagic food webs (Lowry and Frost 1984; Hoekstra et al. 2002). Testing for such a connection is important to understanding how and where the tremendous amounts of carbon being released from thawing permafrost over the coming decades (Chapin et al. 2005) may subsidize the downstream pelagic food webs of the Beaufort Sea (Chapin et al. 2005; Zimov et al. 2006; Guo et al. 2007).

We wanted to determine whether riverine POM represents a food source for pelagic organisms in the riverine, estuarine, or marine environments. In order to do this, we measured $\delta^{13}C$ and $\delta^{15}N$ of POM and of selected riverine, estuarine, and marine pelagic consumers along a transect across the freshwater–marine transition zone. If riverine exports are preferentially assimilated, then both POM and metazoan $\delta^{13}C$ and $\delta^{15}N$ signatures should reflect the riverine POM signature regardless of where the taxa were collected. This would be evidence of heretofore underappreciated connections between the terrestrial and marine arctic environments and have important implications for whether the warming of the arctic climate will affect coastal marine productivity.

Methods

Site Description

The hierarchical agglomerative clustering of sample sites based on salinity measurements from CTD casts was used to assign the 12 sample sites along a transect from the freshwater portion of the Mackenzie River delta to the marine environment of the inner Beaufort shelf off of Kugmallit Bay during the ice-free period between July 26 and August 3, 2004 to one of the three salinity zones: sites 1–4 were grouped as riverine (0 practical salinity unit (PSU)), sites R5a–R5e fell in the transition zone (5–15 PSU), and sites 7–9 were greater than 20 PSU and are designated as marine (Fig. 1). This transect follows the eastern route through the Mackenzie delta past Tuktoyaktuk (N.W.T.) which exports ~30 % of the freshwater discharge of the river with another ~25 % passing through the western channels to enter Mackenzie Bay, and another 45 % passing around Richards Island (Carmack et al. 2004). The sampled eastern route terminates at a broad, shallow, transverse terminal bar (mean depth ~2 m) that extends more than 10 km offshore and is typical of many arctic delta/estuaries (Carmack et al. 2004; Reimnitz 2002; Macdonald and Yu 2006). Despite the erosion and resuspension of soft sediments by winter storms and pack ice movements, this shallow terminal ramp is a stable and persistent feature that is maintained by riverine POM that arrives during the ice-free period between June and November (Reimnitz 2002; O'Brien et al. 2006). The shallow estuarine zone and accompanying terminal bar form the transition between the riverine zone and the marine environment of the Beaufort shelf zone (Fig. 2).

Sampling, Preservation, and Stable Isotopic Analysis

Three replicate POM samples were collected at a subset of 9 of the 12 sites. The subset of sites was chosen to best represent the riverine, estuarine, and marine salinity zones. At each of these 9 sites, one set of three replicate POM samples was taken from a meter below the surface and a second set of three

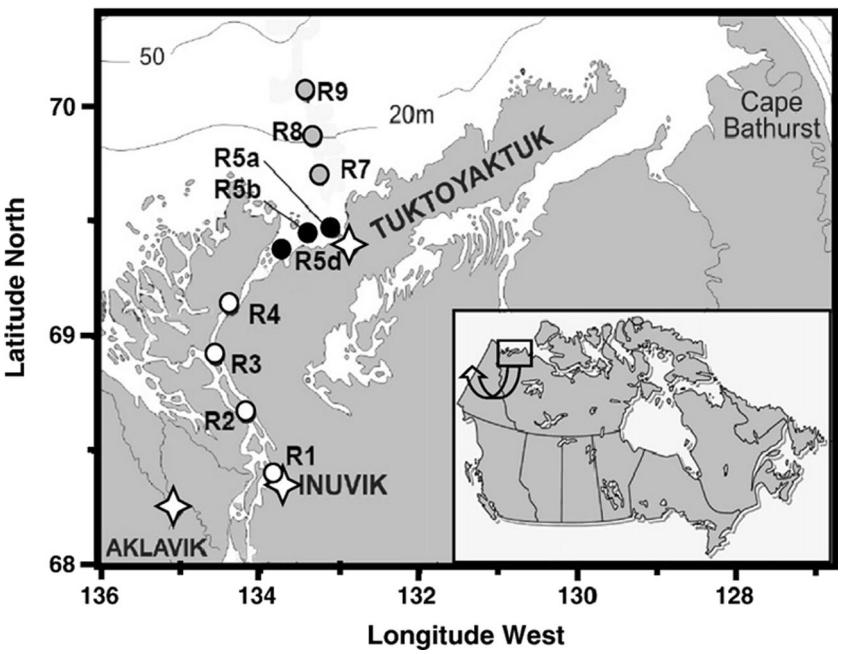

Fig. 1 Sample transect from the Mackenzie River to the Beaufort continental shelf. *Sites R1–R4* are part of the riverine salinity grouping and are represented with *white circles*. *Sites R7–R9*, all with >20 PSU, are considered part of the marine salinity group and are represented with *gray circles*. The salinity at *sites R5a*, *R5b*, and *R5d* varied from 5 to 15 PSU (R5c and e are not shown) and are designated as estuarine and represented with *black circles*

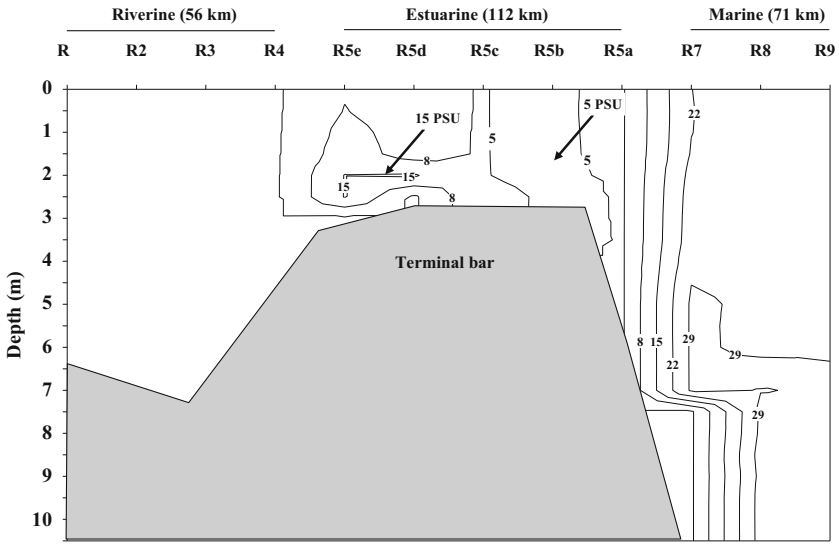

Fig. 2 Schematic representation of the salinity structure of the freshwater–marine transition of the Mackenzie River delta based on 12 CTD casts taken between July 27 and August 3, 2004. *Numbers on the isopleths* refer to salinity in practical salinity units (PSU). The *top axis* shows sample stations and the salinity groupings; however, the distance between *hash marks* is not to scale. *Arrows* indicate anomalous parcels of water mentioned in the text

replicates from 2 to 3 m below the surface using a submersible pump. Sample volumes filtered to collect POM for $\delta^{13}C$ and $\delta^{15}N$ analysis varied from 1 to 20 L depending on the amount of POM present and which of the two mesh sizes (5 μm and 100 μm) were being used. Subsamples of POM for isotopic analysis were pre-filtered through either a 100-μm mesh sieve (referred to as "<100 μm") or a 100-μm mesh sieve plus a 5-μm mesh sieve (referred to as "<5 μm") during pumping. After pre-filtration, the remaining seston was then trapped on precombusted (500 °C, 1 h) 47-mm Whatman GF/F filters using a standard vacuum manifold and stored at −20 °C for laboratory isotopic analysis (three replicates per each site× depth×filter mesh combination for a study total of 108 GF/F filters). Zooplankton was estimated from three replicate horizontal 500-μm mesh net tows collected at roughly the middle of the water column with a specific depth varying with a total depth of each site along with tidal and wind conditions. The presence of variable tidal heights and flows during net deployment means we cannot know the precise depth of a given sample, thus mid-column sample nets were deployed at roughly half the sonar-measured depth (~1–3 m). All zooplankton were kept alive in filtered water for 2–4 h following collection in order to allow for some gut clearance. After the gut clearance interval, either single individuals (for larger fish and insect larvae) or a composite (for copepods) was placed in separate microcentrifuge tubes and frozen at −20 °C for transportation and storage prior to $\delta^{13}C$ and $\delta^{15}N$ analysis. The selection of specific plankton taxa for the analysis was based on a combination of known feeding habits, total number captured (three or more replicates whenever possible), and whether representatives of the same taxa were collected in two or more salinity zones (i.e., freshwater, estuarine, marine).

The ultimate source of organic carbon is the fixation of inorganic carbon via photosynthesis; however, different enzymatic pathways involved in photosynthesis (e.g., terrestrial versus aquatic, marine versus freshwater) result in different carbon ($\delta^{13}C$) signatures. These source-specific $\delta^{13}C$ signatures are preserved as the carbon passes through the food web, creating a signature of $\delta^{13}C$ source that an individual consumed (Onstad et al. 2000). In coastal systems, $\delta^{13}C$ values can range from −32‰ in POM to −12‰ in sea grasses, with emergent aquatic macrophytes and marine phytoplankton falling in the −22 to −19‰ range (Raymond and Bauer 2001a, b). The presence carbonates on the outer surfaces of animals can lead to enrichment in the $\delta^{13}C$ signature; therefore, all animals were acidified with 10 % 12 N HCl solution then rinsed with distilled water and oven-dried at 40 °C for 24 h (Bunn et al. 1995; Lorrain et al. 2003). The trophic position of an organism can significantly affect $\delta^{13}C$ signatures, especially in the case of a consumer who exploits a particular food source; thus, $\delta^{13}C$ data needs to be corrected for trophic level. Trophic position can be inferred from another stable isotope, $\delta^{15}N$, which increases with increasing number of links between carbon source and the consumer in question. Primary consumers that assimilate bacteria and phytoplankton and other seston generally range from 0 to 3‰, while secondary and tertiary consumers can often range from 10 to 15‰ depending on how many levels of consumers are found in a particular ecosystem. Because acidification is known to cause enrichment in $\delta^{15}N$ values, a separate subsample, which was not acidified, was used for $\delta^{15}N$ analysis (Pinnegar and Polunin 1999). Carbonates were removed from the filtered POM by fuming samples with 36 % HCl (Yamamuro and Kayanne 1995; Kendall et al. 2001). This method was selected because it showed no loss of organic C or N. Isotopic analyses were carried out by the Commission Géologique du Canada using an Isotope Ratio Mass Spectrometer (Fisons Instruments, model VG Prism Isotech) coupled with an Elemental Analyzer (NA 2500 series).

Analysis

The mean $\delta^{13}C$ and $\delta^{15}N$ signatures of three replicate POM surface samples and a separate three replicates of mid-water column samples at each site were compared with a three-factor multivariate analysis of variance (MANOVA) using R software (version 2.15.1) and procedures (Crawley 2012, p. 487) to determine whether the mean values varied among salinity categories. Subsequently, $\delta^{13}C$ and $\delta^{15}N$ differed from each other in their responses; thus, a separate three-factor ANOVA for each isotope was also conducted. The independent variables used as factors in the model are salinity group, size fraction (100 or <5 μm), and sample depth. These were used as both the main effects and interactions with an alpha of 0.05 as the significance threshold. To make the ultimate interpretation of whether the different POM types were assimilated differentially by pelagic animals, mean $\delta^{13}C$ and $\delta^{15}N$ bi-plots of the most widely distributed planktonic metazoans (collected from at least two of the three salinity zones) were plotted using the mean and standard error of the POM from each respective salinity zone.

Results

CTD casts show that the 100+ km estuarine transition zone is centered over shallow (2–3 m) terminal ramp and extending to where depths descend to 8–10 m on to the Beaufort shelf (Fig. 2). Two important aspects of the salinity structure of the transition zone were seen. The first is a small parcel of higher salinity water enclosed by the 15-PSU isopleths over the upstream end of the terminal ramp (Fig. 2). The second is a 5-PSU parcel of water located at the seaward edge of the shallow ramp. Both of these water parcels are likely the result of incomplete tidal mixing and/or wind-driven currents. Once formed, these ephemeral anomalies may require multiple tidal cycles to dissipate completely in a micro-tidal system like Mackenzie (Tilburg and Gravine 2003; Yankovsky 2004).

MANOVA of POM $\delta^{13}C$ and $\delta^{15}N$ values revealed significant main effects for $\delta^{13}C$ and the interaction, but not for the $\delta^{15}N$ main effect (Table 1). Following the procedures of Crawley (2012, p.487), we produced single-dependant factor ANOVAs that show the $\delta^{13}C$ difference between size fraction (<100 versus <5 μm) and among salinity group (river, estuarine, and marine), although the $\delta^{13}C$ and $\delta^{15}N$ interaction effect is influenced by sample depth (surface versus mid-column) alone (Table 2). However, the two isotopes did not vary in the same manner; $\delta^{13}C$ site values decreased as distance downstream increased, while $\delta^{15}N$ values showed comparatively little trend (Fig. 3). When these results are considered with graphs of the mean and standard error of the signatures (Fig. 3a–d), we can make three conclusions. Firstly, there is the aforementioned declining trend in $\delta^{13}C$ seston with distance downstream, but the values of <100 μm seston increase in the marine zone (Fig. 3b). Additionally, the means and standard errors show that there is no difference between surface and mid-column values for seston <5 um (Fig. 3a). In contrast, signatures of seston <100 μm from surface and mid-column depths begin to diverge in the estuarine zone and continue to do so in the marine zone, while this is not true for seston <5 μm (Fig. 3b). However, the significant third-order interaction also indicates that the spatial response of <100 μm fraction differed from the <5 μm fraction by sample depth. Specifically, that the response of the <5 and <100 μm size fraction diverge in the estuarine and marine zones. When the $\delta^{13}C$ and $\delta^{15}N$ POM values are plotted together (Fig. 4), the strongest differentiation is between the marine and riverine end members of the gradient with the estuarine being intermediate. Although both POM size fractions generally cluster tightly together along both axes, there are two anomalies worth noting: both marine <100 μm and estuarine <100 μm are considerably more $\delta^{13}C$ enriched than the other samples from their respective salinity categories.

Table 1 Three-factor multiple analysis of variance (MANOVA) of seston $\delta^{13}C$ and $\delta^{15}N$ isotope values collected from the Mackenzie River July 27–August 4, 2004 using salinity group, size fraction (100 μm or <5 μm), and sample depth as main-effects variables

	df	Wilks	Approx *F*	Num *df*	Denom *df*	Prob>*F*
$\delta^{13}C$	1	0.642	5.570	3	30	0.004
$\delta^{15}N$	1	0.996	0.041	3	30	0.989
$\delta^{13}C$:$\delta^{15}N$	1	0.753	3.282	3	30	0.034
Residuals	32					

Table 2 Separate one-factor analysis of variance (ANOVA) of the $\delta^{13}C$ and $\delta^{15}N$ isotope signature of the seston in response to salinity group, size fraction, and sample depth. Samples collected from the Mackenzie River July 27–August 4, 2004

Response to	Factor	*df*	SS	MS	*F*	Prob>*F*
Depth	$\delta^{13}C$	1	0.003	0.003	0.013	0.910
	$\delta^{15}N$	1	0.004	0.004	0.019	0.891
	$\delta^{13}C$:$\delta^{15}N$	1	2.044	2.044	9.413	0.004
	Residuals	32	6.949	0.217		
Size fraction	$\delta^{13}C$	1	1.309	1.309	5.570	0.025
	$\delta^{15}N$	1	0.021	0.021	0.090	0.767
	$\delta^{13}C$:$\delta^{15}N$	1	0.152	0.152	0.647	0.427
	Residuals	32	7.518	0.235		
Salinity group	$\delta^{13}C$	1	4.657	4.657	8.494	0.006
	$\delta^{15}N$	1	0.019	0.019	0.035	0.853
	$\delta^{13}C$:$\delta^{15}N$	1	0.000	0.000	0.001	0.983
	Residuals	32	17.546	0.548		

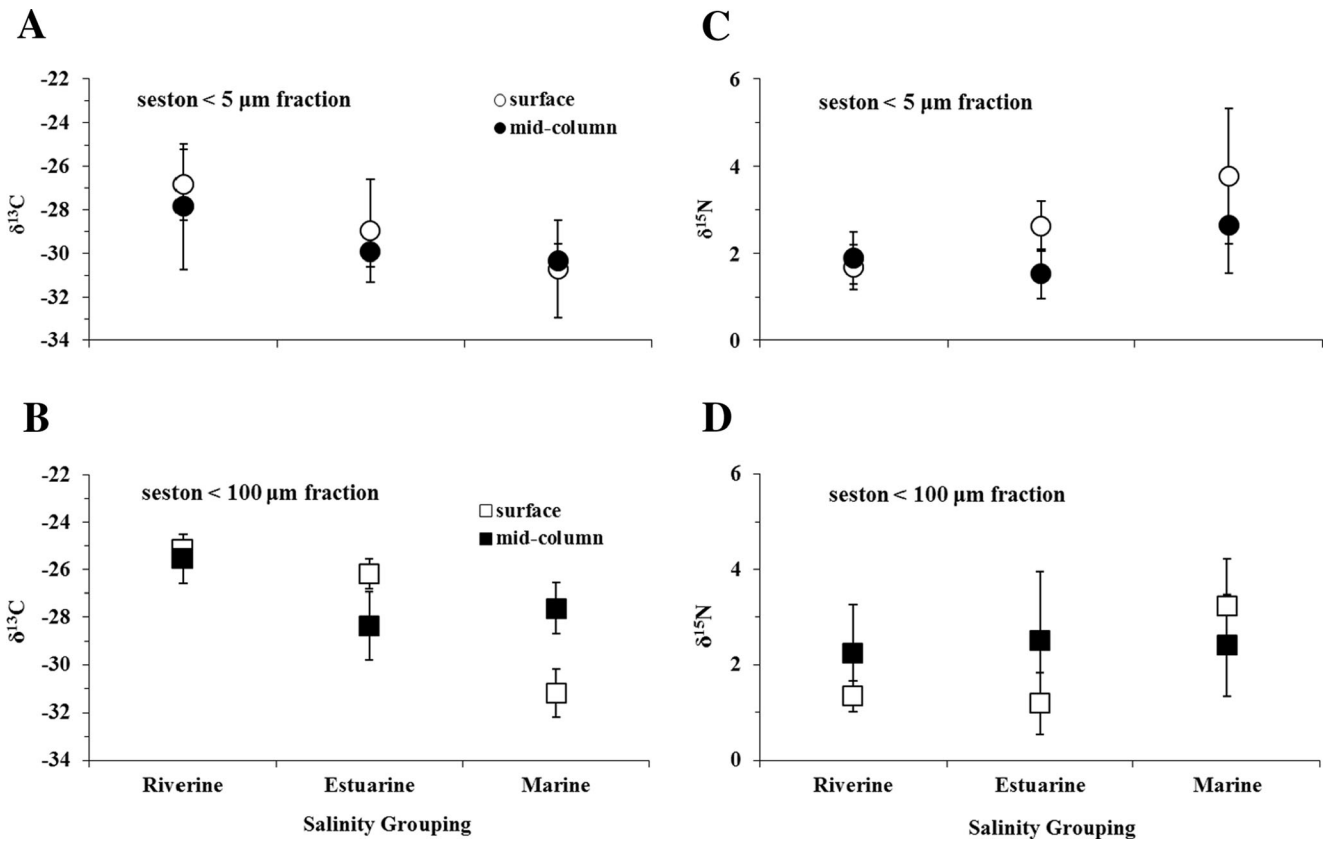

Fig. 3 Isotopic signature (mean±standard error) of different types of sestonic POM as a function of salinity grouping: **a** δ^{13}C isotopic signature of the <5 µm seston, **b** δ^{13}C isotopic signature of the <100 µm seston, **c** δ^{15}N isotopic signature of the <5 µm seston, and **d** δ^{15}N isotopic signature of the <100 µm seston

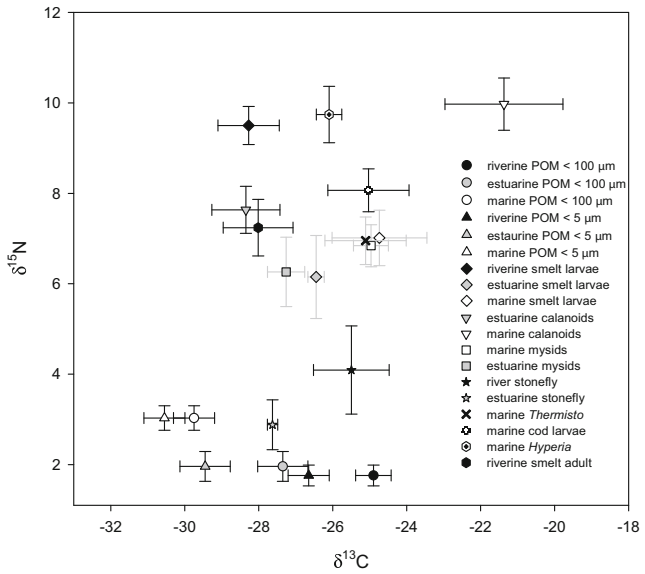

Fig. 4 Bi-plot of δ^{13}C and δ^{15}N isotopic signatures (mean±standard error) of a subset of the pelagic and two size classes of POM collected across the freshwater–marine transition of the Mackenzie River delta between July 27 and August 3, 2004. *Symbols* indicate either different taxa or different types of sestonic POM, while color patterns indicate the salinity zone from which the sample was collected. Some *error bars* are grayed to make interpretation easier

Comparing the δ^{13}C and δ^{15}N signatures of the metazoans collected from two or more salinity zones shows that the spatial pattern for consumer does not always mirror that of local POM (Fig. 4). In fact, all the consumers collected were more closely aligned with the riverine and estuarine POM δ^{13}C signatures and thus appear to be assimilating little of either of the size fractions of marine POM. When stoneflies, a freshwater taxon, collected from the river and estuary sites are compared, their trophic position (δ^{15}N) overlaps inferring no change in feeding habits despite the difference in food resource (δ^{13}C) signatures between the two salinity zones. Furthermore, the δ^{13}C signature of both estuarine and riverine stoneflies overlaps the range of POM values of the riverine zone, implying the main carbon source is riverine (Fig. 4). The trophic signature of both Mysid decapods and calanoid copepods from the marine salinity zone overlapped, though there is also overlap when Mysids and calanoids from the estuarine zone are contrasted with those from the marine zone, though the amount is much less for the latter (Fig. 4). However, when these two taxa are compared with POM, those metazoans from the marine zone are more closely aligned with δ^{13}C values for riverine POM than marine. The representatives of the same two taxa sampled from the estuarine zone fell closer to values found where riverine and estuarine POM

ranges overlap. Planktivorous smelt larvae were collected in all three zones and were also the highest trophic level sampled based on δ^{15}N values. As with the invertebrates, there was strong divergence in δ^{13}C values between smelt from the marine zone and those from the estuarine and riverine zones, which were equivalents. However, the δ^{13}C enrichment and variability for the marine samples of this highly mobile vertebrate planktivore was much stronger than that of either the marine POM or the marine invertebrates. From a subset of taxa that were only collected in one of the three salinity zones, there is further evidence of selective carbon food source choice and assimilation. For example, two types of marine amphipods (*Thermisto* and *Hyperia*) and several cod larvae were collected in the marine zone alone and were δ^{13}C enriched to a higher level than that of either estuarine or marine POM, suggesting that they too are assimilating riverine-exported carbon even though they live outside the obvious influence of the freshwater plume (Table 3, Fig. 4). However, from their δ^{15}N values, these three are all inferred to be predators, and their δ^{13}C values also closely match that of a common prey item, calanoid copepods. Thus, their assimilation of riverine POM is likely due to this food web connection instead of the direct ingestion of freshwater POM (Table 3, Fig. 4).

Discussion

In arctic seas, the sedimentation of the POM exported by rivers represents a major connection between the terrestrial/continental and marine environments (Schell 1983; Walker 1998; Kattner et al. 1999; Dagg et al. 2004). In the case of the Mackenzie delta–Beaufort shelf system, previous research has shown that benthic productivity is strongly influenced by the Mackenzie River plume (Peterson and Curtis 1980; Renaud et al. 2007), but whether this subsidy is also important to pelagic productivity is less well understood. Previous work showed that there is both a discrete estuarine zooplankton community feeding on POM colonized by bacteria and a separate offshore zooplankton community that relies on marine diatoms (Parsons et al. 1988, 1989), implying a spatial disconnect in the carbon they assimilate. However, δ^{13}C data we present extends this idea. We show instead that organisms from the riverine, estuarine, and marine communities have a single dominant carbon source, riverine POM. However, these two data sets may not be contradictory as they might seem: the marine organisms of the Parsons et al. (1988, 1989) studies were actually collected much further offshore, >71° N, whereas our sampling transect ended closer to 70° N. At first glance, there is a stronger separation between riverine and marine POM and organism signatures in Parson et al. (1989) data than ours, particularly on the δ^{15}N axis. However, given that this data was collected further north in the Arctic Ocean, bacterial enrichment of POM δ^{15}N is much more likely. In fact, when the difference in distance offshore sampling location is considered, Parson et al.'s (1989) δ^{13}C data, particularly the marine amphipod values, tends to suggest that riverine POM is still being assimilated in the marine food web even at a great distance from the Mackenzie delta. Based on the evidence for the direct pelagic assimilation of riverine POM we and Parsons et al. (1989) both demonstrate, we suggest that changes in the amount of POM exported by rivers are likely producing a concurrent increase in pelagic productivity across the Beaufort coastal shelf zone.

Evidence shows that secondary production in large rivers and estuaries is disproportionally driven by a small pool of local autochthonous primary production (Deegan and Garritt 1997; Thorp and Delong 2002; Martineau et al. 2004; Sobczak et al. 2005; Delong and Thorp 2006). In a large river like the Mackenzie, transport of this small pool of local autochthonous carbon through the estuary and into the coastal zone has the potential to be a sizeable trophic subsidy. If there is also deferential assimilation of these riverine exports in the downstream salinity zones, then the same δ^{13}C signature seen in the riverine POM and organisms should also be found in the estuarine and marine zones, which is in fact what our results show. For example, the δ^{13}C signature of the marine calanoids and Mysids overlap that of both riverine stoneflies and POM <100. Our data indicate increasingly negative δ^{13}C values as the more δ^{13}C depleted estuarine and marine POM mixes with and dilutes the riverine POM (MacDonald et al. 1998; Dagg et al. 2004; Dunton et al. 2006). However, unlike the downstream progression of POM, the metazoan consumer δ^{13}C values did not decline. For example, the marine calanoid and Mysid δ^{13}C signatures track riverine POM more closely than marine POM, and subsequently, the planktivorous larval smelt sampled off shore had much more elevated δ^{13}C values than that of the marine and estuarine POM and potential prey items. Thus, our results confirm that POM sampled in the marine zone is not different from that from the riverine and estuarine zones. In addition, our results show that there is the widespread preferential assimilation of riverine POM among estuarine and marine consumers, including both fish (smelt

Table 3 δ^{13}C/δ^{15}N isotope signatures for metazoan consumers whose collection was restricted to only one of the three salinity zones (Fig. 2) of the Mackenzie delta transition zone

Salinity zone	Taxa	Number	δ^{15}N		δ^{13}C	
			Mean	SE	Mean	SE
Riverine	Smelt (adult)	4	7.2	0.6	−28.0	0.9
	Mayfly (larvae)	4	4.6	1.0	−29.0	1.8
Marine	*Hyperia*	3	9.7	0.6	−26.1	0.3
	Cod (larvae)	11	8.1	0.5	−25.0	1.1
	Themisto	13	7.0	0.5	−25.1	1.1

and cod larvae) and plankton (Mysids and calanoids). Furthermore, even the marine amphipods *Hyperia* and *Thermisto* had signatures squarely in the riverine range and no overlap with either estuarine or marine POM values. Thus, we conclude that selective uptake of river exports by estuarine and marine organisms creates a significant link between riverine transported POM, and coastal food webs and secondary production in the Mackenzie-Beaufort system.

The Arctic Ocean has large coastal shelves that are strongly influenced by riverine outflows, subsequently the materials that these rivers export (Walker 1998; Dunton et al. 2006; Macdonald and Yu 2006). Our data show that in the estuarine and marine zones, pelagic consumers assimilate autochthonous POM exported by the Mackenzie River, providing a significant subsidy to consumers at higher trophic levels. Any changes in the amount of these subsidies, such as those resulting from on-going regional climate shifts (Rouse et al. 1997; Freeman et al. 2004; Piepenburg 2005; Lawrence and Slater 2005; Zimov et al. 2006; Guo et al. 2007), have the potential to change foodwebs across multiple trophic levels (von Biela et al. 2011). Major potential sources of increased riverine POM comes from thermokarst erosion, fluvial erosion, and other types of mass movements of soil organic matter previously locked in the permafrost across the Mackenzie Basin and the Arctic (Baker 1979; Woo and McCann 1994, Gou et al. 2007, and Jolivel and Allard 2013). These land surface processes occur when landslides or destabilized banks that were formerly frozen and inert thaw or are destabilized and exposed (Jolivel and Allard 2013). Numerous studies have documented an accelerating rate of destabilization erosion in many parts of the Arctic, implying that the delivery of POM to rivers and subsequently the coastal zone is also accelerating. In the case of the Mackenzie–Beaufort system, riverine POM input is known to be greater than POM from coastal erosion processes (Rachold et al. 2000), meaning that any climate-related changes in the type of POM exported by the Mackenzie is likely to constitute a significant potential subsidy for marine metazoans (Dunton et al. 2006). By establishing that a link between the climate/landscape dynamics, riverine POM, and marine pelagic productivity, we can begin to better frame questions about complex influence of climate on ecological and food web processes of the coastal Arctic seas (Woo and McCann 1994; Steele 1998; Hobbie 2000).

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