Evidence for the assimilation of ancient glacier organic carbon in a proglacial stream food web

Jason B. Fellman,*[1] Eran Hood,[1] Peter A. Raymond,[2] John Hudson,[3] Maura Bozeman,[2] Mayumi Arimitsu[4]

[1]Environmental Science Program, University of Alaska Southeast, Juneau, Alaska
[2]School of Forestry and Environmental Sciences, Yale University, New Haven, Connecticut
[3]Aquatics Alaska, Juneau, Alaska
[4]U.S. Geological Survey, Alaska Science Center, Juneau, Alaska

Abstract

We used natural abundance δ^{13}C, δ^{15}N, and Δ^{14}C to compare trophic linkages between potential carbon sources (leaf litter, epilithic biofilm, and particulate organic matter) and consumers (aquatic macroinvertebrates and fish) in a nonglacial stream and two reaches of the heavily glaciated Herbert River. We tested the hypothesis that proglacial stream food webs are sustained by organic carbon released from glacial ecosystems. Carbon sources and consumers in the nonglacial stream had carbon isotope values that ranged from -30% to -25% for δ^{13}C and from -14% to 53% for Δ^{14}C reflecting a food web sustained mainly on contemporary primary production. In contrast, biofilm in the two glacial stream sites was highly Δ^{14}C-depleted (-215% to 175%) relative to the nonglacial stream consistent with the assimilation of ancient glacier organic carbon. IsoSource modeling showed that in upper Herbert River, macroinvertebrates (Δ^{14}C $= -171\%$ to 22%) and juvenile salmonids (Δ^{14}C $= -102\%$ to 17%) reflected a feeding history of both biofilm ($\sim 56\%$) and leaf litter ($\sim 40\%$). We estimate that in upper Herbert River on average 36% of the carbon incorporated into consumer biomass is derived from the glacier ecosystem. Thus, ^{14}C-depleted glacial organic carbon was likely transferred to higher trophic levels through a feeding history of bacterial uptake of dissolved organic carbon and subsequent consumption of ^{14}C-depleted biofilm by invertebrates and ultimately fish. Our findings show that the metazoan food web is sustained in part by glacial organic carbon such that future changes in glacial runoff could influence the stability and trophic structure of proglacial aquatic ecosystems.

Climate warming will likely alter the physical and chemical characteristics of stream ecosystems across a wide range of biomes. Understanding how shifts in physicochemical drivers will alter the structure and function of stream ecosystems is a key challenge facing ecologists. In high-latitude and high-elevation ecosystems, changes in glacier extent and runoff are expected to be primary drivers of change in stream ecosystems (Moore et al. 2009). Glaciers, which currently cover $\sim 11\%$ of Earth's surface, are losing mass across much of the globe (Gardner et al. 2013). With glacier mass loss expected to continue and increase in most regions of the world (Radic and Hock 2011), the ongoing loss of ice could have considerable hydrological consequences (e.g., water resources, Laghari 2013) and alter watershed land-cover, leading to changes in biogeochemistry (Hood and Scott 2008), biodiversity (Milner and Petts 1994; Jacobsen et al. 2012), and food web structure in proglacial streams (Zah et al. 2001).

Glacial runoff typically has low concentrations of dissolved organic carbon (DOC) that is enriched in aliphatic material compared with the aromatic DOC derived from vascular plants that commonly dominates nonglacial rivers (Spencer et al. 2008; Bhatia et al. 2010). Glacier-derived DOC is also old (typically 2000-5000 years B.P., Hood et al. 2009; Singer et al. 2012; Bhatia et al. 2013), but surprisingly bioavailable to aquatic microbes over relatively short time scales. For example, laboratory bioassays of glacier ice and meltwater have found that, on average, more than 50% of glacier DOC was bioavailable to aquatic microbes (Hood et al. 2009; Singer et al. 2012), which is noticeably higher than DOC lability in temperate U.S. Rivers (Volk et al. 1997; Kaplan et al. 2006). These lability studies provide compelling evidence that glacier DOC entering proglacial streams and coastal marine ecosystems will likely stimulate heterotrophic activity. In support, a glacial foreland food web study in southern Norway showed that terrestrial spiders and beetles were feeding on aquatic Chironomid midges that were

*Correspondence: jbfellman@uas.alaska.edu

consuming ancient organic C released from the glacial eco-system (Hagvar and Ohlson 2013). However, whether the incorporation of ancient glacial organic C into proglacial stream food webs is a widespread phenomenon remains largely unknown because the importance of glacial DOC to consumers (i.e., invertebrates and fish) relative to other sources of streamwater DOC is not well quantified.

Stable isotopes of C (δ^{13}C) and N (δ^{15}N) have been the foundation of our evolving understanding of aquatic food webs because these can be good indicators of food source and trophic level (Vander Zanden and Rasmussen 2001; Finlay et al. 2002; Post 2002). However, isotopic overlap of C sources as well as high variability among stream habitats (e.g., riffle/pool, open/shaded) can still make identifying the key basal C sources for metazoa problematic in some streams (Finlay et al. 1999; Vander Zanden and Rasmussen 2001; Finlay 2004). Alternatively, the combined use of δ^{13}C and natural abundance radiocarbon (Δ^{14}C) is a promising approach for tracking noncontemporary C incorporation into aquatic food webs because Δ^{14}C values do not vary among local habitats and are not influenced by isotopic fractionation, as is the case for δ^{13}C (McCallister et al. 2004; Caraco et al. 2010; Ishikawa et al. 2012). This multi-isotope approach is particularly appropriate for tracking the incorporation of glacier organic C into the metazoan food web because of the unique isotopic signature of glacier-derived DOC, which is typically ^{13}C-enriched and ^{14}C-depleted relative to other watershed sources (Hood et al. 2009).

Coastal Mountain glaciers of southeast Alaska are currently experiencing some of highest rates of mass loss on Earth (Larsen et al. 2007; Berthier et al. 2010). The resulting changes in the timing and magnitude of runoff have the potential to influence stream ecosystems, including food web structure, by altering biogeochemical inputs to streams (Hood and Scott 2008) in a region where many proglacial streams currently provide rearing habitat for juvenile Pacific salmon. Here, we combine δ^{13}C, δ^{15}N, and natural abundance Δ^{14}C to compare trophic linkages between potential producers, aquatic macro-invertebrates, and juvenile salmonids in two reaches of the heavily glaciated Herbert River as well as a contrasting non-glacial stream. We tested the hypothesis that proglacial stream food webs are sustained by ^{14}C-depleted yet bioavailable organic C released from glacial ecosystems. Moreover, our study design allowed us to evaluate whether food web structure would shift support from mainly old organic C to that of one sustained by contemporary primary production. Our findings provide insight into the role of glaciers as drivers of ecosystem C cycling as well as how climatically driven changes in glacier volume may alter the stability and trophic structure of proglacial stream ecosystems.

Methods
Site description
Food web samples were collected from the glaciated Herbert River watershed, located near Juneau in coastal southeast Alaska (Fig. 1). The study area is part of the coastal temperate rainforest that extends along the coastal margin of the Pacific Northwest of the United States and British Columbia through the Gulf of Alaska. Juneau has a cool, maritime climate and persistent cloud cover with a mean annual temperature of 4.7°C and mean annual precipitation of 1400 mm at sea level. Most of this precipitation falls as rain in the autumn or as snow at upper elevations during the winter. The region has experienced numerous glacial epochs that have sculpted the Coast Mountains leaving heavily incised watersheds with steep slopes but also extensive lowlands containing water-logged peatlands and coniferous forest.

The Herbert River watershed (49% watershed glacier coverage) encompasses an area of 152 km^2 and contains a major outlet glacier (Herbert Glacier) from the 3800 km^2 Juneau Icefield. Watershed geology is mainly schistose bedrock that consists primarily of meta volcanic basalts and meta clastic sediments of the Taku Terrane. The upper Herbert River site is located $\sim$ 1 km downstream of the glacier terminus in a large floodplain ($\sim$ 0.25 km^2) that is dominated by unstable gravel, cobble, and glacial silt with sporadic colonizing plants. The floodplain is low gradient ($<$ 5%) and can be completely flooded during high flow events, but numerous side channels that are connected to the main channel exist during periods of lower flow. Side channels are generally shallow, contain more stable substrate and have lower flow than the main channel, thus moderating the harsh physical conditions that typically prevent extensive epilithic biofilm from developing in the main channel. The floodplain is ringed by a developing deciduous forest dominated by *Alnus* spp., *Salix* spp., and *Populus trichocarpa*.

The lower Herbert River site is located $\sim$ 8 km downstream of the upper site, near the watershed outlet to the intercoastal marine waters (Fig. 1). The lower reaches of the river contain an older landscape of mixed coniferous forest (*Picea sitchensis* and *Tsuga heterophylla*) and small areas of wetland. There are few braided side channels but extensive parafluvial gravel bars and abundant log jams create favorable habitat for aquatic invertebrates and juvenile salmonids. Abandoned side channels and point gravel bars at or above the sampling site contain a developing deciduous forest of *Alnus* spp., and *Salix* spp. that likely contribute allochthonous organic matter to the river. The low order, nonglacial stream site drains into Herbert River and contains similar dominant vegetation to the upper Herbert River site. This recently formed stream ranges in width from 2 m to 3 m and has sediments dominated by gravels and large cobbles. The stream channel was characterized by a sequence of riffles or small waterfalls and small pools. A thick riparian forest of mainly deciduous trees (*Alnus* spp. and *Salix* spp.) provides partial shading of the channel and abundant litterfall to the stream. All three stream sites contain Coho salmon (*Oncorhynchus kisutch*) and Dolly Vardon (*Salvelinus malma*).
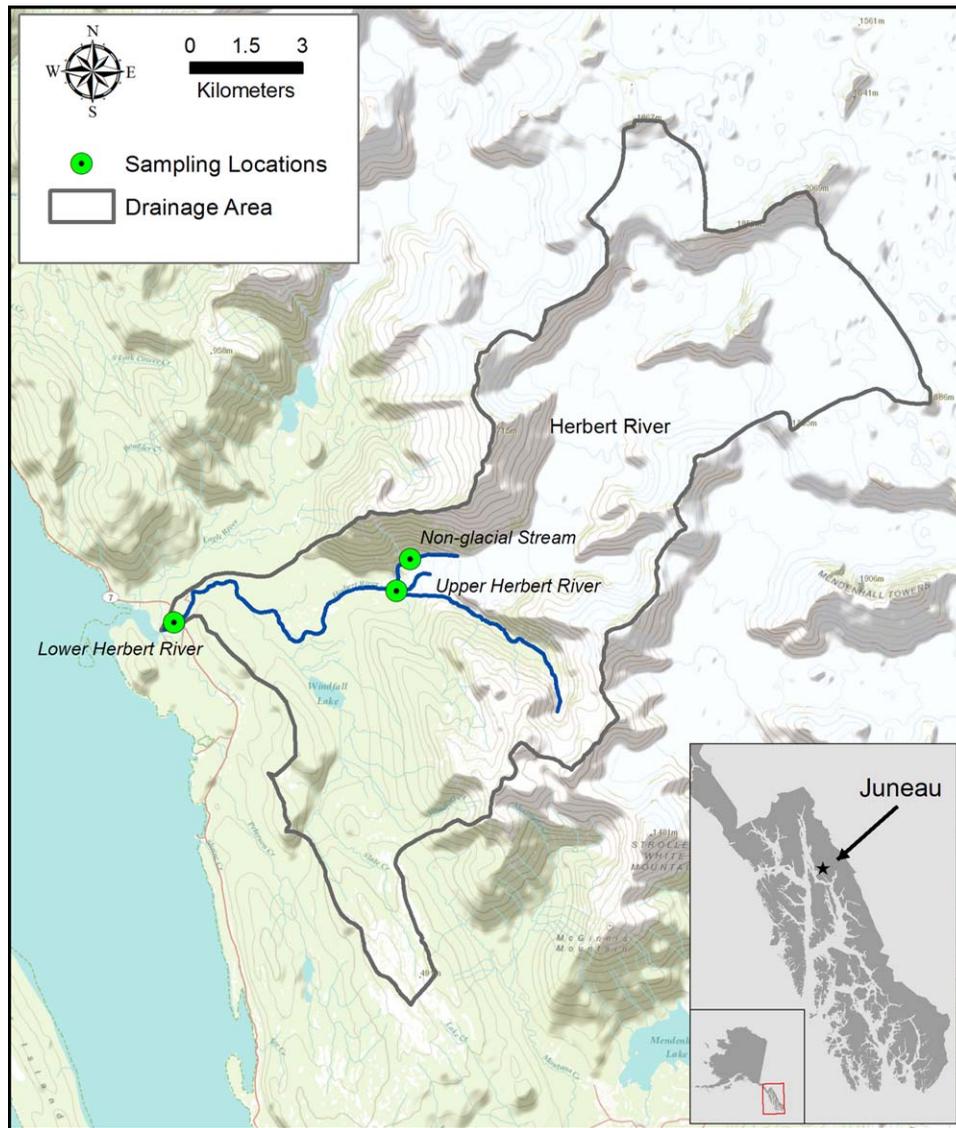
Fig. 1. Map of the Herbert River watershed and three sampling sites located $\sim$ 30 km north of the city center of Juneau, Alaska.

Sample collection

Food web sampling at the three sites occurred over a four-day period in the first week of August 2012. This time period was chosen to coincide with the typical seasonal peak in glacier runoff (Fellman et al. 2014). Given that seasonal changes in the magnitude of glacial runoff are likely to influence macroinvertebrate diversity and abundance and the main C source supporting stream metazoa (Robinson et al. 2001; Burgherr et al. 2002), our findings are likely representative of food web dynamics only at the height of the glacial runoff period. Sources and consumers (fish and macroinvertebrates) were collected from at least two locations within each site to encompass the range of available habitats and ensure that samples were representative of the biota

occurring at each site. For sources, samples were composited to yield two samples per site. In the upper Herbert River site, side channels in the extensive floodplain that receive surface flow directly from the mainstem were sampled rather than the main channel itself.

The three potential organic C sources collected from each site were epilithic biofilm, leaf litter from in-stream leaf packs, and particulate organic matter (POM). For each C source, two samples were collected for $\delta^{15}N$ and $\delta^{13}C$ analysis but only one sample was analyzed for $\Delta^{14}C$. Epilithic biofilm was collected by scraping the entire surface of submerged rocks with visible organic material using a scalpel. Biofilm was collected in a beaker filter with Milli-Q water and filtered onto a precombusted quartz filter. The

POM was collected by field-filtering streamwater (sampled by disturbing stream sediments and collecting the water immediately downstream) through a precombusted quartz filter (as much water that could pass through the filter). In addition, benthic algae was collected from a small patch of algal growth in the upper Herbert River site (the only site with visible benthic algal growth) by scraping algae from rocks into a beaker filled with streamwater and allowed to settle. A 100 mL aliquot was then drawn off the top and filtered onto a precombusted quartz filter. Our algal sample likely contains some terrestrial material, although it is estimated to be less than 30% by weight (Rasmussen 2010).

Benthic macroinvertebrates were collected at each site by physically disturbing sediments upstream of a 500 μm mesh D-net. Three macroinvertebrate taxa were live picked from samples and stored in separate glass vials filled with streamwater: *Baetis* (Ephemeroptera: Baetidae), *Zapada* (Plecoptera: Nemouridae), and Chironomid midges (Diptera: Chironomidae). Multiple individuals of the same taxa were collected and composited for each site to ensure sufficient biomass for isotope analysis. These three taxa were selected because they were the most common macroinvertebrates found at each of the three sites and are also common in glacial and nonglacial streams in the region (Wipfli et al. 1998; Chaloner et al. 2002; Wesener et al. 2011). Chironomid midges and *Baetis* are considered biofilm grazers and *Zapada* a shredder (Merritt et al. 2008). Three juvenile salmonids, either Coho salmon or Dolly Varden, were collected from each site using minnow traps baited with salmon eggs. The fish, which represents higher order, generalist predators, ranged in size from 4 cm to 7 cm across the three sites.

To assist in the interpretation of the C sources incorporated into epilithic biofilm, one sample of DOC and dissolved inorganic carbon (DIC) were collected from each site and analyzed for $\delta^{13}C$ and $\Delta^{14}C$. Streamwater for DOC was field-filtered through a precleaned Whatman Polycap 36TC filter (0.20 μm) and stored in acid-washed polycarbonate bottles. For DIC, filtered water was stored in precombusted amber glass bottles with zero headspace and stabilized with mercuric chloride.

Laboratory procedures and isotope analyses

All samples for isotope analyses were returned to the laboratory the same day as collected and processed immediately. Leaves collected from in-stream leaf packs were lightly rinsed with Milli-Q water and dried in an oven for 24 h, ground in a coffee grinder to a fine powder, and stored in precombusted (450°C for 4 h) glass vials. Quartz filters for biofilm, POM, and benthic algae (upper Herbert River only) analyses were oven-dried at 50°C for 48 h and stored in precombusted foil packages. Live aquatic macroinvertebrates collected in glass vials were stored with streamwater overnight to purge stomach contents. Invertebrates were next rinsed with Milli-Q water and placed in four-milliliter

precombusted glass vials. Samples were dried whole at 50°C for 48 h and hand ground in the glass vials (yield one composite sample per invertebrate taxa) using a precombusted glass stirring rod. Dorsal muscle tissue samples from fish were excised with a scalpel and dried at 50°C for at least 48 h before being transferred to four-milliliter precombusted glass vials and hand ground with a glass stirring rod.

The $\delta^{15}N$ and $\delta^{13}C$ analyses of stream sources and consumers were performed at the UC Davis Stable Isotope Facility by continuous-flow Isotope Ratio Mass Spectrometry. Samples were initially treated to remove inorganic C by a repeated Sulfurous acid addition. Replicate analyses of reference samples yielded standard deviations of $< 0.1‰$ for $\delta^{13}C$ and $< 0.2‰$ for $\delta^{15}N$. The $\delta^{13}C$ of DOC ($\delta^{13}C$-DOC) and DIC ($\delta^{13}C$-DIC) were analyzed on a O.I. Analytical Model 1010 TOC Analyzer (OI Analytical, College Station, Texas) interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon, Cheshire, United Kingdom). The $\Delta^{14}C$ for all samples was measured as described in Raymond and Bauer (2001). Briefly, following inorganic C removal and sample oxidation, the evolved CO_2 was collected cryogenically and purified on a vacuum extraction line. $\Delta^{14}C$ analysis of purified CO_2 was performed by accelerator mass spectrometry (AMS) at the National Ocean Sciences AMS at Woods Hole Oceanographic Institution. All $\Delta^{14}C$ values were corrected for sample $\delta^{13}C$. Isotope ratios are presented using delta (δ) notation as:

$$\delta^{15}N, \delta^{13}C, \text{ or } \Delta^{14}C = [(R_{sample} - R_{standard}) - 1] \times 1000$$

where $R = {}^{15}N/{}^{14}N, {}^{13}C/{}^{12}C, \text{ or } {}^{14}C/{}^{12}C$.

Isotope food source models

The relative contribution of different sources of organic matter (in-stream leaf litter, biofilm, and POM) to invertebrate and fish diets was assessed using a three isotope ($\delta^{15}N$, $\delta^{13}C$, and $\Delta^{14}C$), IsoSource model (Phillips and Gregg 2003). The IsoSource model, which solves iteratively for possible food source combinations, is well-tested and is commonly used in aquatic food web studies (e.g., Caraco et al. 2010; Cole et al. 2011). We used tolerance parameters of 1-3‰, which reflect the high uncertainty in sources (Cole et al. 2011). We used a trophic enrichment factor for $\delta^{15}N$ of 3.4‰ for each trophic level and 0.4‰ for $\delta^{13}C$ (Post et al. 2000). However, there was no trophic adjustment used for $\Delta^{14}C$ because values were corrected by their respective $\delta^{13}C$ values (Caraco et al. 2010).

There are two pathways by which ^{14}C-depleted C could be incorporated into biofilm: (1) aquatic heterotrophs associated with epilithic biofilms could assimilate ancient, glacier-derived DOC or POM and/or (2) benthic algae associated with epilithic biofilm could fix ^{14}C-depleted DIC likely derived from carbonate weathering in the watershed. We used a three source (DOC, DIC, and POM) IsoSource model

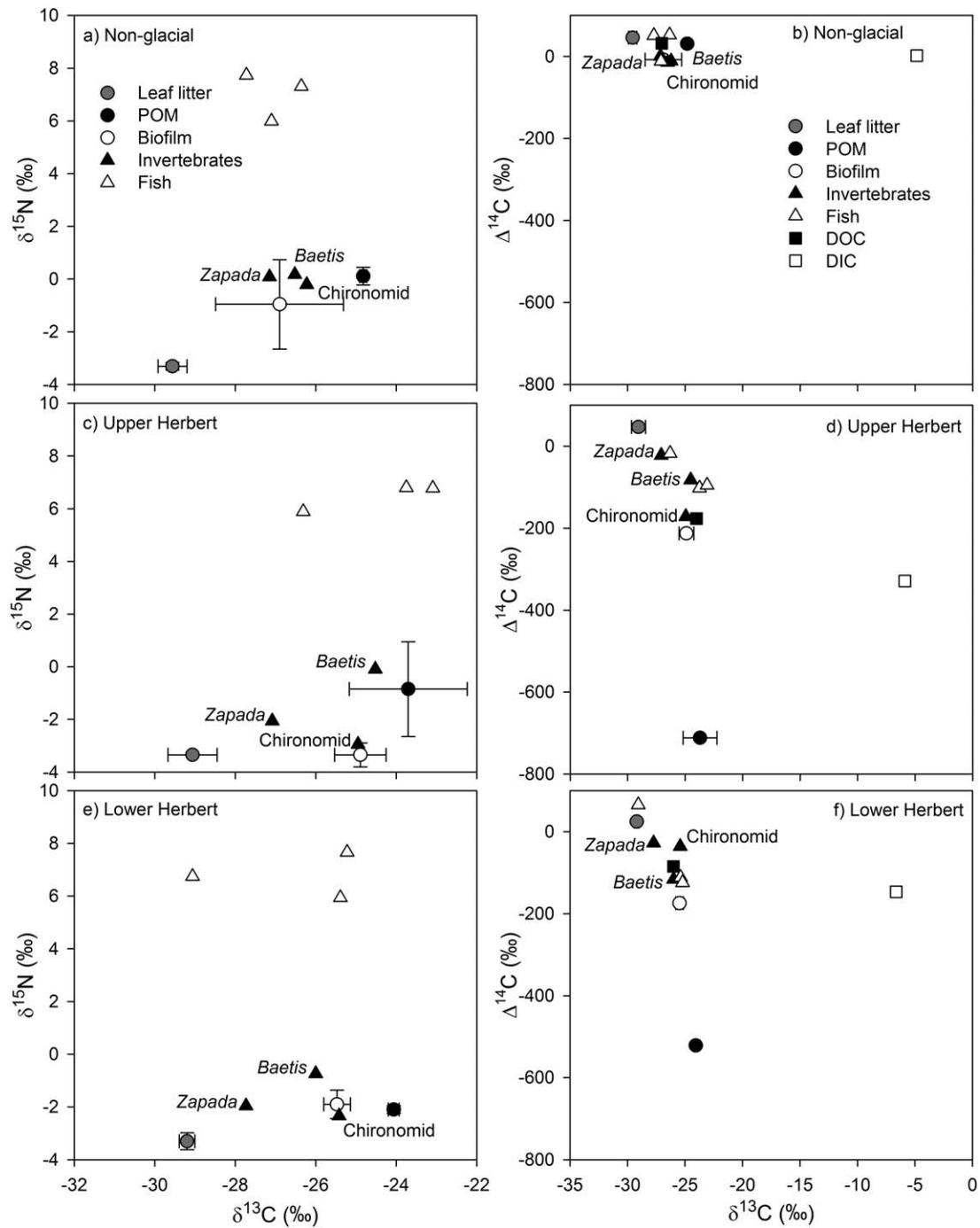**Fig. 2.** Isotope biplots of $\delta^{13}C$ vs. $\delta^{15}N$ and $\delta^{13}C$ vs. $\Delta^{14}C$ for the three organic matter sources ($\pm$ 1 SD for $\delta^{13}C$ and $\delta^{15}N$) and consumers in the (a, b) nonglacial stream, (c, d) upper Herbert River, and (e, f) lower Herbert River.

following Small et al. (2011) to determine if the isotopic signature of biofilm was more strongly related to benthic algae or bacteria. Our goal for this model was to determine the main C source contributing to epilithic biofilm where we treated biofilm as the consumer and DOC, DIC, and particulate organic C (POC) as the potential C sources. The

methods were identical to invertebrate and fish food source modeling, except models were run using only $\delta^{13}C$ and $\Delta^{14}C$ because we do not have $\delta^{15}N$ for DOC and DIC. Prior to running the model, we calculated algal fractionation of $\delta^{13}C$ from assimilation of DIC according to Finlay (2004). Using the $\delta^{13}C$ of benthic algae collected at the upper Herbert

Table 1. IsoSource model results showing the % contribution of three organic matter sources to macroinvertebrates and fish for the three study sites, based on $\delta^{13}C$, $\delta^{15}N$, and $\Delta^{14}C$ values. The models include combinations of possible sources shown as the mean and (1-99) percentiles. Coho refers to Coho salmon (*Oncorhynchus kisutch*) and dolly refers to Dolly Varden (*Salvelinus malma*).

Site	Source	Chironomid	*Baetis*	*Zapada*	Fish 5 cm Dolly	Fish 6 cm Coho	Fish 7 cm Dolly
Nonglacial	Biofilm	57 (52-62)	52 (42-62)	76 (68-82)	3 (0-9)	96 (96-99)	3 (0-12)
	POM	15 (0-29)	20 (0-42)	10 (0-22)	12 (0-49)	0 (0-3)	18 (0-51)
	Leaf litter	27 (16-38)	28 (0-56)	13 (0-30)	84 (60-99)	0 (0-3)	75 (48-93)
					4 cm Dolly	5 cm Dolly	7 cm Coho
Upper Herbert	Biofilm	81 (78-84)	67 (62-76)	19 (13-25)	79 (69-89)	68 (50-86)	20 (2-44)
	POM	1 (0-2)	3 (0-5)	2 (0-4)	2 (0-4)	6 (0-12)	6 (0-14)
	Leaf litter	18 (16-20)	29 (24-33)	79 (75-83)	18 (12-24)	26 (14-38)	68 (56-84)
					6 cm Dolly	7 cm Coho	6 cm Dolly
Lower Herbert	Biofilm	80 (74-86)	76 (64-82)	6 (0-16)	68 (62-78)	68 (52-84)	8 (4-10)
	POM	2 (0-4)	2 (0-6)	4 (0-6)	4 (0-6)	6 (0-12)	0 (0-2)
	Leaf litter	18 (14-22)	22 (18-30)	90 (84-94)	28 (22-32)	25 (16-36)	92 (90-94)

River site ($\delta^{13}C = -25.9$), we calculated algal fractionation of $\delta^{13}C$-DIC to be $-19.6‰$. Although algal fractionation of $\delta^{13}C$-DIC can vary widely in streams (Finlay et al. 1999; Finlay 2004), our estimated value is similar to other studies (Chanton and Lewis 1999; Finlay 2004).

Results

The sources and consumers in the nonglacial stream had stable isotope values that ranged from $-3.1‰$ to $7.8‰$ for $\delta^{15}N$ and $-29.5‰$ to $-24.2‰$ for $\delta^{13}C$ (Fig. 2a). The $\Delta^{14}C$ values ranged from $-11‰$ to $46‰$ for the sources and $-14‰$ to $52‰$ for the consumers, consistent with the fixation of modern atmospheric carbon dioxide (Fig. 2b). IsoSource model results of isotope values for the organic C sources and consumers in the nonglacial stream showed that epilithic biofilm was likely the main C source to all three macroinvertebrate taxa (42-82%, Table 1). However, there was high uncertainty about the relative importance of POM and leaf litter to macroinvertebrate diets. Model results indicate that fish had a feeding history that strongly reflected either biofilm (6 cm Coho salmon, 96-99%) or leaf litter (5 cm and 7 cm Dolly Varden, 60-99%) with POM (0-51%) less likely to be important (Table 1).

In the heavily glaciated upper Herbert River, biofilm, DOC, and particularly POM had an isotopic signature that was ^{13}C-enriched and highly ^{14}C-depleted relative to the nonglacial stream, reflecting the incorporation of ancient C into biofilm biomass (Fig. 2c,d). Moreover, the $\delta^{13}C$ and $\Delta^{14}C$ values for DOC and POM are consistent with those collected from other glacial streams in the region (Hood et al. 2009; Spencer et al. 2014) as well as with studies of glacier DOC from around the world (Singer et al. 2012; Bhatia et al. 2013). This suggests that streamwater organic C in upper Herbert River is derived mainly from the glacier ecosystem.

In-stream leaf litter in upper Herbert River had an isotopic signature similar to leaf litter collected from dominant riparian vegetation ($\delta^{15}N = -3.1‰$, $\delta^{13}C = -29.8‰$, and $\Delta^{14}C = 42.3‰$) indicating little to no biofilm growth on in-stream leaf litter. The $\delta^{13}C$ values across all consumers in upper Herbert River ranged from $-27.1‰$ to $-23.1‰$ (mean $= -24.9‰$) and were significantly enriched (*t*-test, $p = 0.01$, $N = 6$) compared with the nonglacial stream (Fig. 2c). Consumer $\delta^{15}N$ ($-0.1‰$ to $6.8‰$) values in upper Herbert River did not differ from the nonglacial stream (*t*-test, $p = 0.66$, $N = 6$) but $\Delta^{14}C$ values ($-171.4‰$ to $-17.2‰$, mean $= -81.6‰$) were significantly depleted (*t*-test, $p < 0.01$, $N = 6$) compared with the nonglacial stream (Fig. 2d). These $\Delta^{14}C$ values correspond to a radiocarbon age of modern to 1434 yr B.P. for the Chironomid midge indicating ancient C is efficiently transferred to higher trophic levels. IsoSource modeling showed high variability in the proportional contribution of each C source to consumers (Table 1). Biofilm was likely the main C source to *Baetis* (62-76%) and Chironomid midge (78-84%), but *Zapada* (75-83%) was likely consuming leaf litter. Fish reflected a feeding history of a mixture of biofilm (2-89%) and leaf litter (12-84%) with POM (0-14%) less likely to be important.

The $\delta^{13}C$ and $\Delta^{14}C$ values for the sources (except leaf litter) and consumers in lower Herbert River were in general intermediate between the nonglacial and the upper Herbert River site (Fig. 2e,f). Consumer $\delta^{15}N$ and $\delta^{13}C$ values in lower Herbert River did not differ from the nonglacial stream (*t*-test, $p > 0.60$, $N = 6$), but $\Delta^{14}C$ values were significantly depleted (*t*-test, $p < 0.05$, $N = 6$) compared with the nonglacial stream. The $\Delta^{14}C$ values for macroinvertebrates and fish in lower Herbert River ranged from $-124.4‰$ (radiocarbon age of 994 yr B.P.) to $6.6‰$ (modern C) reflecting high variability in their feeding history (Fig. 2f). Mixing model results were similar to upper Herbert River where macroinvertebrates and fish reflect
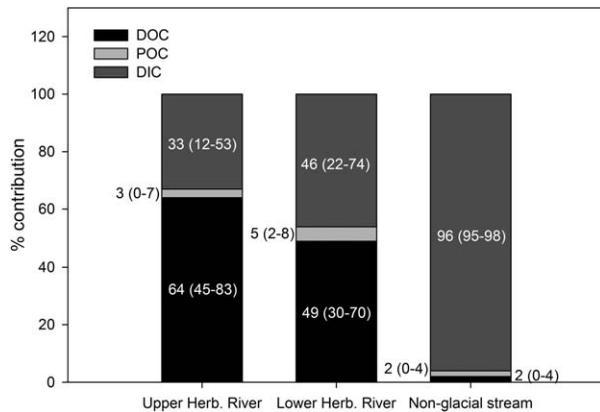
Fig. 3. IsoSource model results showing the % contribution of DOC, POC, and DIC to biofilm biomass, based on δ^{13}C and Δ^{14}C values in upper and lower Herbert River and the nonglacial stream. The models include combinations of possible sources shown as the mean and (1 and 99) percentiles.

a feeding history of both biofilm and leaf litter with POM (0-12%) less likely to be important (Table 1). However, in several instances, consumers (e.g., *Zapada*) appeared to be consuming substantial leaf litter.

Epilithic biofilm in both upper and lower Herbert River was highly ^{14}C-depleted relative to the nonglacial stream reflecting the assimilation of ^{14}C-depleted C. Moreover, Δ^{14}C values for DOC, POM, and DIC were all highly ^{14}C-depleted (Fig. 2) relative to the nonglacial stream. Using an IsoSource model to determine the proportion of each potential C source contributing to biofilm C demand (*see* Methods), we estimate that the isotopic signature of biofilm in upper Herbert River strongly reflected consumption of DOC (45-83%) and to a lesser extent fixation of DIC (12-53%) with POM (0-7%) less likely to be an important C source (Fig. 3). In lower Herbert River, DOC (30-70%) and DIC (22-74%) showed a similar contribution to the isotopic signature of biofilm with POM (2-8%) again unlikely to be important. In contrast, biofilm in the nonglacial stream strongly reflected the isotopic signature of DIC (95-98%, Fig. 3).

To estimate the contribution of glacier organic C to consumer diets in the upper and lower Herbert River sites, we used the relative proportion of biofilm to consumer diets determined from IsoSource modeling (Table 1) together with the calculated proportion of DOC that contributes to biofilm biomass (Fig. 3). IsoSource modeling showed that the relative proportion of biofilm across all consumer diets averaged 56% ($N = 6$) in upper Herbert River and 51% ($N = 6$) in lower Herbert River (Table 1). Using the calculated proportion of C from bulk DOC contributing to biofilm biomass, we estimate that on average 36% of the C incorporated into consumer biomass in upper Herbert River is from glacial organic C and 25% in lower Herbert River. For our high estimate, we calculate that in upper Herbert River 52% of the Chironomid

midge diet and 51% of the 4 cm Dolly Varden diet is from glacier organic C. For lower Herbert River, our high estimate is 39% of the Chironomid midge diet and 34% of the 7 cm Coho salmon diet is from glacial organic C.

Discussion

Importance of glacial organic C to proglacial stream food webs

Our finding that $\sim 36\%$ of the C incorporated into macroinvertebrates and juvenile salmonids in upper Herbert River is glacier-derived supports our initial hypothesis that the metazoan food web is sustained in part by bioavailable organic C released from the upstream glacial ecosystem. Previous field and laboratory experiments have shown that glacier-derived DOC is readily metabolized at low trophic levels (Hood et al. 2009; Singer et al. 2012; Hagvar and Ohlson 2013). Our findings expand this view to higher trophic levels by providing evidence that ancient glacial organic C is transferred from one trophic level to the next. The Δ^{14}C values of C sources and consumers represent the mean sample age and, therefore, our findings do not unequivocally show assimilatory uptake of the ancient fraction, as bulk Δ^{14}C values likely represent an amalgamation of C of different ages. However, our findings clearly show that organic C released from the upstream glacial ecosystem has the potential to contribute to ecosystem productivity in inland waters that receive glacier runoff.

Glacier organic C could be incorporated by consumers either through the direct uptake of POC or by consumption of biofilm, which contains heterotrophs metabolizing glacier-derived DOC. However, IsoSource modeling showed that POC was unlikely to be a main C source for consumers in our glacial river sites. This finding was somewhat surprising given that POC concentrations are typically higher than DOC in proglacial streams. Moreover, macroinvertebrate gut contents in proglacial streams have been shown to contain large amounts of fine glacial rock fragments (Clitherow et al. 2013) suggesting unintentional uptake while grazing biofilm rather than assimilatory uptake of POC. Thus, ^{14}C-depleted glacial organic C was likely transferred to higher trophic levels through a feeding history of bacterial uptake of DOC and subsequent consumption of ^{14}C-depleted biofilm by grazing invertebrates (*Baetis* and Chironomid midges) and ultimately fish.

The large contribution of biofilm to *Baetis* and Chironomid midge diets was not surprising because biofilm is considered to be a preferred food source to invertebrate grazers (Milner and Petts 1994; Battin et al. 2003), even in proglacial streams (Füreder et al. 2003; Clitherow et al. 2013). Moreover, our finding that the isotopic signature of biofilm in the two glacial sites more strongly resembled that of bulk DOC than DIC suggests that biofilms were dominated by heterotrophic biomass assimilating glacier-derived DOC. In small,

heavily shaded streams (Findlay et al. 1993; McNeely et al. 2006) or in turbid proglacial streams with low channel stability, benthic algal biomass is generally low and biofilms are probably dominated by heterotrophic organisms assimilating DOC (Uehlinger et al. 1998; Burgherr and Ward 2001). However, in glacial streams that contain shallow side channels with low turbidity or during the shoulder seasons of the summer glacial runoff period (late spring and early fall) when meltwater inputs are low, benthic algal growth can be high (Zah et al. 2001) such that biofilm along with invertebrate grazers could assume the isotopic signature of benthic algae (Füreder et al. 2003).

Macroinvertebrates and fish appeared to have a feeding history of a mixture of leaf litter and biofilm at the glacial sites, although IsoSource modeling did not consistently elucidate the extent to which consumers were supported by both C sources. These results contribute to the growing body of evidence suggesting that terrestrial support of the metazoan food web in inland waters is widespread (Cole et al. 2006, 2011; Berggren et al. 2010). In coastal southeast Alaska, abundant riparian forests and heavily vegetated mountain slopes adjacent to glaciers provide substantial allochthonous C inputs to proglacial streams. Furthermore, given the severe energy limitations consumers likely experience in proglacial streams, we propose that glacial organic C is a particularly important cross-ecosystem subsidy that helps moderate energy limitations set by contemporary primary production.

There were no obvious trends in feeding preference for fish species (Coho salmon vs. Dolly Varden) and fish size across sites. Dolly Varden commonly consume salmon eggs in streams in the region although this marine-derived subsidy was not likely important because no spawning salmon were observed during the period of sampling as well as the salmon run in Herbert River is thought to be small. The harsh physical conditions and limited energy supply (both from terrestrial and algal sources) common to glacial streams constrain food sources for consumers (Uehlinger et al. 1998; Zah et al. 2001). It is likely that consumer feeding preferences are highly variable and that there are several C transfer pathways through trophic levels within proglacial stream food webs. For instance, aquatic invertebrates in proglacial streams have been known to adapt their feeding behavior to available food sources (Zah et al. 2001). In our study, *Zapada* typically had a feeding preference of leaf litter and Chironomid midges of biofilm. However, both taxa have been shown to feed on salmon carcasses in nonglacial streams during brief periods when carcasses are locally abundant (Chaloner et al. 2002). Moreover, invertebrate diversity and abundance in proglacial streams can exhibit high spatio-temporal variation because of seasonal shifts in glacial runoff and food availability (Burgherr and Ward 2001; Burgherr et al. 2002). Therefore, the main C source fueling consumers in proglacial streams is likely to vary in space and time. In this context,

our findings are likely representative of food web dynamics only at the height of the glacial runoff period when sampling occurred.

Our findings are consistent with studies of glacial ecosystems showing that ancient C is incorporated into microbial and metazoan food webs (Bardgett et al. 2007; Hagvar and Ohlson 2013). These results support a growing number of studies that contradict the dominant view, that freshly produced DOC is preferentially metabolized, in showing that ancient DOC supports heterotrophy in both terrestrial (Fontaine et al. 2007; Gurwick et al. 2008) and aquatic ecosystems (Schell 1983; Caraco et al. 2010; McCallister and Del Giorgio 2012). Collectively, our findings raise the question of whether the incorporation of ancient C into aquatic food webs is more common than previously assumed, particularly in organic C poor environments such as glacial forelands (Hagvar and Ohlson 2013) or in high-latitude ecosystems where destabilization of ancient peat is occurring (Schell 1983). Moreover, our findings support the emerging paradigm that organic C persistence in the terrestrial environment may be more related to its stabilization in "partial refuges," such as in permafrost soils or glacier ice, rather than its chemical recalcitrance (Ekschmitt et al. 2005; Fontaine et al. 2007; McCallister and Del Giorgio 2012). In this context, the melting of glaciers can be viewed as a pathway to release previously stabilized ancient C that can be assimilated by aquatic heterotrophs upon delivery to proglacial streams.

Implications of watershed deglaciation for metazoan food webs

Mountain and subpolar glaciers have experienced widespread recession over the last century (Gardner et al. 2013). This has led to the creation of many new streams and inland aquatic habitats that are being colonized by aquatic primary producers and biota during primary succession (Milner et al. 2011). Glacier volume loss is predicted to continue and even increase in many regions (Radic and Hock 2011) resulting in landcover changes on regional and local scales as glaciers are replaced by forested ecosystems. This transition will alter the dominant sources and reactivity of organic C inputs to proglacial streams. We hypothesize that as glaciers recede in the region and contribute less meltwater to streamflow, food web structure would shift support from mainly old organic C to that of one sustained by contemporary primary production.

Our findings suggest that the bioavailable DOC released from glaciers contributes to ecosystem C cycling such that future changes in glacial runoff will alter the stability and trophic structure of proglacial ecosystems. For instance, our previous research has shown that bioavailable DOC concentrations in forested and wetland streams in the region generally range from 1 mg C L^{-1} to 4 mg C L^{-1} (Fellman et al. 2009). In glacial streams, the bioavailable fraction is typically 2-5 times more than in forested and wetland streams,

although bioavailable DOC concentrations generally range from 0.3 mg C L^{-1} to 0.8 mg C L^{-1} (Hood et al. 2009). Thus, future ice mass loss that results in decreasing runoff from glaciers could lead to an increased flux of less bioavailable DOC (lower percentage of bioavailable C but higher concentration) delivered to streams. However, it is still unclear how this predicted shift in the magnitude and fraction of bioavailable DOC might affect heterotrophic metabolism, which is a critical link in organic C transfer from low to high trophic levels. The fact that glacier DOC can be as much as five times more labile than nonglacier DOC (Hood et al. 2009) magnifies this uncertainty because even relatively small changes in glacial runoff could substantially alter the metabolic balance of proglacial streams.

In conclusion, our results expand the well-documented role of glaciers as drivers of watershed hydrology and physical water properties (e.g., temperature and turbidity) by showing that glacier organic C may also be an effective driver of secondary production through the bacterial uptake of DOC and subsequent consumption of ^{14}C-depleted biofilm by macroinvertebrates. This feeding history provides a key link between production at low trophic levels with rearing juvenile salmonids such as Coho salmon, which as adults when returning to spawn in their natal streams are thought to be a keystone species in coastal watersheds along the Gulf of Alaska (Helfield and Naiman 2006). In this context, our findings suggest that future climate warming and associated glacier wastage will affect downstream ecosystems through not only changes in glacial runoff but also to biogeochemical inputs that, in turn, could influence the structure of metazoan food webs. This may have previously unrecognized impacts on the stability and biodiversity of proglacial stream ecosystems.

References

Bardgett, R. D., A. Richter, R. Bol, M. H. Garnett, R. Baumler, X. Xu, E. Lopez-Capel, D. A. C. Manning, P. J. Hobbs, I. R. Hartley, and W. Wanek. 2007. Heterotrophic microbial communities use ancient carbon following glacial retreat. Biol. Lett. **3**: 487-490. doi:10.1098/rsbl.2007.0242

Battin, T. J., L. A. Kaplan, J. D. Newbold, and C. M. E. Hansen. 2003. Contribution of microbial biofilms to ecosystem processes in stream mesocosms. Nature **426**: 439-442. doi:10.1038/nature02152

Berggren, M., and others. 2010. Lake secondary production fueled by rapid transfer of low molecular weight organic carbon from terrestrial to aquatic sources. Ecol. Lett. **13**: 870-880. doi:10.1111/j.1461-0248.2010.01483.x

Berthier, E., E. Schiefer, G. K. C. Clarke, B. Menounos, and F. Remy. 2010. Contribution of Alaskan glaciers to sea-level rise derived from satellite imagers. Nat. Geosci. **3**: 92-95. doi:10.1038/ngeo737

Bhatia, M. P., S. B. Das, K. Longnecker, M. A. Charette, and E. B. Kujawinski. 2010. Molecular characterization of dissolved organic matter associated with the Greenland ice sheet. Geochem. Cosmochim. Acta **74**: 3768-3784. doi:10.1016/j.gca.2010.03.035

Bhatia, M. P., S. B. Das, L. Xu, M. A. Charette, J. L. Wadham, and E. B. Kujawinski. 2013. Organic carbon export from the Greenland ice sheet. Geochim. Cosmochim. Acta **109**: 329-344. doi:10.1016/j.gca.2013.02.006

Burgherr, P., and. J. V. Ward. 2001. Longitudinal and seasonal distribution patterns of the benthic fauna of an alpine glacial stream (Val Roseg, Swiss Alps). Freshwater Biol. **46**: 1705-1721. doi:10.1046/j.1365-2427.2001.00853.x

Burgherr, P., J. V. Ward, and C. T. Robinson. 2002. Seasonal variation in zoobenthos across habitat gradients in an alpine glacial floodplain (Val Roseg, Swiss Alps). J. North Am. Benthol. Soc. **21**: 561-575. doi:10.2307/1468430

Caraco, N., J. E. Bauer, J. J. Cole, S. Petsch, and P. A. Raymond. 2010. Millennial-aged organic carbon subsidies to a modern river food web. Ecology **91**: 2385-2393. doi:10.1890/09-0330.1

Chaloner, D. T., M. S. Wipfli, and J. P. Caouette. 2002. Mass loss and macroinvertebrate colonization of Pacific salmon carcasses in south-eastern Alaska streams. Freshwater Biol. **47**: 263-273. doi:10.1046/j.1365-2427.2002.00804.x

Chanton, J. P., and F. G. Lewis. 1999. Plankton and dissolved inorganic carbon isotopic composition in a river-dominated estuary: Apalachicloa Bay, Florida. Estuaries **22**: 575-583. doi:10.2307/1353045

Clitherow, L. R., J. L. Carrivick, and L. E. Brown. 2013. Food web structure in a harsh glacier-fed river. PLoS ONE **8**: e60899. doi:10.1371/journal.pone.0060899

Cole, J. J., S. R. Carpenter, J. Kitchell, M. L. Pace, C. T. Solomon, and B. Weidel. 2011. Strong evidence for a terrestrial support of zooplankton in small lakes based on stable isotopes of carbon, nitrogen and hydrogen. Proc. Natl. Acad. Sci. USA **108**: 1975-1980. doi:10.1073/pnas.1012807108

Cole, J. J., S. R. Carpenter, M. L. Pace, M. C. Van de Bogert, J. L. Kitchell, and J. R. Hodgson. 2006. Differential support of lake food webs by three types of terrestrial organic carbon. Ecol. Lett. **9**: 558-568. doi:10.1111/j.1461-0248.2006.00898.x

Ekschmitt, K., M. Liu, S. Vetter, O. Fox, and V. Wolters. 2005. Strategies used by soil biota to overcome soil organic matter stability – why is dead organic matter left over in the soil? Geoderma **128**: 167-176. doi:10.1016/j.geoderma.2004.12.024

Fellman, J. B., E. Hood, R. T. Edwards, and D. V. D'Amore. 2009. Changes in the concentration, biodegradability and fluorescent properties of DOM during stormflows in coastal temperate watersheds. J. Geophys. Res. **114**: G01021. doi:10.1029/2008JG000790

Fellman, J. B., S. Nagorski, S. Pyare, A. W. Vermilyea, D. Scott, and E. Hood. 2014. Stream temperature response to variable glacier coverage in coastal watersheds of

Southeast Alaska. Hydrol. Process. **28**: 2062-2073. doi: 10.1002/hyp.9742

Findlay, S. E. G., K. Howe, and D. Fontvieille. 1993. Bacterial-algal relationships in streams of the Hubbard Brook experimental forest. Ecology **74**: 2326-2336. doi:10.2307/1939585

Finlay, J. C. 2004. Patterns and controls of lotic algal stable carbon isotope ratios. Limnol. Oceanogr. **49**: 850-861. doi:10.4319/lo.2004.49.3.0850

Finlay, J. C., S. Khandwala, and M. E. Power. 2002. Spatial scales of carbon flow in a river food web. Ecology **83**: 1845-1859. doi:10.1890/0012-9658(2002)083[1845:SSOCFI]2.0.CO;2

Finlay, J. C., M. E. Power, and G. Cabana. 1999. Effects of water velocity on algal carbon isotope ratios: implications for river food web studies. Limnol. Oceanogr. **44**: 1198-1203. doi:10.4319/lo.1999.44.5.1198

Fontaine, S., S. Barot, P. Barre, N. Bdioui, B. Mary, and C. Rumpel. 2007. Stability of organic carbon in deep soil layers controlled by fresh carbon supply. Nature **450**: 277-281. doi:10.1038/nature06275

Füreder, L., C. Welter, and J. K. Jackson. 2003. Dietary and stable isotope (δ^{13}C, δ^{15}N) analyses in alpine stream insects. Int. Rev. Hydrobiol. **88**: 314-331. doi:10.1002/iroh.200390028

Gardner, A. S., and others. 2013. A reconciled estimate of glacier contributions to sea level rise: 2003-2009. Science **340**: 852-857. doi:10.1126/science.1234532

Gurwick, N. P., D. M. McCorkle, P. M. Groffman, A. J. Gold, D. Q. Kellogg, and P. Seitz-Rundlett. 2008. Mineralization of ancient carbon in the subsurface of riparian forests. J. Geophys. Res. **113**: G02021. doi:10.1029/2007JG000482

Hagvar, S., and M. Ohlson. 2013. Ancient carbon from a melting glacier gives high ^{14}C age in living pioneer invertebrates. Sci. Rep. **3**: 1-4. doi:10.1038/srep02820

Helfield, J. M., and R. J. Naiman. 2006. Keystone interactions: salmon and bear in riparian forests of Alaska. Ecology **9**: 167-180. doi:10.1007/s10021-004-0063-5

Hood, E., J. B. Fellman, R. G. M. Spencer, P. J. Hernes, R. T. Edwards, D. D'Amore, and D. Scott. 2009. Glaciers as a source of ancient and labile organic matter to the marine environment. Nature **462**: 1044-1047. doi:10.1038/nature08580

Hood, E., and D. Scott. 2008. Riverine organic matter and nutrients in southeast Alaska affected by glacial coverage. Nat. Geosci. **1**: 583-586. doi:10.1038/ngeo280

Ishikawa, N. F., M. Uchida, Y. Shibata, and I. Tayasu. 2012. Natural C-14 provides new data for stream food-web studies: a comparison with C-13 in multiple stream habitats. Mar. Freshwater Res. **63**: 210-217. doi:10.1071/MF11141

Jacobsen, D., A. M. Milner, L. E. Brown, and O. Dangles. 2012. Biodiversity under threat in glacier-fed river systems. Nat. Clim. Change **2**: 361-364. doi:10.1038/nclimate1435

Kaplan, L. A., J. D. Newbold, D. J. Van Horn, C. L. Dow, A. K. Aufdenkampe, and J. K. Jackson. 2006. Organic matter transport in New York City drinking-water-supply watersheds. J. North Am. Benthol. Soc. **25**: 912-927. doi:10.1899/0887-3593(2006)025[0912:OMTINY]2.0.CO;2

Laghari, J. R. 2013. Melting glaciers brings energy uncertainty. Nature **502**: 617-618. doi:10.1038/502617a

Larsen, C. F., R. J. Motyka, A. A. Arendt, K. A. Echelmeyer, and P. E. Geissler. 2007. Glacier changes in southeast Alaska and northwest British Columbia and contribution to sea level rise. J. Geophys. Res. **112**: F01007. doi:10.1029/2006JF000586

McCallister, S. L., J. E. Bauer, J. E. Cherrier, and H. W. Ducklow. 2004. Assessing sources and ages of organic matter supporting river and estuarine bacterial production. A multiple-isotope (Δ^{14}C, δ^{13}C, and δ^{15}N) approach. Limnol. Oceanogr. **49**: 1687-1702. doi:10.4319/lo.2004.49.5.1687

McCallister, S. L., and P. A. Del Giorgio. 2012. Evidence for the respiration of ancient terrestrial organic C in northern temperate lakes and streams. Proc. Natl. Acad. Sci. USA **109**: 16963-16968. doi:10.1073/pnas.1207305109

McNeely, C., S. M. Clinton, and J. M. Erbe. 2006. Landscape variation in C sources of scraping primary consumers in streams. J. North Am. Benthol. Soc. **25**: 787-799. doi:10.1899/0887-3593(2006)025[0787:LVICSO]2.0.CO;2

Merritt, R. W., K. W. Cummins, and M. G. Berg. 2008. An introduction to the aquatic insects of North America, 4th ed. Kendall/Hunt Publishing Company.

Milner, A. M., and G. E. Petts. 1994. Glacial rivers: physical habitat and ecology. Freshwater Biol. **32**: 295-307. doi:10.1111/j.1365-2427.1994.tb01127.x

Milner, A. M., A. L. Robertson, L. E. Brown, S. H. Sonderland, M. McDermott, and A. J. Veal. 2011. Evolution of a stream ecosystem in recently deglaciated terrain. Ecology **92**: 1924-1935. doi:10.1890/10-2007.1

Moore, R. D., S. W. Fleming, B. Menounos, R. Wheate, A. Fountain, K. Stahl, K. Holm, and M. Jakob. 2009. Glacier change in western North America: influences on hydrology, geomorphic hazards and water quality. Hydrol. Process. **23**: 42-61. doi:10.1002/hyp.7162

Phillips, D. L., and J. W. Gregg. 2003. Source partitioning using stable isotopes: Coping with too many sources. Oecologia **136**: 261-269. doi:10.1007/s00442-003-1218-3

Post, D. M. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. Ecology **83**: 703-718. doi:10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

Post, D. M., M. L. Pace, and N. G. Hairston, Jr. 2000. Ecosystem size determines food-chain length in lakes. Nature **405**: 1047-1049. doi:10.1038/35016565

Radic, V., and R. Hock. 2011. Regionally differentiated contribution of mountain glaciers and ice caps to future sea-level rise. Nat. Geosci. **4**: 91-94. doi:10.1038/ngeo1052

Rasmussen, J. B. 2010. Estimating terrestrial contribution to stream invertebrates and periphyton using a gradient-based mixing model for δ^{13}C. J. Anim. Ecol. **79**: 393-402. doi:10.1111/j.1365-2656.2009.01648.x

Raymond, P. A., and J. E. Bauer. 2001. Use of ^{14}C and ^{13}C natural abundances as a tool for evaluating freshwater, estuarine and coastal organic matter sources and cycling. Org. Geochem. **32**: 469-485. doi:10.1016/S0146-6380(00)00190-X

Robinson, C. T., U. Uehlinger, and M. Hieber. 2001. Spatio-temporal variation in macroinvertebrate assemblages of glacial streams in the Swiss Alps. Fresh. Biol. **46**: 1663-1672.

Schell, D. M. 1983. Carbon-13 and carbon-14 abundances in Alaskan aquatic organisms: Delayed production from peat in arctic food webs. Science **219**: 1068-1071. doi:10.1126/science.219.4588.1068

Singer, G. A., C. Fasching, L. Wilhelm, J. Niggemann, P. Steier, T. Dittmar, and T. J. Battin. 2012. Biogechemically diverse organic matter in alpine glaciers and its downstream fate. Nat. Geosci. **5**: 710-714. doi:10.1038/NGEO1581

Small, G. E., R. Bixby, C. Kazanci, and C. M. Pringle. 2011. Partitioning stoichiometric components of epilithic biofilm using mixing models. Limnol. Oceanogr.: Methods **9**: 185-193. doi:10.4319/lom.2011.9.185

Spencer, R. G. M., G. R. Aiken, K. P. Wickland, R. G. Striegl, and P. J. Hernes. 2008. Seasonal and spatial variability in DOM quantity and composition from the Yukon River basin, Alaska. Global Biogeochem. Cycles **22**: GB4002. doi:10.1029/2008GB003231

Spencer, R. G. M., A. Vermilyea, J. B. Fellman, P. Raymond, A. Stubbins, D. Scott, and E. Hood. 2014. Seasonal variability of organic matter composition in an Alaskan glacier outflow: Insights into glacier carbon sources. Environ. Res. Lett. **9**: 055005-055014. doi:10.1088/1748-9326/9/5/055005

Uehlinger, U., R. Zah, and H. Burgi. 1998. The Val Roseg project: Temporal and spatial patterns of benthic algae in an alpine stream ecosystem influence by glacial runoff, p. 419-425. In K. K. U. Tappeiner, N. E. Peters, and R. G. Craig [eds.], Hydrology, water resources and ecology in headwaters. IAHS Press.

Vander Zanden, M. J., and J. B. Rasmussen. 2001. Variation in δ^{15}N and δ^{13}C trophic fractionation: Implications for aquatic food web Studies. Limnol. Oceanogr. **46**: 2061-2066. doi:10.4319/lo.2001.46.8.2061

Volk, C. J., C. B. Volk, and L. A. Kaplan. 1997. Chemical composition of biodegradable dissolved organic matter in streamwater. Limnol. Oceanogr. **42**: 39-44. doi:10.4319/lo.1997.42.1.0039

Wesener, M. D., R. W. Merritt, E. Y. Campbell, M. E. Benbow, E. C. Norberg, and R. T. Edwards. 2011. Hyporheic and benthic macroinvertebrate communities in glacial, clearwater, and brownwater streams in Alaska. Pan-Pac. Entomol. **87**: 145-160. doi:10.3956/2011-06.1

Wipfli, M. S., J. Hudson, and J. Caouette. 1998. Influence of salmon carcasses on stream productivity: Response of biofilm and benthic macroinvertebrates in southeast Alaska, U.S.A. Can. J. Fish. Aquat. Sci. **55**: 1503-1511. doi:10.1139/f98-031

Zah, R., P. Burgherr, S. M. Bernasconi, and U. Uehlinger. 2001. Stable isotope analysis of macroinvertebrates and their food sources in a glacier stream. Freshwater Biol. **46**: 871-882. doi:10.1046/j.1365-2427.2001.00720.x