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A melting glacier feeds aquatic and terrestrial invertebrates with ancient carbon and supports early succession

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ABSTRACT

More than 5000-yr-old organic material was released by a melting glacier in central southern Norway. The ancient carbon was bioavailable and supported early food chains. This was shown through high radiocarbon age in living aquatic and terrestrial invertebrates. Young ponds acted as biological oases, where ancient carbon was assimilated by larvae of various Diptera: mainly Chironomidae, but also Tipulidae and Limoniidae. Within ponds, even predatory diving beetles had a high radiocarbon age. Adult chironomid midges with a radiocarbon age of 1040 yr transported ancient carbon to terrestrial predators among beetles, spiders, and harvestmen. Ancient carbon was also assimilated by chironomid larvae downstream in the glacier-fed river, and radiocarbon dating of chironomid larvae from glacial rivers will thus be an easy way to check whether a given glacier releases bioavailable ancient carbon. Our study indicates that the ancient organic particles were very small. We refer to studies from other countries showing that glaciers collect and release ancient carbon in the form of tiny, long-transported and biodegradable aerosol particles, which stem from the incomplete combustion of radiocarbon-depleted fossil fuels. All our results would fit with this mechanism.

INTRODUCTION

Recent studies show that glaciers play a role in the global carbon cycle as they collect, produce, store, transform, and release organic matter (Anesio et al., 2009; Anesio and Laybourn-Parry, 2012; Hood et al., 2015). Long-transported aerosols, originating from the incomplete combustion of fossil fuels, make up a part of the organic matter that glaciers collect by surface accumulation (Stubbins et al., 2012). These aerosols are radiocarbon depleted and ^{14}C dating will consequently reveal that they are very old (Stubbins et al., 2012; Fellman et al., 2015a). Thus, ancient ice-locked carbon will eventually be released into glacial rivers and dissolved organic matter that is several thousand years old can become bioavailable to support downstream microbial life (Singer et al., 2012; Stubbins et al., 2012), as well as invertebrates and fish (Fellman et al., 2015b). Actually, heavily glaciated watersheds can transport ancient carbon all the way to oceans where marine microorganisms assimilate the old carbon (Hood et al., 2009), and in a recent review, it was concluded that mountain and polar glaciers represent a quantitatively important store of organic carbon (Hood et al., 2015). Due to climate warming, it is reasonable to expect that the annual loss and river transport of glacial dissolved organic carbon will increase in the future.

Ancient carbon is, however, not only transported away by glacial rivers, but may also play a role in the glacier foreland by supporting the establishment of pioneer organisms. As glaciers are melting and retreating worldwide due to climate change (Oerlemans, 2005; Jomelli et al., 2011; Malcomb and Wiles, 2013), large, barren foreland areas are made available for pioneer communities. In Norway, for example, the mean retreat of 24 glaciers during the period 2000–2014 was 270 m, that is, about 20 m per year (Hallgeir Elvehøy, personal communication, Norwegian Water Resources and Energy Directorate). Forelands near receding glaciers are unique "natural laboratories" for the study of primary succession and have received increasing attention by ecologists (e.g., Kaufmann, 2001; Gobbi et al., 2006; Hågvar et al., 2009a; König et al., 2011; Ingimarsdóttir et al., 2012; Vater, 2012; Bråten et al., 2012; Hågvar, 2010, 2012; Raso et al., 2014). In a glacier foreland in the Austrian Alps, Bardgett et al. (2007) documented that terrestrial microbial communities used ancient and recalcitrant carbon as an energy source, along with modern carbon, during the first 50 years after deglaciation. Hågvar and Ohlson (2013) were the first to document that ancient carbon released from a glacier can be assimilated by pioneer animals, resulting in high radiocarbon age in living invertebrates. Initially, they showed that freshly deposited sand and silt close to the receding Hardangerjøkulen glacier in southern Norway contained ancient carbon. This carbon turned out to be bioavailable, which was illustrated by high radiocarbon age of living predatory invertebrates. The carabid beetles, *Nebria nivalis* and *Bembidion hastii*, were 690 and 1100 yr "old," respectively. The harvestman, *Mitopus morio*, had a radiocarbon age of 570 yr, and the wolf spider, *Pardosa trailli*, 340 yr. Studies of the gut content in the two beetles and the harvestman revealed remnants of adult chironomid midges. Furthermore, adult chironomids taken in pitfall traps had a radiocarbon age of no less than 1040 yr. Hågvar and Ohlson (2013) assumed that chironomid larvae could assimilate the ancient carbon in recently established ponds in the glacier foreland, and that adult midges subsequently transferred the carbon to terrestrial predators.

Here we present new radiocarbon data to test the following hypotheses:

1. Detritus-eating chironomid larvae in young ponds assimilate ancient carbon released by the glacier.
2. Young ponds function as "biological oases" on barren, pioneer ground. They produce food to pioneer predators and support early succession.
3. Also, chironomid larvae in the glacier river assimilate ancient carbon.

MATERIAL AND METHODS

The Midtdalsbreen glacier snout (60°34′N; 7°28′E) is part of the 73 km^2 large Hardangerjøkulen glacier in central southern Norway. Situated nearly 1400 m a.s.l., its foreland endures harsh environmental conditions with an annual snow-free period of 3–4 months. An aerial photo of the foreland, with dated sampling sites, was given by Bråten et al. (2012). Between 2001 and 2011, Midtdalsbreen retreated 154 m (Atle Nesje, personal communication). Samples of freshly deposited silt and sand for age analyses of organic matter were taken in September 2010 about 20 m from the ice edge. However, since the actual bedrock contains the mineral phyllite, which may include graphite particles that will influence the radiocarbon dating by being dead in a radiocarbon perspective, new samples were taken close to the receding ice edge in August 2014. These samples were pretreated in two different ways to isolate the possible influence of graphite. The standard accelerator mass spectrometry (AMS) procedure included heating to >800 °C, where possible graphite would be combusted and included in the analyses, but a second sample was pretreated at 466 °C to avoid the graphite particles being combusted. In both cases, combustion was performed under active O_2 flow.

Our main study area for invertebrates was a marked moraine that was pushed up in 2005 during a temporary advance of the glacier snout. Terrestrial invertebrates for radiocarbon dating were sampled in pitfall traps in this area. Beetles (Coleoptera), spiders (Aranea), and harvestmen (Opiliones) were sampled alive and frozen, while adult Diptera (Chironomidae and Limoniidae) and springtails (Collembola) were preserved in 70% ethanol. Analyses of carabid beetles from older terrain (40 and 63 yr old, respectively) were on ethanol-preserved pitfall material. The ethanol used was produced from modern plant material and did not contain ancient carbon. Samples were thoroughly rinsed with water to remove ethanol before analysis. Each sample for radiocarbon dating of beetles, spiders, or harvestmen consisted of 7–25 individuals; of Limoniidae, 22 individuals; of Chironomidae larvae, hundreds; and of springtails and adult midges, thousands.

Ponds of varying size on the 2005 moraine were sampled using a sieve. Adult diving beetles were frozen, while larvae of diving beetles, as well as larvae of Chironomidae and Tipulidae, were preserved in ethanol. Sediment from a dried-up pond, about 0.5 m in diameter, was kept dry until analysis. Just outside the 1934 moraine, fully grown diving beetle larvae creeping ashore from an 80-yr-old pond to pupate were taken in pitfall traps and alcohol-preserved. In August 2014, benthic chironomid larvae, and some pupae, were collected at three sites in the glacial river using a standardized kicking technique (Brittain et al., 2001), combined with brushing of stones.

Except for the chironomid larvae from the two 8-yr-old ponds (Table 1), gut contents were removed from larvae of chironomids and tipulids before radiocarbon dating. This was to ensure that the measured ancient carbon was a part of their body tissue, and not only an effect of, for instance, graphite particles in the gut.

In August 2015, tail flesh was collected from 10 specimens of Arctic charr (*Salvelinus alpinus*), 5–6 km downstream of the glacier snout, since charr could be a potential predator on chironomid larvae (Fjeld, 1985). However, this locality was suboptimal, being influenced by a nonglacial tributary.

In order to eliminate the possible influence of the carbon-containing phyllite bedrock, two types of sample were taken in other southern Norwegian glacial forelands with nonphyllite bedrock. Close to the receding ice edge at the Hellstugubreen glacier snout in Lom municipality, situated on gabbro bedrock, silt/sand samples were taken in 2014 and 2015 for radiocarbon dating. Furthermore, ethanol-preserved chironomid larvae collected in October 1996 from the glacier-fed river from Brigsdalsbreen (part of the Jostedalsbreen ice cap in Stryn municipality, situated on gneiss bedrock), were radiocarbon dated.

An overview of all radiocarbon-dated material from the foreland of the Hardangerjøkulen glacier is given in Table 1. All ^{14}C results are corrected for isotopic fraction using δ^{13}C values. Ages are reported as the Conventional Radiocarbon Age. Each δ^{13}C value is from the sample material itself, measured by isotope ratio mass spectrometry (IRMS). Material from river, ponds, and terrestrial habitats are distinguished, and invertebrates are listed as predators, decomposers, or grazers.

Radiocarbon dating was done by Beta Analytic, an ISO 17025-accredited radiocarbon dating laboratory in Miami, Florida.

RESULTS

Influence of Bedrock on Radiocarbon Dating of Organic Material in Silt and Sand

Radiocarbon dating of silt and sand in 2014 confirmed that the standard AMS method gave too high of an age due to graphite particles from phyllite bedrock (Table 1). When graphite was not allowed to combust during the pretreatment, the real age of organic material was measured to be 5160 yr, compared to 17,750 yr by the standard AMS method. Consequently, the standard AMS datings from 2010 (Hågvar and Ohlson, 2013), between 17,950 and 24,340 yr, were also considered to be too high.

Silt and sand collected in front of the receding Hellstugubreen glacier situated on a nonphyllitic bedrock (i.e., gabbro) contained ancient carbon. Here, the two samples from 2014 and 2015 had a radiocarbon age of 3220 ± 30 and 1450 ± 30 yr, respectively.

Assimilation of Ancient Carbon in the Glacier-Fed River

At the glacier snout, the following water chemistry parameters were measured: pH 7.1, conductivity 2.94 mS m^{-1}, Cl 0.36 mg L^{-1}, SO$_4$ 5.04 mg L^{-1}, total P 150 μg L^{-1}, total N 69 μg L^{-1}, and Ca 4.8 mg L^{-1}. This indicates the influence of calcium-rich bedrock beneath the glacier.

Chironomid larvae from the upper sampling site, in a fast-flowing reach about 0.8 km downstream from the glacier snout, had a radiocarbon age of 1190 yr. The next sampling station was 1.4 km downstream, in a slow-running brook emerging from a 200-m-wide lake in which larger particles would have the possibility to sediment. However,

FIGURE 1. An 8-yr-old pond, less than 1 m^2 in area and only a few centimeters deep. The soft bottom sediments were rich in chironomid larvae that assimilated ancient carbon.

ancient carbon had evidently passed through the lake, since chironomid larvae were 1260 yr "old." The lowest sampling site was in a fast-flowing reach 4.0 km downstream from the glacier snout, after having joined another glacial river. Even here, ancient carbon had been assimilated, resulting in 290-yr-"old" larvae.

Tail flesh from Arctic charr 5–6 km downstream did not contain ancient carbon. Neither did chironomid larvae from the glacier river emerging from Brigsdalsbreen, situated on gneiss rocks.

Assimilation of Ancient Carbon in Young Ponds

Small, 8-yr-old ponds with silty, soft sediments were investigated in July 2013. Some of the ponds were only 0.5–1 m wide and a few cm deep (Fig. 1). Fine sediments from a newly dried pond, only 0.5 m wide, had a radiocarbon age of 14,050 yr by standard AMS method. Since graphite particles were not removed in this analysis, the radiocarbon age of organic matter alone must have been lower. In several small ponds, tube-living chironomid midge larvae were observed in the bottom sediments (Fig. 2, part a). Figure 2, part b, shows the larvae partly freed from their tubes, with gut content visible. Chironomid larvae from the pond in Figure 1 had a radiocarbon age of 3270 yr, and larvae from a larger pond of about 8 m^2 had a radiocarbon age of 1420 yr. The latter larval sample contained impurities of inblown synthetic fibers, so the age was underestimated. Among 50 DNA-identified larvae, 49 belonged to *Tanytarsus* cf. s*inuatus* Goetghebuer 1936, and one to *Parakiefferiella scandica* Brundin 1956 (Torbjørn Ekrem, personal communication).

Chironomid larvae from the ponds were radiocarbon dated with their gut content in situ. Ideally, the gut content should be removed in order to document that ancient carbon had been assimilated into the body tissue. In 2014, larvae of Tipulidae (Fig. 2, part c, lower part) collected in pond sediments were radiocarbon dated after removal of their gut contents. A radiocarbon age of 1610 yr demonstrated that ancient carbon had been assimilated into their tissue. Figures 2, parts c and d, show larva and adult of the predatory water beetle *Agabus bipustulatus* from ponds, which also contained an-

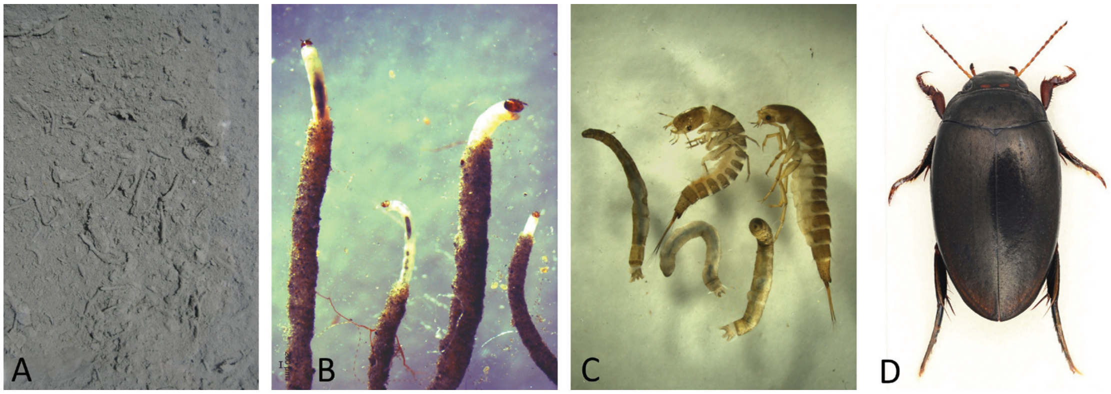

FIGURE 2. Pond-living invertebrates containing ancient carbon released by the glacier. (A) The sediment surface of the pond in Figure 1, showing the numerous tubes in which chironomid larvae are living. (B) Chironomid larvae partly freed from their tubes. (C) Two predacious larvae of the diving beetle *Agabus bipustulatus*, together with three cylindrical larvae of Tipulidae (Diptera). (D) Adult predacious diving beetle, *Agabus bipustulatus.*

cient carbon (Table 1). The hunting behavior of the larvae along mud surfaces indicated that they prey on midge larvae. Also adult *Agabus* larvae from an 80-yr-old pond contained ancient carbon, having a radiocarbon age of 350 yr (Table 1).

In addition to Chironomidae and Tipulidae, ancient carbon was detected in a third group of Diptera. Adult Limoniidae collected by pitfall traps on 6-yr-old ground in 2011 had a radiocarbon age of 1820 yr. The sample contained two species, *Symplecta scotica* (Edwards 1938) (22 specimens) and *Dicranomyia incisurata* Lackschewitz 1928 (7 specimens).

Gut Contents of Chironomid Larvae

Gut contents of chironomid larvae from river and pond, respectively, were dominated by small mineral particles, with very few signs of algae (Fig. 3, parts a and b). Visually, the gut contents were similar to the fine-grained sediment isolated from water at the glacial river outlet (Fig. 3, part c). Some darker elements in all three figures are of unknown origin.

Ancient Carbon in Terrestrial Predators

Predatory carabid beetles, harvestmen, and spiders living on 6-yr-old ground had radiocarbon ages between 340 and 1100 yr (Table 1, Fig. 4). On 40-yr-old ground, ancient carbon was still present in the carabid beetle *Nebria nivalis* (radiocarbon age 260 yr), but absent after 63 yr.

DISCUSSION

Assimilation or Contamination?

The possible presence of small graphite particles in guts of aquatic invertebrates would influence radiocarbon dating. By removing gut contents before analysis, true assimilation of ancient carbon into the tissue was proved for Chironomidae larvae in the river and for Tipulidae larvae in pond sediments. High radiocarbon age in adult Chironomidae (1040 yr) and Limoniidae (1820 yr) is also a proof of assimilation. Adults do not bring with them any gut contents from their larval life in water, and they cannot contaminate terrestrial predators with graphite.

A Pioneer Invertebrate Food Web

Ancient carbon released by the melting Hardangerjøkulen glacier can be followed through food chains by a combination of radiocarbon dating of living invertebrates and studies of their gut contents. Our data show that the ancient carbon was initially assimilated by aquatic Diptera larvae, mainly Chironomidae, but also Tipulidae and Limoniidae. Larvae of Limoniidae develop in moist soil or mud, may be in shallow ponds, and feed on decaying organic material (Jukka Salmela, personal communication). Algae were almost absent in guts of chironomid and tipulid larvae in young ponds, and in guts of chironomid larvae in the glacier-fed

TABLE 1

Conventional radiocarbon age and $\delta^{13}C$ values of invertebrates and substrates in the foreland of the Hardangerjøkulen glacier, southern Norway. For modern age, percent modern carbon (pMC) is given. River, ponds, and terrestrial habitats are distinguished, and animals are grouped according to trophic level. For river, distance from glacier outlet is along the water course. Data with a star are previously unpublished.

	River				Ponds				Terrestrial			
	Taxon	Distance from glacier outlet (km)	$\delta^{13}C$ (‰)	Radiocarbon age BP	Taxon	Age of pond (yrs)	$\delta^{13}C$ (‰)	Radiocarbon age BP	Taxon	Age of ground (yrs)	$\delta^{13}C$ (‰)	Radiocarbon age BP
Predators	*_Salvelinus alpinus_ (fish, Arctic charr, tail meat)	5–6	–25.4	Modern 102.8 ± 0.3 pMC	_Agabus bipustulatus_ larvae (diving beetle)	7	–21.6	1200 ± 30	_Nebria nivalis_ (ground beetle)	6	–25.4	690 ± 30
					Agabus bipustulatus adults	7	–20.2	1130 ± 30	*_Nebria nivalis_	40	–25.5	260 ± 30
					*_Agabus bipustulatus_ larvae (diving beetle)	80	–17.3	350 ± 30	*_Nebria nivalis_	63	–24.5	Modern 103.0 ± 0.3 pMC
									Bembidion hastii (ground beetle)	6	–24.5	1100 ± 30
									*_Bembidion hastii_	40	–24.3	20 ± 30
									Mitopus morio (harvestman)	6	–23.6	570 ± 30
									Pardosa trailli (wolf spider)	6	–24.5	340 ± 30
Decomposers	*Chironomidae larvae	0.8	–32.1	1190 ± 30	*Chironomidae larvae pond 1	8	–20.9	3270 ± 30	Chironomidae (Diptera) adults	6	–19.5	1040 ± 30
	*Chironomidae larvae	1.4	–28.4	1260 ± 30	*Chironomidae larvae pond 5	8	–21.9	1420 ± 30	*Limoniidae (Diptera) adults	6	–24.5	1820 ± 30
	*Chironomidae larvae	4.0	–26.6	290 ± 30	*Tipulidae larvae small ponds	9	–22.9	1610 ± 30	*_Omphalina rivulicola_ (Mushroom, Agaricales)	6	–26.5	Modern 105.1 ± 0.3 pMC

TABLE 1

Continued

	River				Ponds				Terrestrial			
	Taxon	Distance from glacier outlet (km)	δ^{13}C (‰)	Radiocarbon age BP	Taxon	Age of pond (yrs)	δ^{13}C (‰)	Radiocarbon age BP	Taxon	Age of ground (yrs)	δ^{13}C (‰)	Radiocarbon age BP
Substrate					*Sediment of pond 4 (dry), 2013, standard AMS	8	–25.2	14,050 ± 60	Silt and sand near ice edge, 2010, standard AMS (5 values)	0	–24.2 to –25.1	17,950–24,340 ± 80–110
									*Silt and sand near ice edge, 2014, standard AMS	0	–25.0	17,750 ± 60
									*Silt and sand near ice edge, 2014, graphite particles not included in AMS	0	–29.6	5160 ± 40
Grazers									Collembola: moss- and fungal feeders	6	–24.4	40 ± 30
									Collembola: biofilm feeders	6	–25.5	0 ± 30

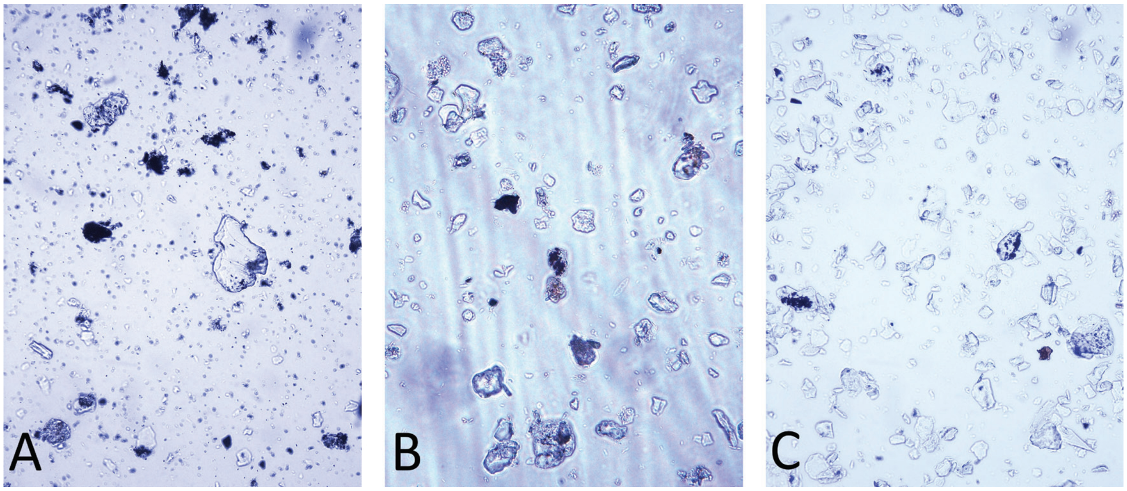

FIGURE 3. Photomicrographs, ×400. (A) Typical gut contents of chironomid larva living in the upper part of the glacial river. (B) Typical gut contents of chironomid larva living in the sediment of an 8-yr-old pond. (C) Fine-grained sediment from water collected at the outlet of the glacial river.

river. As shown in Figure 3, parts a–c, typical gut contents of chironomid larvae in ponds and upper river reaches were very similar to sediment transported in the water column, indicating uncritical ingestion of particles released by the glacier. This suggests direct assimilation of ancient organic matter, or digestion of bacteria that feed on the organic matter.

Chironomidae are not only key organisms for assimilation of ancient carbon, but also for further transport of ancient carbon to the predator level, both in aquatic and terrestrial environments (Table 1). Within recently established ponds, larvae and adults of predacious diving beetles had a radiocarbon age of 1100–1200 yr, and ancient carbon was still present in diving beetle larvae in an 80-yr-old pond. Adult chironomids, with a radiocarbon age of 1040 yr, transferred ancient carbon to terrestrial predators like carabid beetles, spiders, and harvestmen. Thus, ancient carbon delivered by the glacier supports a pioneer food web that combined aquatic and terrestrial habitats. Even on 40-yr-old ground, the carabid beetle *Nebria nivalis* contained some ancient carbon. Because younger ponds seem to be key habitats for inclusion of ancient carbon into pioneer food webs, glacier fore-

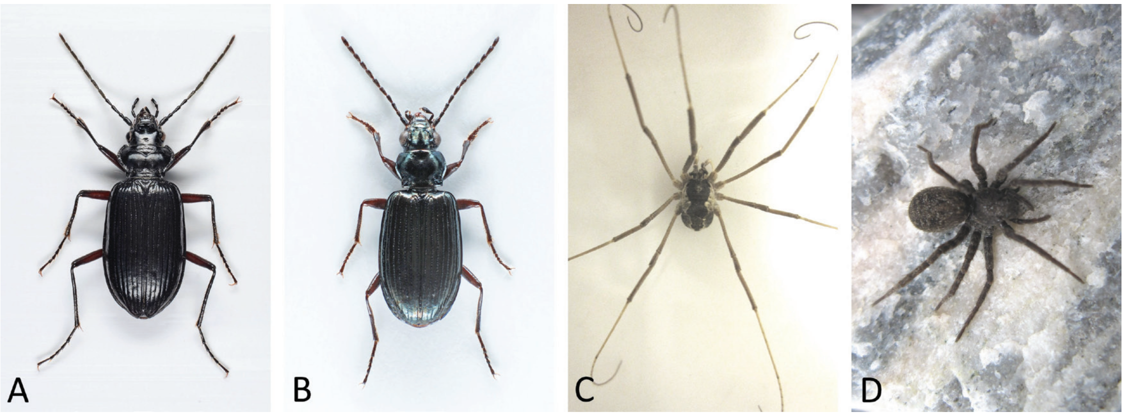

FIGURE 4. Terrestrial predators containing ancient carbon released by the glacier. (A) The carabid beetle *Nebria nivalis*. (B) The carabid beetle *Bembidion hastii*. (C) The harvestman *Mitopus morio*. (D) The wolf spider *Pardosa trailli*.

lands lacking such ponds may be unable to take advantage of ancient carbon in early faunal succession.

Chironomids were consumed by terrestrial predators throughout the snow-free season (Hågvar and Pedersen, 2015). These small midges often fall to the ground and are probably easier to catch than jumping springtails. As shown by Hågvar and Ohlson (2013), springtails, although abundant (Hågvar 2010, 2012), were unimportant as food at this site. Furthermore, springtails turned out not to be significant carriers of ancient carbon (Table 1), and their gut content revealed that they were mainly herbivores on biofilm or tiny pioneer mosses (Hågvar and Ohlson, 2013; Hågvar and Pedersen, 2015). In the foreland of the Rotmoos glacier in Austria, however, where ponds were lacking, pioneer predators relied to a high degree on springtails, and intraguild predation was common (Raso et al., 2014).

Close to the glacier, the snow bunting (*Plectrophenax nivalis* [L.]) might assimilate ancient carbon from both ponds and the river, as various Diptera including mud-living Tipulidae larvae are included in the diet (Hågvar et al., 2009b).

In a glacial foreland on Svalbard, Hodkinson et al. (2001) pointed to the fertilizing effect of airborne spiders and midges on nutrient-poor pioneer ground. In our site, also, locally produced midges, partly raised on ancient carbon, may contribute to early soil development and fertilization of pioneer plants.

A "Decomposer-First" Food Web

As remarked by Hågvar and Ohlson (2013), the use of ancient carbon sheds light on the so-called "predator-first paradox," which is that terrestrial predators like spiders, carabid beetles, and harvestmen colonize pioneer ground before herbivores and visible plants. It has been commonly assumed that these predators are fed by airborne input of invertebrate prey (Hodkinson et al., 2001, 2002; Coulson et al., 2003), or by pioneer springtails (Collembola) that decompose inblown debris (König et al., 2011). However, in the Hardangerjøkulen glacier foreland, terrestrial predators rely to a large degree on locally produced chironomids. As decomposers, chironomid larvae can use ancient organic material in pond sediments, immediately after the creation of ponds. Thus, the pioneer predators are part of a "decomposer-first" food web.

In this context, it is worth noting that the small, saprophagous fungus *Omphalina rivulicola* on a 6-yr-old moraine did not contain ancient carbon (Table 1). It has probably used recent organic material embedded in the moraine soil, and ancient organic material may have been too fine-grained and dispersed for the fungus.

Ponds as Biological Oases

Ponds act as carbon traps. First, fine particulate material in glacial meltwater tend to aggregate in depressions just outside the ice edge, resulting in ponds with soft sediments in which dipteran larvae may thrive. Second, also various windblown organic materials tend to aggregate in ponds. Flø and Hågvar (2013) showed that fragments and diaspores of pioneer mosses are blown into pioneer ground. The sediment of several ponds contained pioneer mosses of the genus *Pohlia,* that had germinated from wind-transported bulbils. These young moss plants soon die, partly being covered by fine sediments, and because they are adapted to the terrestrial environment. However, the accumulated moss biomass, as well as other windblown organic matter trapped by the water surface, contributes recent carbon to the ponds. Together with the chironomid tubes constructed by larval silk, the sediment of these 8-yr-old ponds contained a mixture of ancient and recent carbon. During sunny, still weather, water temperature can be high in such shallow ponds with dark sediments, creating good breeding conditions for chironomids. Thus, these ponds can be characterized as biological oases on barren ground, although their supporting role in terrestrial succession may easily be overlooked.

Ancient Carbon in Glacier-Fed Rivers

In Alaska, Hood et al. (2009) found that organic matter containing ancient carbon was transported all the way from glaciers to the Gulf of Alaska, supporting microbial life both in the river and in the marine ecosystem. The oldest particles had the highest bioavailability. In the European Alps, Singer et al. (2012) documented that all of 26 glaciers released biogeochemically diverse organic matter, up to 8500 yr old, which was used by microbial heterotrophic organisms in glacial rivers. Also here, the oldest particles were the most bioavailable.

Our data show that not only microbial organisms, but also invertebrates like chironomid larvae may use ancient carbon in glacial rivers. This opens the possibility of further transport to predator level, both within the river channel and in riparian terrestrial habitats. Fellman et al. (2015b) recently showed that chironomid larvae and predatory fish in an Alaskan glacier river assimilated ancient carbon. The larvae were probably feeding on a ^{14}C-depleted biofilm containing bacteria. However, chironomid larvae in glacier-fed river do not always contain ancient carbon. For example, there was a lack of ancient carbon in chironomid larvae collected in the Brigsdalsbreen glacial river, perhaps because this glacier was in an advancing phase when the study was done (Brittain et al., 2001). In addition, a proglacial lake is located at the front of Brigsdalsbreen, and particulate ancient carbon may therefore not reach the river due to sedimentation. Nonetheless, radiocarbon dating of chironomids from glacial rivers will be an easy way to check whether a given glacier releases bioavailable ancient carbon.

Age and Origin of the Ancient Carbon

Radiocarbon dating of organic material in sand and silt from the Hardangerjøkulen glacier changed from about 17,000–24,000 yr to 5160 yr when graphite particles from the phyllite bedrock were excluded. That was an important correction, but 5160 yr may still be the result of a mix of old and recent carbon, since the melting glacier also releases inblown, recent organic material. A mix of very old carbon and recent carbon can give many different radiocarbon ages, depending on the relative fraction of the two components. What "5160 yr" tells us is that the released organic material does contain ancient carbon. Likewise, the different radiocarbon ages from silt at the Hellstugubreen glacier in two different samples (3220 and 1450 yr, respectively) may be explained by different ratios between ancient and recent organic matter in the two samples.

There is a theoretical possibility that old, inorganic carbon from bedrock could enter aquatic food chains via dissolved $CaCO_3$. Certain aquatic algae are able to transform calcium bicarbonate to CO_2, which they use in photosynthesis. In this way, ancient carbon could be incorporated into algae-eating larvae. However, algae were absent or very rare in larval guts. Furthermore, ancient carbon was already present in freshly deposited silt at the ice edge, before ponds were created.

Hågvar and Ohlson (2013) suggested that the ancient carbon released from the Hardangerjøkulen glacier originated from soil and vegetation in periods when the glacier was absent. In that respect, the corrected age of 5100 yr corresponds well with the fact that the glacier was periodically absent 4000–8000 yr ago (Nesje et al., 2008). However, recent studies have shown that glaciers in different areas of the world collect and release degradable aerosols, which are long-transported anthropogenic combustion products from fossil fuels (Singer et al., 2012; Stubbins et al., 2012; Fellman et al., 2015a). In a case study from Alaska, Stubbins et al. (2012) revealed deposition of a high variety of radiocarbon-depleted aerosols on the glacier surface, and that the glacier outflow contained dissolved organic matter with corresponding molecular signatures. Of special interest were highly biodegradable long-chained fatty acids associated with soot. Fellman et al. (2015a) confirmed deposition of combustion products on snow in Alaska, and transport to the ocean.

Long-distance transport of such biodegradable aerosols could explain the basis of all our results: the old carbon in silt close to the ice edge, assimilation of ancient carbon by chironomid larvae in ponds and rivers, as well as further transport to aquatic and terrestrial predators. The transport of ancient carbon through a lake in the investigated river system without full sedimentation indicates very small particles, which is in accordance with the aerosol hypothesis. It would also explain why both glaciers in our study, on bedrock with and without carbon, released ancient carbon.

More Case Studies

Along with increasing melting rate of glaciers, the release and biological use of glacier-derived carbon deserves closer attention, both in forelands, in rivers, and in certain coastal areas. The possibility of supporting pioneer food webs at the ice edge is a fascinating aspect. More case studies are needed to see whether this is a general or special phenomenon. This can be tested by radiocarbon dating of easily-collected invertebrate predators. Perhaps invertebrate communities in pond-free forelands are unable to use ancient carbon delivered by the glacier. Many forelands lack ponds, in which case the assimilation of released, ancient carbon could be restricted to organisms in the glacial river. The documentation of the use of ancient carbon by chironomid larvae in glacial rivers opens for further studies, both among other invertebrate groups, and the possible transfer of ancient carbon to predators, within and along the river channel.

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