

## ECOLOGICAL PATTERNS ALONG TWO ALPINE GLACIAL STREAMS IN THE FITZPATRICK WILDERNESS, WIND RIVER RANGE, USA

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**ABSTRACT.**—Most alpine glaciers worldwide are receding rapidly, revealing new streams to be colonized by aquatic organisms. Several major questions are whether these new streams are colonized by aquatic organisms, how fast this colonizing occurs, which organisms are colonizing, and what factors constrain dispersal. We examined longitudinal patterns (over a length of 5 km) in physicochemistry, as well as periphyton and macroinvertebrate composition in 2 glacier streams (Dinwoody, Gannett) in the Wind River Range wilderness, home to the few remaining glaciers in the contiguous USA. We found that newly emerged streams near the glacial snout were inhabited by periphyton and macroinvertebrates, suggesting rapid colonization by biota. Longitudinal (distance from the glacier) patterns were documented in water temperature (increasing), particulate organic carbon (decreasing), particulate phosphorus (decreasing), and benthic organic matter (increasing in Dinwoody). Macroinvertebrate total density and operational taxonomic units (OTUs) also increased with distance from the glacier. Chironomids (Diamesinae) dominated the macroinvertebrate assemblages, a result supporting the importance of water temperature as a controlling factor influencing macroinvertebrates. Sixteen OTUs were documented, with low-elevation mayflies, stoneflies, and caddisflies occurring at sites with warmer temperatures (>3.0 °C). Only Diamesinae were found at sites nearest the glacial source where water temperature was <2.0 °C. As glaciers recede, the physicochemistry of alpine streams will change and likely differ among glacial streams. The mechanistic basis for the consequent effects of these physicochemical changes on freshwater biodiversity is still poorly understood.

**RESUMEN.**—La mayoría de los glaciares alpinos de todo el mundo están desapareciendo con rapidez, lo cual da origen a la existencia de nuevos arroyos que pueden ser colonizados por organismos acuáticos. Es importante determinar si dichos organismos acuáticos pueden colonizar los nuevos arroyos, qué organismos los están colonizando, con qué rapidez y cuáles son los factores fundamentales que frenan la dispersión. Examinamos patrones longitudinales (aproximadamente 5 km) en fisicoquímica, perifiton y macroinvertebrados en dos arroyos glaciares (Dinwoody, Gannett) en Wind River Range, donde se encuentran los glaciares que quedan en los Estados Unidos Continentales. Encontramos que los nuevos arroyos que se encuentran cerca de la orilla del glaciar estaban habitados por perifiton y macroinvertebrados, lo cual sugiere una rápida colonización de biota. Los patrones longitudinales (según la distancia al glaciar) se documentaron en la temperatura del agua (en aumento), carbono orgánico particulado (en disminución), fósforo particulado (en disminución) y materia orgánica bentónica (en aumento, en Dinwoody). La densidad total de macroinvertebrados y las unidades taxonómicas operacionales (OTUs) también se incrementaron al aumentar la distancia al glaciar. Los quironómidos (Diamesinae) dominaban entre los grupos de macroinvertebrados, lo cual refuerza la importancia de la temperatura del agua como factor de control que influye en los macroinvertebrados. Se documentaron dieciséis OTUs donde se encontraron efemerópteros, plecópteros y frígneas en terrenos con temperaturas más cálidas (>3.0 °C). Sólo se encontró Diamesinae en lugares cercanos al nacimiento del glaciar, donde la temperatura del agua era <2.0 °C. La estructura fisicoquímica de los arroyos alpinos se modificará y probablemente será diferente entre los arroyos glaciares, a medida que los glaciares desaparezcan, lo cual traerá consecuencias para la biodiversidad de agua dulce, para la cual las bases funcionales están poco comprendidas.

Glaciers are the earth's largest freshwater reservoirs, covering ca. 10% of the earth's surface (Knight 1999). However, most alpine glaciers globally are receding rapidly, and many are expected to be gone by 2050 (Zemp et al. 2006, IPCC 2007). Consequently, many alpine glacial systems are threatened (Jacobsen et al.

2012). For example, the remaining 25 glaciers (of 150 glaciers estimated in 1850) in Glacier National Park, USA, are expected to disappear within the next 50 years (Hall and Fagre 2003). This loss of glaciers has been linked with a concurrent loss in biotic diversity of alpine stream macroinvertebrates in particular

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(Finn et al. 2012, Jacobsen et al. 2012). Because many glacial systems exist in remote areas that have never been studied, it is important that baseline studies be undertaken to document the ecological changes influencing these ecosystems.

Receding glaciers reveal stream channels that can be colonized over time by aquatic biota (Milner et al. 2009, Finn et al. 2010). Some glacial streams may predate the formation of glaciers, while other streams may be formed quite recently via glacial erosion. Glacial stream water sources (proportions of snowmelt, ice melt, and groundwater) and stream flow dynamics (such as timing, discharge, and extreme flows) also will change as glaciers recede (Milner et al. 2009). Such changes will allow the colonization of some alpine streams by nonalpine macroinvertebrates, such as those requiring warmer water temperatures (Brown et al. 2007). Climate change predictions further suggest that precipitation patterns will change, resulting in alterations in alpine floodplain hydrology and a greater potential for some streams to become intermittent (Hannah and McGregor 1997, Robinson and Matthaei 2007). Large changes in the timing and discharge of meltwater from alpine glaciers will put further stress on glacial streams and their associated biota. Glaciers are powerful agents of physical erosion (Patterson 1994). An earlier and larger runoff from rapidly melting snowfields not buffered by the ice mass of alpine glaciers will change the quantity, grain size, and timing of sediment delivery, potentially altering the physical disturbance regimes in glacial streams.

Glacial streams, in general, show strong longitudinal zonation in physical and chemical characteristics (e.g., changes in bed stability, solute concentration, and temperature) that is reflected in the biota inhabiting particular reaches (Milner and Petts 1994, Milner et al. 2001). As glaciers recede, sites once near the glacier snout will be further downstream and more distant from the glacial water source. Depending on the recession rate, this in-stream distance from the glacier will change the physicochemical nature of a stream site over space and time. Thus, downstream sites will exhibit not only the longitudinal zonation (spatial perspective) found in most glacial streams but also successional development (temporal perspective) as the glacier continues

to recede. For instance, specific sites along a stream exhibit changes over time as the degree of glacial influence changes over time (see Milner et al. 2008).

This study documents the colonization by macroinvertebrates of recently emerged streams following glacial recession in Wyoming wilderness streams. As alpine landscapes are transformed by glacial recession, the colonization of newly revealed alpine streams by aquatic biota, macroinvertebrates in particular, will ultimately occur. The question arises as to the variation in colonization among glacial stream systems (*sensu* Finn et al. 2012) and whether patterns over space and time follow the general predictions of earlier models, such as that of Milner et al. (2001). A primary goal of this study was to assess the longitudinal development (i.e., distance from the glacial snout) of 2 glacial streams in the Wind River Range, Wyoming, USA, a remote alpine region with almost no existing ecological information on the freshwater systems.

## METHODS

### Study Area

The Wind River Range trends northwest, rising above both the western Green River valley, a tributary to the Colorado River system, and the eastern Wind River valley, a tributary to the Missouri/Mississippi system. The Wind River Range, a protected wilderness, forms the continental divide 500–2200 m above the surrounding high arid plains that lie at an elevation of ca. 2000 m asl. The continental divide forms a physiographic barrier that collects precipitation. Because of the mountainous location and high elevation, most precipitation in the range falls as snow. Two confluent glacier source streams in the central part of this remote range were selected for study. The glacier sources are ca. 40 km from the nearest town and ca. 100 km from the nearest significant industrial emission source. The 2 glacier-melt streams are in the neighboring Gannett Creek and Dinwoody Creek drainages, with flows originating from respective glacial snouts at ca. 3400 m asl (Fig. 1). These glacial streams flow from the largest (Gannett) and fourth-largest (Dinwoody) glaciers in the Wind River Range, home to the most extensive concentration of glaciers (63) in the USA Rocky Mountains (Meier 1951).

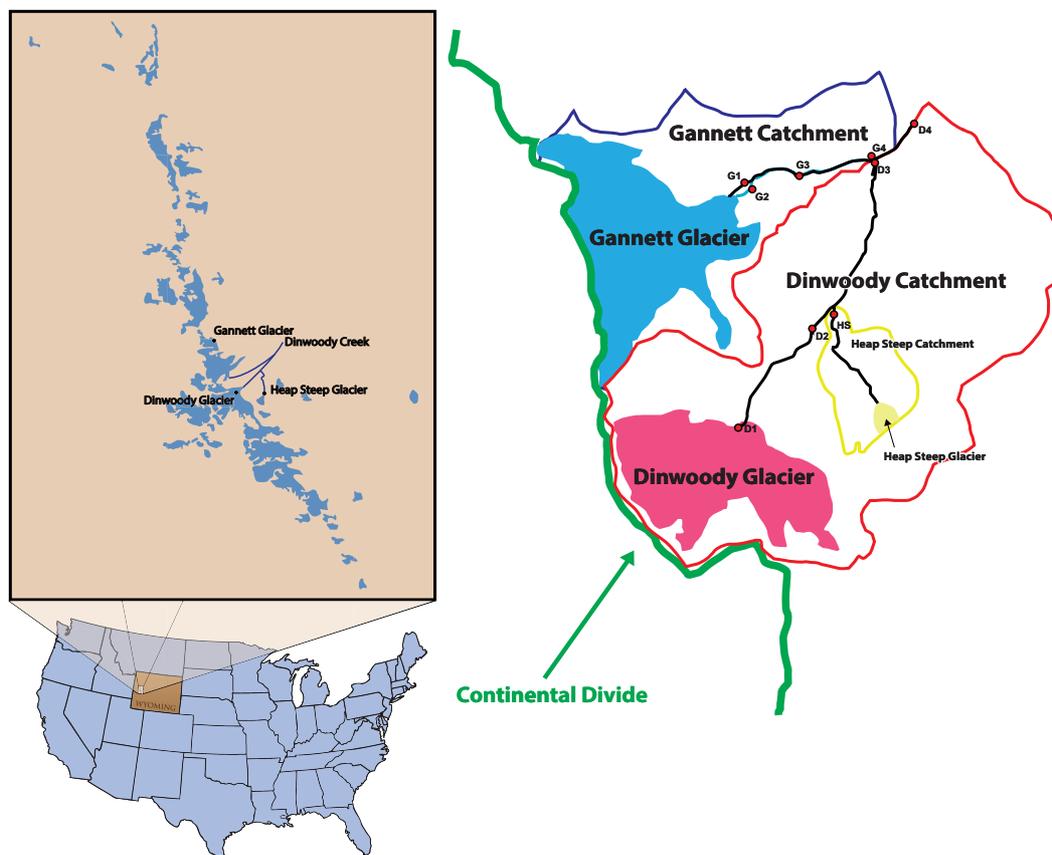


Fig. 1. Map of the of the study sites within the Wind River Range, Wyoming, USA. The Dinwoody glaciers (sites labeled D) and Gannett glaciers (sites labeled G) are in adjacent catchments on the eastern flank of the range. Site HS flowed from Heap Steep Glacier into the Dinwoody system.

Although there are a few cirque glaciers on the windward (southwestern) side, most Wind River Range glaciers are cirque glaciers on the leeward side, a few are valley glaciers, and 2 glaciers span the continental divide.

The Dinwoody and Gannett glaciers were formed in cirques below the range's highest peaks: Gannett Peak, Mount Helen, and Mount Warren. Wyoming's highest point, Gannett Peak (4205 m asl), lies along the continental divide and is the SW divide of the Gannett Creek catchment (area 71 km<sup>2</sup>, 39% glaciated). Similarly, Dinwoody Peak is in the SW corner of the Dinwoody catchment (area 137 km<sup>2</sup>, 19% glaciated) and captures precipitation in the Dinwoody Creek valley. Both catchments trend to the northeast. The confluence of Gannett and Dinwoody Creeks is at the eastern end of Floyd Wilson Meadow at ca. 3040 m asl

(Fig. 1). The cirques of Gannett and Dinwoody glaciers are geologically composed of the oldest granitic gneiss in the Wind River Range (Love and Christiansen 1985). While Dinwoody Creek flows to the confluence with Gannett Creek entirely in this geologic province, Gannett Creek originates in the same rock type but also flows over a bisecting 2600 Ma rock composed of grandiorite to porphyritic and equigranular granite. Feldspar containing minerals such as apatite, sometimes associated with pegmatite and occurring in granitic bedrock, are sources of particulate phosphorus (PP) that when dissolved in water become ortho-phosphorus (PO<sub>4</sub>-P). Upstream of the confluence, Dinwoody Creek flows from Dinwoody Glacier for ca. 4.5 km with an elevation loss of 450 m (10% slope), while Gannett Creek flows from Gannett Glacier for

TABLE 1. General site description with field-recorded spot measures.

Site	Site name	Coordinates	Distance from glacier (m)	Elevation (m asl)	Temperature (°C)	Turbidity (NTU)	pH	Conductivity ( $\mu\text{S} \cdot \text{cm}^{-1}$ at 20 °C)	Dissolved oxygen ( $\text{mg} \cdot \text{L}^{-1}$ )
D1	Dinwoody below snout	No GPS data	10	3390	1.6	9.35	5.9	4.3	12.2
D2	Dinwoody Ck 2	43°11.133' N, 109°37.560' W	1480	3311	3.7	43	6.4	9.4	10.8
HS	Heap Steep tributary	43°11.188' N, 109°37.351' W	1325	3283	4.1	3.4	6.7	16.5	10.7
D3	Dinwoody Ck 3	43°12.391' N, 109°36.888' W	4370	3064	5.4	10.5	6.4	18.8	10.9
D4	Dinwoody below confluence	43°12.841' N, 109°36.438' W	4450	3010	4.3	11.5	6.9	14.9	10.4
G1	Gannett snout north	43°12.245' N, 109°38.220' W	243	3363	3.4	22.8	6.5	8.1	10.8
G2	Gannett snout south	43°12.216' N, 109°38.184' W	20	3373	1.3	23.9	5.9	4.3	13
G3	Gannett Ck 3	43°12.304' N, 109°37.686' W	2100	3213	3.0	13.8	6.1	10.1	11.9
G4	Gannett Ck 4	43°12.440' N, 109°36.910' W	3150	3051	4.0	19.2	5.9	8.8	11.2

ca. 2.0 km with an elevation loss of 324 m (18% slope).

### Study Sites

Nine sites were selected along the 2 study streams to incorporate longitudinal patterns in stream development with distance from the glacier (Fig. 1, Table 1). Four sites were sampled on the mainstem Gannett Creek (G1–G4), and 4 sites were sampled on the mainstem Dinwoody Creek (D1–D4). Uppermost sites (ca. 3380 m asl) were located as close to the glacier snout as practical (D1, G2), in most cases within 10–30 m. An exception was G1 where the stream flowed over an exposed rock face upstream of the study site; this site was ca. 240 m below the glacial snout. The lowest-elevation site was downstream of the confluence of Dinwoody Creek and Gannett Creek at 3010 m asl, referred to as D4 on Dinwoody Creek and ca. 5 km distant from D1. A second glacial tributary (HS) was sampled in the Dinwoody catchment, and this tributary flowed from Heap Steep Glacier and was used to compare with an adjacent site (D2) on the Dinwoody mainstem. Streams were sampled during the first week of September 2010, with each site representing 20–30 m of stream channel.

### Physicochemistry

At each site, electrical conductivity (at 20 °C), water temperature, pH, and turbidity were spot-measured by using portable field meters. In addition, a water sample (1 L) was collected, kept in an iced cooler, and returned to the laboratory for analysis. In the laboratory, alkalinity, sulfate ( $\text{SO}_4$ ), nitrate ( $\text{NO}_3\text{-N}$ ), nitrite ( $\text{NO}_2\text{-N}$ ), dissolved nitrogen (DN), particulate nitrogen (PN), phosphorus ( $\text{PO}_4\text{-P}$ ), particulate phosphorus (PP), dissolved organic matter (DOC), and particulate organic matter (POC) were analyzed following methods detailed in Tockner et al. (1997). Sulfate, DN, and DOC were below analytical detection limits at all sites and are not discussed further.

### Seston, Periphyton Biomass, and Benthic Organic Matter

Seston ( $n = 3$ ) was collected at each site using a drift net (1 m long, 100  $\mu\text{m}$  mesh, aperture diameter 11 cm). Water velocity (MiniAir2, Schiltknecht Ag, Switzerland) was recorded at the net aperture to calculate the volume of water filtered. Following collection,

the contents of the net were filtered (Whatman GFF filters) and any macroinvertebrates removed. In the laboratory, the filter was dried at 60 °C, weighed, ignited at 550 °C, and reweighed, with the difference in weights giving the ash-free dry mass (AFDM) of each sample.

Periphyton biomass was quantified by using a metal brush to scrape a known area from the surface of 5 randomly selected stones from the stream bottom within each study reach. The brush was rinsed with distilled water, and the periphyton slurry was filtered through Whatman GFF filters and frozen until analyzed in the laboratory as AFDM (as above).

#### Macroinvertebrates

Macroinvertebrates were collected from each site by using a Hess sampler (0.04 m<sup>2</sup>, 250 µm mesh,  $n = 3$ ) and were preserved in the field with 70% ethanol. In the laboratory, all macroinvertebrates were handpicked from each sample, identified (usually subfamily or genus), and counted. Due to the varying level of taxa identification, taxa were classified as operational taxonomic units (OTUs) in the analysis. The remaining material in each sample was used to estimate the amount of benthic organic matter as AFDM. Identifications were based on Merritt and Cummins (1984).

#### Data Analyses

Data were examined for longitudinal patterns in each system, as well as for differences between each stream. Longitudinal patterns were assessed using regression (linear or non-linear for best fit), with distance from the glacier as the independent factor, and between-stream differences were tested using a standard *t* test (Zar 1984). Data were  $\log(x + 1)$  transformed prior to analysis to meet assumptions of normality. Macroinvertebrate assemblages also were examined using nonmetric dimensional scaling analysis (NMDS) on taxa (as OTUs) relative abundance data to illustrate any spatial differences between sites. All statistics were computed with Statistica software (Statsoft, version 7).

## RESULTS

### Physicochemistry

Water temperature ranged from 1.3 to 5.4 °C among sites (Table 1). The lowest recorded

temperatures (1.3, 1.6 °C) were at the highest-elevation sites (G2, D1) nearest the glacier snouts of Gannett and Dinwoody Glaciers, respectively (Fig. 1). A warmer temperature was noted at upper site G1 (3.4 °C) where the stream flowed over an exposed rockface upstream of the study site. Water temperature increased as each stream flowed down valley and gained heat through solar radiation absorption and air temperature exchange (Fig. 2a). Primarily because of the low temperatures, dissolved oxygen concentrations were at saturation or supersaturation with values all above 10.4 mg · L<sup>-1</sup>. Electrical conductivity ranged from 4.3 to 18.8 µS · cm<sup>-1</sup>, with highest values in Dinwoody Creek. Turbidity values ranged between 3.4 (HS) and 43 NTUs (D2) but were usually between 10 and 20 NTUs. Values for pH ranged from 5.9 to 6.9.

Particulate organic carbon (POC) ranged from 0.11 mg C · L<sup>-1</sup> to 0.39 mg C · L<sup>-1</sup> and averaged 0.21 mg C · L<sup>-1</sup> in both catchments. Using all sites, POC significantly decreased with distance from the glacier (Fig. 2b). Nitrite concentrations were below detection (<1.0 µg N · L<sup>-1</sup>) in Gannett and averaged only 1.4 µg N · L<sup>-1</sup> in Dinwoody. Nitrate concentrations averaged 289 µg N · L<sup>-1</sup> in Dinwoody and 319 µg N · L<sup>-1</sup> in Gannett. Particulate nitrogen (PN) ranged from 11.3 µg N · L<sup>-1</sup> (G1) to 29.8 µg N · L<sup>-1</sup> (D1), excluding an outlier of 125.1 µg N · L<sup>-1</sup> at D2, and averaged 18.4 µg N · L<sup>-1</sup> overall. PO<sub>4</sub>-P concentrations averaged 1.7 µg P · L<sup>-1</sup> in Dinwoody Creek, while being significantly higher and averaging 5.5 µg P · L<sup>-1</sup> in Gannett Creek (*t* test:  $P < 0.0001$ ). Particulate phosphorus (PP) averaged 16.3 µg P · L<sup>-1</sup> in Dinwoody and 30.6 µg P · L<sup>-1</sup> in Gannett. Highest PP values were found at sites nearest the glacier (>35 µg P · L<sup>-1</sup>), and values decreased downstream (5.4 µg P · L<sup>-1</sup> at D3, 15.4 µg P · L<sup>-1</sup> at G4; Fig. 2c). PP increased at site D4 because of inputs from Gannett Creek.

### Seston, Periphyton Biomass, and Benthic Organic Matter

Seston concentrations were low in both systems, averaging 0.029 g · m<sup>-3</sup> in Dinwoody and 0.046 g · m<sup>-3</sup> in Gannett, with no discernable longitudinal patterns. Periphyton biomass, measured as AFDM, was ca. 2-fold higher in Dinwoody Creek sites above the confluence ( $\bar{x} = 4.80$  g · m<sup>-2</sup>) than in Gannett Creek ( $\bar{x} = 1.97$  g · m<sup>-2</sup>; *t* test:  $P = 0.027$ ).

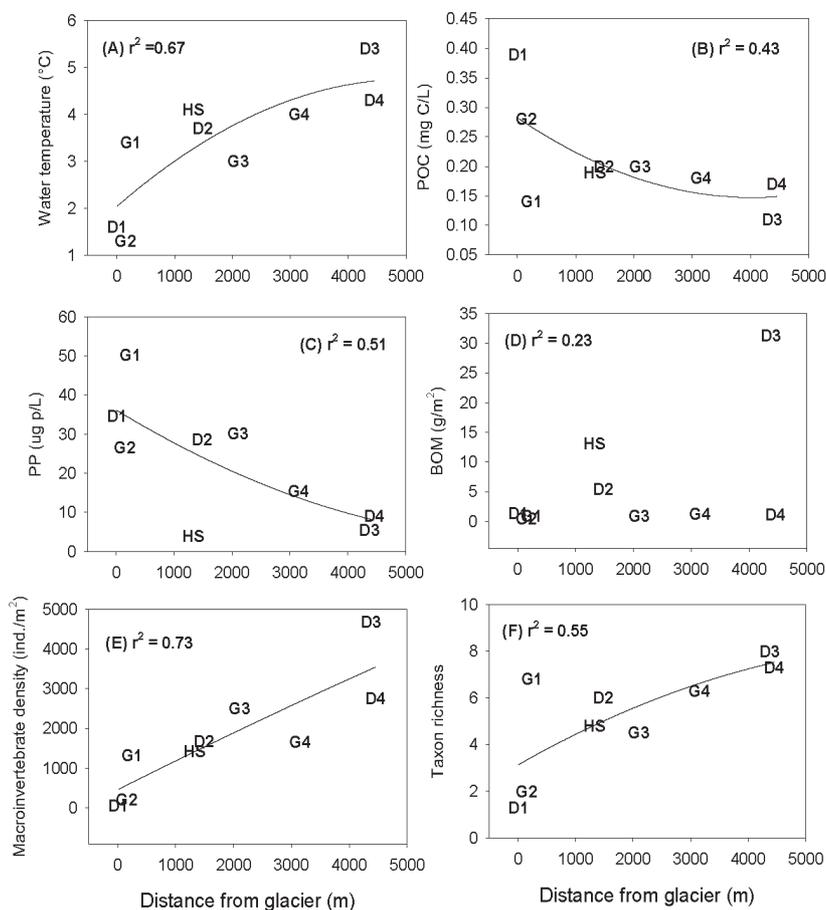


Fig. 2. Regressions (linear or nonlinear for best fit) of (A) water temperature, (B) particulate organic carbon (POC), (C) particulate phosphorus (PP), (D) benthic organic matter (BOM), (E) macroinvertebrate total density, and (F) OTUs against distance from the glacier source. Sites are labeled as in the text: D = Dinwoody, G = Gannett, and HS = Heap Steep. Regression lines are displayed only for significant regressions, except for plot B which was nearly significant.

Periphyton levels displayed no significant longitudinal patterns in either system (overall  $\bar{x} = 1.90 \text{ g} \cdot \text{m}^{-2}$ ). The amount of benthic organic matter (BOM) was 11-fold higher in Dinwoody ( $\bar{x} = 10.49 \text{ g} \cdot \text{m}^{-2}$ ) than in Gannett ( $\bar{x} = 0.90 \text{ g} \cdot \text{m}^{-2}$ ;  $t$  test:  $P < 0.0001$ ). Excluding site D4, BOM increased substantially downstream in Dinwoody, averaging  $1.35 \text{ g} \cdot \text{m}^{-2}$  at the snout to  $31.33 \text{ g} \cdot \text{m}^{-2}$  at D3 (Fig. 2d). BOM values in Gannett were low, ranging from  $0.52$  to  $1.30 \text{ g} \cdot \text{m}^{-2}$ , and showed no longitudinal pattern.

#### Macroinvertebrates

Macroinvertebrate total density ranged from an average of  $61 \text{ individuals} \cdot \text{m}^{-2}$  at Dinwoody glacial snout site (D1) to  $4686 \text{ individuals} \cdot \text{m}^{-2}$

at D3. Total density significantly increased with distance from the glacier in each stream (Fig. 2e). Sites near the snouts had the lowest average macroinvertebrate total densities, except for the relatively warm site G1, with an average density of  $1331 \text{ individuals} \cdot \text{m}^{-2}$ . Average total densities were similar between catchments (Dinwoody  $\bar{x} = 2119 \text{ individuals} \cdot \text{m}^{-2}$ ; Gannett  $\bar{x} = 1423 \text{ individuals} \cdot \text{m}^{-2}$ ;  $t$  test:  $P = 0.49$ ).

Macroinvertebrate OTUs increased with stream distance from each glacier (Fig. 2f). The number of OTUs ranged from 2 to 15 among sites, and only 2 OTUs were found at the uppermost sites in both glacier streams (sites D1, G2). The warmer G1 site had an average OTU of ca. 7. The highest OTU number was

TABLE 2. Average density (individuals  $\cdot$  m<sup>-2</sup>) of macroinvertebrate operational taxonomic units (OTUs) collected from each site in the Dinwoody and Gannett basins. See map for locations of sites on each stream. Two distinct morphotypes were evident for Diamesinae (morph-1, morph-2).

Order	Family	Subfamily/genus	Dinwoody					Gannett				
			D1	D2	HS	D3	D4	G1	G2	G3	G4	
Coleoptera	Halipidae	<i>Halipias</i>	22	0	0	0	0	0	0	0	0	0
Diptera	Chironomidae	Diamesinae (morph-1)	66	1111	865	1469	2008	737	99	2195	1051	0
Diptera	Chironomidae	Diamesinae (morph-2)	0	330	374	303	396	231	149	171	380	0
Diptera	Chironomidae	Orthocladiinae	0	66	132	1557	39	0	22	22	73	0
Diptera	Simuliidae	<i>Prosimulium</i>	0	59	88	1159	66	127	0	77	22	0
Diptera	Empididae	<i>Chelifera</i>	0	0	44	0	0	0	0	0	0	0
Diptera	Blephariceridae		0	0	0	88	33	0	0	0	0	0
Ephemeroptera	Baetidae	<i>Baetis</i>	0	22	235	248	0	0	0	22	33	0
Ephemeroptera	Heptageniidae	<i>Cinygmula</i>	0	0	0	51	44	0	0	0	66	0
Ephemeroptera	Siphonuridae	<i>Ameletus</i>	0	0	0	33	44	22	0	0	0	0
Ephemeroptera	Heptageniidae	<i>Rhithrogena</i>	0	0	0	0	138	22	0	61	51	0
Hydracarina			0	0	0	73	0	44	22	0	22	0
Plecoptera	Chloroperlidae	<i>Alloperla</i>	0	37	0	44	66	51	0	22	33	0
Plecoptera	Chloroperlidae	<i>Utaperla</i>	0	0	0	88	37	0	0	0	0	0
Plecoptera	Nemouridae	<i>Zapada</i>	0	22	0	22	0	22	0	0	66	0
Trichoptera	Limnephilidae	<i>Allomyia</i>	0	44	0	0	0	138	0	0	0	0

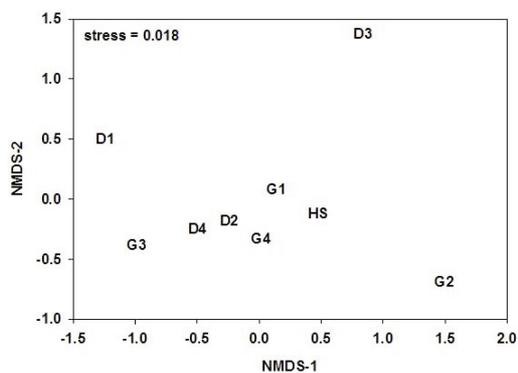


Fig. 3. Scatterplot of the NMDS analysis based on OTU relative abundances at the different sites. Stress level was 0.018, indicating excellent separation of sites.

at sites above (D3 = 15 OTUs) and below (D4 = 13 OTUs) the confluence of Dinwoody and Gannett. Overall, 16 OTUs were identified at the 9 sites. There was no significant difference in OTUs between catchments ( $t$  test:  $P = 0.74$ ).

Chironomidae (mostly Diamesinae: 2 OTUs) were most common at all sites, representing between 35% and 95% ( $\bar{x} = 85\%$ ) of the individuals collected (Table 2). The most frequent genera included the blackfly *Prosimulium*; mayflies *Baetis*, *Cinygmula*, and *Rhithrogena*; and the stoneflies *Alloperla* and *Zapada*. The trichopteran genus *Allomyia* was found in both Dinwoody Creek and Gannett Creek at higher elevations ca. 3300 m asl, and Blephariceridae and the stonefly genus *Utaperla* (Chloroperlidae) were found only at the lowest-elevation sites (D3 and D4). *Alloperla* was missing from the glacier snout sites D1 and G2 but was found in the warmer G1 site. *Rhithrogena* and Hydracarina were found only in the Gannett catchment.

The NMDS analysis reflected these differences in assemblage structure between the sites with a very low stress level (Fig. 3). Sites D1, D3, and G2 were clearly separated from the other sites in the ordination. Both D1 and G2 were nearest the glacial snouts with the coldest water temperature and a taxonomic composition dominated by chironomids (mostly Diamesinae), whereas site D3 had the highest number of OTUs of all the sites. The other sites were grouped closer in the NMDS ordination, with chironomids dominating these assemblages, along with the presence of a variety of other taxa.

## DISCUSSION

Although Dinwoody catchment was 2-fold larger in area than Gannett, the glaciated percentage of each catchment was 2-fold greater in Gannett (39% vs. 19% as of 2009). The greater stream slope (17.5% vs. 10%) and shorter stream length (2.0 km vs. 4.5 km) in Gannett over Dinwoody, respectively, further caused the residence time of water to be longer in Dinwoody Creek (ca. 2 h) than in Gannett (ca. 40 min). Regardless, both systems displayed similar longitudinal trends in temperature, particulate phosphorus, and particulate and benthic organic matter with distance from each glacier. Macroinvertebrate total density and OTUs also showed longitudinal increases with distance from the glacier in both systems.

### Spatial Patterns in Physicochemistry

Sites nearest the glaciers had typically low water temperatures (i.e.,  $<1.5$  °C), as documented for glacier streams globally (Tockner et al. 1997, Milner et al. 2001, Brown et al. 2006, Finn et al. 2010). Somewhat unexpected was the degree of warming within a relatively short distance from the glacier snout, such as the  $>3.4$  °C temperatures at G1 and D2. Site G1, in particular, was only ca. 250 m below the snout, but the water flowed over an exposed rockface that enhanced the thermal warming from solar radiation. At present, most glacial streams originate above treeline, thus potential exposure to direct solar inputs is high. This solar warming allows the colonization of glacier streams at high elevations ( $<3000$  m asl) by aquatic macroinvertebrates not typically found in coldwater systems or at high elevations (see Finn et al. 2010). Glacial recession in concert with environmental warming enhances the potential colonization of alpine streams by low-elevation taxa (Finn et al. 2010) but also the potential loss of cold stenotherms (Muhlfeld et al. 2011, Sauer et al. 2011, Jacobsen et al. 2012).

As expected, water temperature increased longitudinally in both systems. However, the shorter residence time and relative discharge of Gannett Creek caused the lower site on Dinwoody (D4) to actually be colder (ca. 1.1 °C) than Dinwoody above the confluence (site D3) due to the mixing of the colder Gannett Creek water with Dinwoody. In drainages

having a mix of glacier sources, this spatial heterogeneity in water temperatures could be quite complex at the floodplain level (Uehlinger et al. 2003). For instance, warmer streams could flow in rather close proximity to cold glacier streams (e.g., HS with D2), or the merging of glacier streams (e.g., at D4) could alter longitudinal temperature patterns. This temperature mosaic of alpine streams clearly influences the spatial distribution of aquatic macroinvertebrates, as documented in a number of studies (Burgherr et al. 2002, Hieber et al. 2005, Brown et al. 2006).

Solute concentrations produced by physical and chemical weathering are typically low in alpine areas because of low temperatures; short water residence times; and slow weathering of bedrock geology (Hodson et al. 2004), granitic rock in this particular case. Solute concentrations increase, however, when glacial erosion produces fine particulates (glacial flour) with large surface areas that increase the rate of dissolution (Martin and Meybeck 1979). The suspended sediment surface area and solubility strongly affect the solute composition of the stream in which they are suspended. These physical processes are reflected in the overall higher conductivity, alkalinity, and TIC values in Dinwoody than in Gannett Creek. The higher particulate phosphorus in Gannett Creek, in contrast, can be attributed to the greater percentage glaciation in a relatively smaller catchment than Dinwoody, as PP is directly related to the glacier flour in the system (Malard et al. 2000). Furthermore, longitudinal changes in these constituents, PP in particular, provide a good indication of the glacial source water influence at a site.

Nitrogen sources in each catchment likely result from long-term increases in atmospheric deposition in the wilderness area (Grenon et al. 2010). Both PN and  $\text{NO}_3\text{-N}$  were high in both catchments, and most probably are due to this atmospheric deposition of nitrogen. Similar findings have been documented for glacial floodplain streams in the Swiss Alps (Malard et al. 2000, Hieber et al. 2005). The retention of nitrogen in glacial streams has been found to be low (Robinson et al. 2002), with most dissolved forms of nitrogen being transported downriver to lower-elevation streams and rivers.

Phosphorus sources in the proglacial zone originate from snow condensation nuclei,

enmeshed atmospheric particulates captured in snowfall and dust fall, airborne organic matter like plant detritus and insects (Lockwood et al. 1991), sloughing cryoflora and/or microbes from 'cryoconite holes' (Mader et al. 2006), groundwater, and glacier flour. Phosphorus levels ( $\text{PO}_4\text{-P}$ , DP, and PP) were significantly greater in Gannett Creek than in Dinwoody, perhaps again reflecting the higher percentage glaciation and associated processes in the Gannett catchment. Low phosphorus levels in Dinwoody suggest P was limiting or was quickly being taken up by biota. Phosphorus is quickly taken up in streams in the Swiss Alps (Robinson et al. 2002), suggesting that it is a limiting nutrient in many alpine waters (e.g., Tockner et al. 1997).

#### Spatial Patterns in Periphyton Biomass

Hydrologic factors such as the 67% lower water residence time in Gannett Creek catchment may also explain the significantly higher periphyton biomass in Dinwoody than in Gannett Creek. The lower residence time may be indicative of a lower transient storage area in Gannett than Dinwoody, allowing any available nutrient to be quickly transported downstream. For instance, the higher periphyton biomass in Dinwoody Creek may explain the lower phosphorus concentrations in Dinwoody Creek, as nutrients are already removed from the water through biotic uptake. We assume that the removed phosphorus would be taken up by biota in a stoichiometric manner in Dinwoody Creek. Hall and Tank (2003) showed with a stoichiometric model in a similar remote Wyoming alpine environment that areal N uptake was comparable to measured uptake values.

#### Spatial Patterns in Macroinvertebrates

Finn et al. (2010) noted that newly emerged glacial streams were colonized by alpine specialists and that lower sites were colonized by low-elevation species, and our results are consistent with these findings. With the earlier noted exception, the longitudinal zonation pattern (i.e., OTUs, total density, and benthic organic matter increase with distance to the glacier) found in most glacial streams was present in our study streams (see Milner et al. 2001). Lower sites had significantly higher water temperatures that we presume allow lower-elevation species to colonize. The exception to

this trend is the north tributary to Gannett Glacier (site G1). This high-elevation site (3360 m asl) had a much greater number of OTUs (8 vs. 2) and total density (ca. 1330 individuals  $\cdot$  m<sup>-2</sup> vs. <200 individuals  $\cdot$  m<sup>-2</sup>) compared to other colder sites close to the glacial snout (3.4 °C vs. 1.6 °C at D1 and 1.3 °C at G2). This latter pattern reflects current ideas in the spatial heterogeneity in macroinvertebrate diversity among alpine streams with differing degrees of glacial water influence (Finn et al. 2012, Jacobsen et al. 2012).

A primary goal in this study was to document the degree to which newly emerged streams at the glacier snout were colonized by macroinvertebrates and by which taxonomic groups. Additionally, because an endemic alpine invertebrate, the meltwater stonefly (*Lednia tumana*), has been identified in glacial meltwaters in Glacier National Park (Muhlfeld et al. 2011), the closest major glacial concentration outside the Wind River Range, we were interested in the occurrence of the meltwater stonefly in our samples. Stoneflies were found, but they were of different families and were found at lower elevations, rather than at the glacier snout. Regardless, the habitat template of new glacial streams in this study follows the glacial stream model proposed by Milner et al. (2001), in which low sediment stability and temperature limit assemblage structure in glacial headwaters.

Colonization at the uppermost sites was rapid and widespread by some alpine specialists, Diamesinae in particular. Milner et al. (2001) posited that streams below receding glaciers would initially be dominated by glacial stream specialists such as Diamesinae, and our results support this observation. This chironomid group dominated the population of all zoobenthos, ranging in abundance from 35% to 95% ( $\bar{x}$  = 84%). Periphyton and organic matter resources were present in all systems, although at moderately low levels. Regardless, organic matter resources were sufficient for sustaining populations of omnivorous invertebrates (see Zah et al. 2001, Füreder et al. 2003).

Long-term predictions indicate that most alpine glaciers will continue to recede, with many glaciers lost over time (Zemp et al. 2006). The loss of glacier ice mass will alter water source dynamics in alpine systems, particularly those in the arid western USA (Bell

et al. 2011). These alterations will have a significant impact on biota colonizing these systems (Milner et al. 2009). Our data suggest that at high-elevation sites, early macroinvertebrate colonizers are dominated by glacial stream specialists that can sustain their populations with the food resources generated by primary producers. As alpine glacial water sources change from predominantly ice melt to snowmelt, other biota will likely colonize these systems and directly influence biotic interactions, food web structure, and ultimately ecosystem functioning.

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