

Benthic Macroinvertebrate Assemblages in Kryal and Rhithral Lake Outlet Streams in the North Cascade Mountains

Author(s): Kelley L. Turner , Robin A. Matthews and Ashley K. Rawhouser

Source: Northwest Science, 90(2):206-227.

Published By: Northwest Scientific Association

DOI: <http://dx.doi.org/10.3955/046.090.0211>

URL: <http://www.bioone.org/doi/full/10.3955/046.090.0211>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

Kelley L. Turner¹, Hamer Environmental, 1510 South 3rd Street, Mount Vernon, Washington 98273

Robin A. Matthews, Institute for Watershed Studies, Huxley College of the Environment, Western Washington University, 516 High Street, Bellingham, Washington 98225

and

Ashley K. Rawhouser, North Cascades National Park, 810 State Route 20, Sedro-Woolley, Washington 98284

Benthic Macroinvertebrate Assemblages in Kryal and Rhithral Lake Outlet Streams in the North Cascade Mountains

Abstract

Alpine aquatic environments are one of the harshest on earth and are sensitive indicators of climate change. In Washington, the most glaciated state in the contiguous United States, relatively little is known about the effect of loss of glacial water sources on macroinvertebrate communities. Our study compares the water quality conditions and composition of benthic macroinvertebrates from five rhithral (snowmelt-fed) and five kryal (glacially-fed) lake outlet streams in the North Cascade Mountains, WA. Kryal streams were characterized by lower water temperatures, higher discharge rates, higher turbidities, and less stable in-stream channels compared to rhithral sites. A total of 24 985 specimens representing 96 macroinvertebrate taxa were collected. Rhithral lake outlet streams had significantly higher densities and supported more taxa than kryal sites (9049 individuals m⁻² and 82 taxa versus 821 individuals m⁻² and 38 taxa). Chironomidae dominated macroinvertebrate populations at all sites, although densities and taxa richness were significantly lower in kryal sites. Rhithral sites contained higher densities of non-insect taxa such as Acari, Oligochaeta, Nematelminthes, Planariidae, and crustaceans. Kryal sites were dominated by cold stenotherm or cool eurythermal taxa and supported glacial-tolerant taxa such as chironomids *Diamesa* and *Parorthocladius*, and the mayfly *Rhithrogena*. Water temperature, stream discharge, and turbidity were most strongly correlated to macroinvertebrate density and taxa richness. Our results suggest that glacial presence was the dominant factor influencing in-stream environmental conditions and macroinvertebrate assemblages of alpine lake outlet streams. Continued glacial retreat due to climate change may result in an overall loss of specialists and decreased regional diversity.

Keywords: benthic macroinvertebrates, climate change, kryal streams, glacier-fed streams

Introduction

Alpine environments, located between the permanent snow fields and treeline, represent the upper limits of terrestrial and freshwater ecosystems in both a physical and biological sense. They are generally characterized by large areas of exposed rock, steep topography, extreme seasonality, and reduced food resources. The combination of these conditions make alpine environments one of the most harsh on the earth, sensitive indicators to climate change (Brown et al. 2007, Füreder 2007), and result in highly specialized biotic communities adapted to these conditions. Within alpine environments, three general types of stream

systems have been defined based upon their primary water source: kryal streams, which are dominantly glacially-fed; rhithral streams, which are dominated by seasonal snowmelt; and krenal streams, which are dominated by groundwater (Steffan 1971, Ward 1994, Brittain and Milner 2001). Alpine streams often have contributions from two or more of these sources with the relative contribution varying spatially (stream-reach to catchment) and temporally (diel and seasonal; Brown et al. 2007). Studies from Europe, Alaska, South America, and New Zealand have demonstrated that difference in water sources among these streams affects their physical and chemical properties which in turn affect the resident macroinvertebrate communities (Milner and Petts 1994, Tockner et al. 1997, Brittain et al. 2000, Füreder et al. 2000, Füreder et al. 2001, Lods-Crozet et

¹Author to whom correspondence should be addressed.
Email: Kelley@HamerEnvironmental.com

al. 2001, Hieber et al. 2005, Winterbourn et al. 2008, Jacobsen et al. 2010).

Among these stream types, kryal-dominated streams (hereafter referred to as “kryal”) embody a harsh and highly unstable environment for biota, especially during summer when there are high diel fluctuations in water temperature, discharge, and concentrations of suspended solids and nutrients as glaciers melt during the day and refreeze at night (Milner and Petts 1994, Ward 1994, Füreder et al. 2001, Moore et al. 2009). Kryal streams also have highly mobile and unstable substrates (Robinson 2010). In comparison, rhithral-dominated streams (hereafter referred to as “rhithral”) generally have less pronounced fluctuations in discharge, higher maximum temperatures, and greater channel stability (Hieber et al. 2002, Zbinden et al. 2008). In a study conducted in the Swiss Alps, Hieber et al. (2002) found that levels of ammonia, nitrate, particulate phosphorus, and total suspended solids were also significantly higher in glacial-fed systems than those dominated by snowmelt. Not surprisingly, kryal and rhithral streams also support different communities of macroinvertebrate fauna. Rhithral streams have been found to have more diverse and taxon-rich assemblages than kryal streams (Hieber et al. 2005). However, kryal streams support a number of rare and endemic macroinvertebrate species (Snook and Milner 2001, Ilg and Castella 2006, Brown et al. 2007, Winterbourn et al. 2008, Giersch et al. 2015) and contribute to overall regional and genetic diversity (Jacobsen et al. 2010, Finn et al. 2013, 2014; Brown et al. 2015). Certain macroinvertebrate functional traits, such as small body size, streamlined and flattened body, clinger habit, short life cycle, adult mobility, omnivory, and cold-stenothermal specialists. Kryal have been associated with glacial streams (Snook & Milner 2002, Ilg and Castella 2006, Rossaro et al. 2006, Brown et al. 2007, Füreder 2007, Milner et al. 2009). As glacial influence is reduced, the overall diversity of macroinvertebrate functional traits increases, with larger body sizes, less specialized body shapes, lower adult mobility, and species with a larger range of thermal preference observed.

Recent research has also focused on the physical, chemical, and biotic characteristics of alpine lake outlets which are a transition zone between lentic (“still water”) and lotic (“flowing water”) environments (Wotton 1995, Kownacki et al. 1997, Donath and Robinson 2001, Hieber et al. 2001, 2002, 2005; Brunke 2004, Boggero and Lencioni 2006, Maiolini et al. 2006, Kubo et al. 2013). Although the macroinvertebrate fauna of lake outlets is most similar to streams and rivers, the characteristics of the upstream lake (e.g. size, water source, temperature, allochthonous inputs) can affect the lake outlet community (Richardson and Mackay 1991, Wotton 1995, Donath and Robinson 2001). Lakes generally stabilize outlet streams by increasing water temperature and decreasing daily and seasonal temperature, discharge, and suspended sediment fluctuations, especially in glacially-fed systems (Milner et al. 2000, Donath and Robinson 2001, Hieber et al. 2002, Hood and Berner 2009). In the summer, warm epilimnic surface water discharging into the outlet may increase macroinvertebrate metabolism (Richardson and Mackay 1991) and digestive function (Wotton 1995). Lakes also contribute food sources to outlet streams in the form of detritus from decomposition of dead biota, fecal material, and dissolved organic matter (Wotton 1988). Research has shown that non-glacial lake outlets had more diverse and abundant macroinvertebrate communities (Hieber et al. 2005, Kubo et al. 2013) than their respective non-outlet streams and supported higher densities of non-insect taxa such as Oligochaeta, Nematelminthes, and crustaceans (Hieber et al. 2005). Burgherr and Ward (2000) and Maiolini et al. (2006) found more Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa in kryal lake outlet streams when compared to non-outlet streams, whereas Hieber et al. 2005 found no general differences in macroinvertebrate assemblages.

While studies from Europe, Alaska, South America, and New Zealand have demonstrated the relationship between dominant water source to environmental conditions and macroinvertebrate community composition, relatively little is known about this relationship in Washington State, the most glaciated state in the contiguous United

States. The North Cascades National Park, which contains approximately one-third of all the glaciers in the lower 48 states (Post et al. 1971) has lost on average more than 9.5 meters in ice thickness and 20 to 40% of total ice volume between 1984 and 2005 (Pelto 2006). This rapid glacial retreat has the potential to cause widespread loss of regional biodiversity (Jacobsen et al. 2010, 2012). Thus, the primary objective of our study was to compare benthic macroinvertebrate assemblages, including trait composition and unique taxa, between kryal and rhithral lake outlet streams in the North Cascade Mountains of Washington State. We focused on lake outlet streams because, despite their prominence in alpine landscapes, very little is known about their role in alpine environments (Donath and Robinson 2001). When differences were found between kryal and rhithral macroinvertebrate assemblages, we sought to determine which, if any, physical and water quality parameters were associated with these differences. Our study broadens the geographical scope of glacial and alpine lake outlet research and allowed us to make comparisons to similar research from other temperate zones. In addition, this study adds to the relatively few trait-based studies that have been conducted on kryal streams. Finally, this study provides a base-line of kryal and rhithral lake outlet data for the North Cascades that can be used to measure the effects of climate change.

Methods

Study Sites

Five kryal and five rhithral lake outlet streams were sampled between 31 August and 20 September 2007 when sites were relatively snow-free and accessible. The sites were located at or above treeline between 1117 and 1755 m on the western slope of the North Cascade Mountain range within the North Cascades National Park boundary (Figure 1, Figure 2, Table 1). All lake outlets were fishless, first-order streams (Wetzel 2001). Kryal lake outlet sites were located in five different catchments throughout the western region of the park. Four of the five rhithral lake outlet sites were in the Little Beaver Creek watershed. Dominant water source was determined by the

presence of either a glacier for kryal sites or a snowfield for rhithral sites. All kryal sites were less than 800 meters from the nearest glacier in their watershed. Lake surface area ranged from 0.9 to 21.3 ha with discharge ranging from 0.01 to $3.77 \text{ m}^3 \text{ s}^{-1}$ based on one measurement during the survey period taken between 08:00 and 18:00. All sites were located within the subalpine/alpine ecoregions of the park where continuous forest is replaced by alpine heaths, meadows, barren rock, permanent snow and ice fields, and are inaccessible most of the year (Acker et al. 2010, Rochefort et al. 2012). At each site, a sampling area was selected that began 10 m downstream from the lake outlet and extended 30 m farther downstream.

Physical/Chemical Measurements

We assessed channel stability in the field using the channel bottom component of the Pfankuch stability index (PSI; Pfankuch 1975) to classify stream reaches into four categories of channel bottom stability (≤ 15 = excellent, 16–30 = good, 31–45 = fair, 46–60 = poor). This index is based on several qualitative observations of the stream bottom including rock angularity, consolidation, size distribution, and aquatic vegetation cover and was selected so that results could be compared to studies from Europe (Hieber et al. 2002). Lake outlet discharge was measured using the neutrally buoyant object procedure (EPA 2004) in which the movement of a neutrally buoyant object was timed through a measured length of channel. Discharge in cubic meters per second was determined using the formula

$$\text{Flow} = \text{ALC}/T$$

where A is the average cross-sectional area of the stream (meters), L is the float length (meters), C is 0.8, the correction factor for rocky bottom streams, and T is the average time (seconds) for the object to float the length. The relative percent cover of each substrate type was visually estimated for the entire stream reach. Substrate types were delineated based upon size fractions and included percent fine sediment (< 0.06 to 2 mm) and bedrock/boulder (256 to > 4906 mm).

Water quality measurements and samples were collected midway along the stream reach.

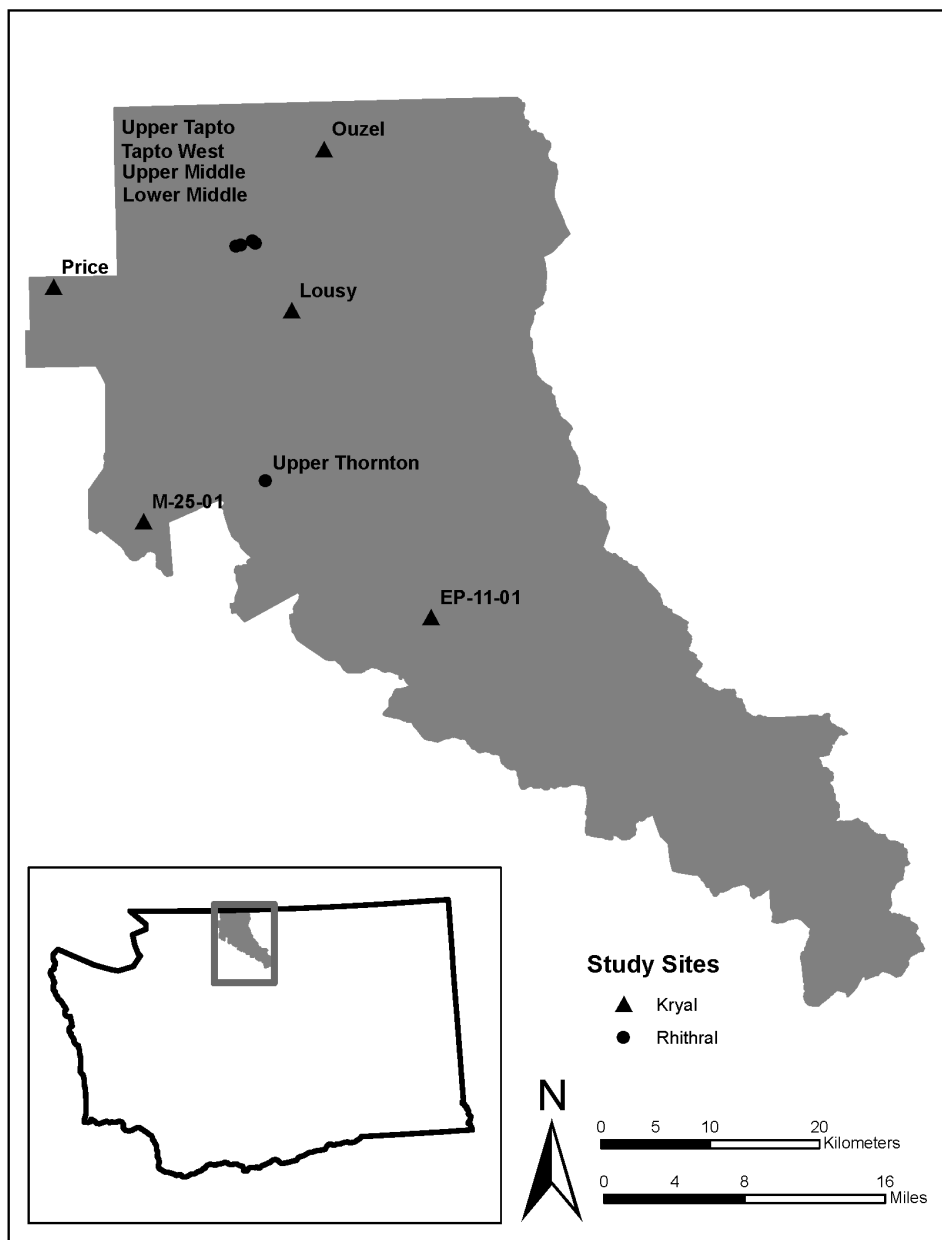


Figure 1. Kryal and rhithral lake outlet stream site locations in the North Cascades National Park, Washington.

Water temperature and dissolved oxygen were measured in the field using a Yellow Springs Instrument field meter or a field thermometer and Hach Dissolved Oxygen kit (Model OX-2P). Water samples were collected to measure alkalinity, chlorophyll, conductivity, nutrients (total persulfate nitrogen, nitrate/nitrite, ammonium,

total persulfate phosphorus, orthophosphate), pH, total suspended solids, and turbidity using the methods summarized in Table 2. A portion of each sample was filtered in the field (Whatman GF/F filters; 0.45- μ m) to measure chlorophyll, orthophosphate, nitrate/nitrite, and ammonium. All water samples were stored in cooler bags or

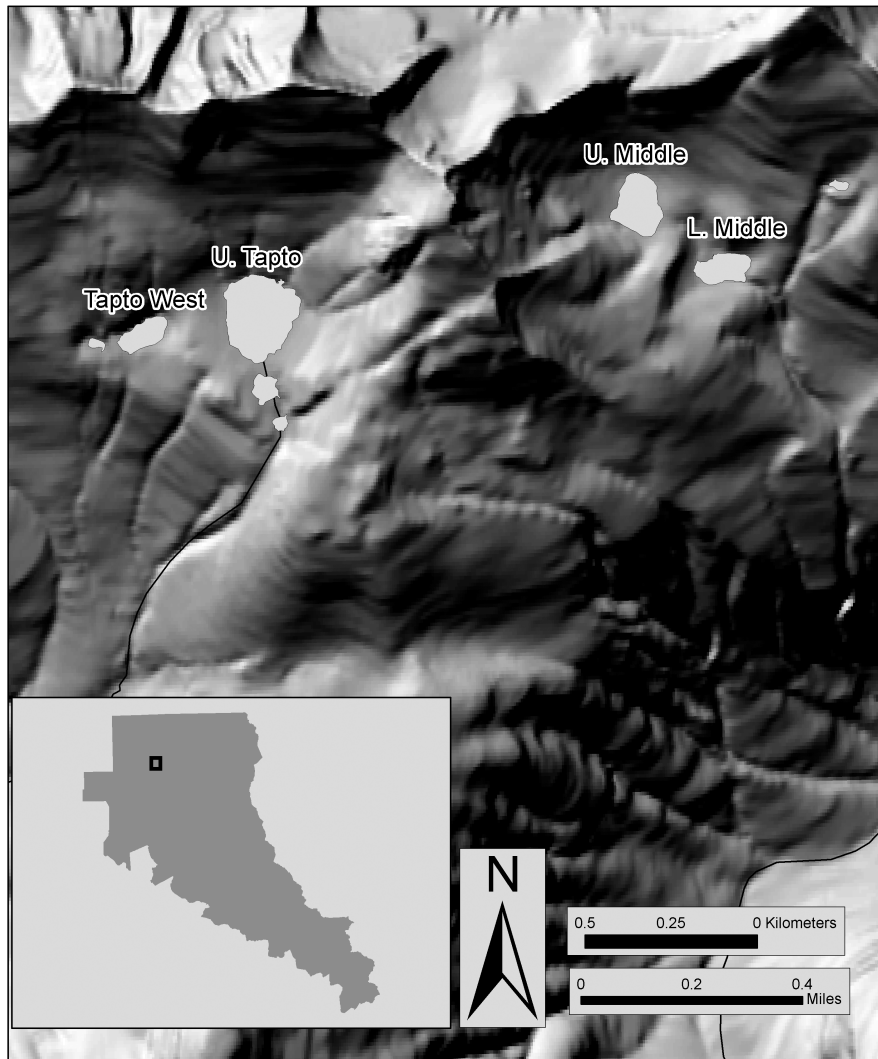


Figure 2. Rhithral lake outlet stream sites located in the Little Beaver Creek watershed, North Cascades National Park, Washington.

dry bags packed with snow and kept cold until they were transported to the laboratory. No more than three days elapsed between water collection and storage in the laboratory. Once in the laboratory, water samples were split based on the chemical parameter, and stored and processed according to the Standard Methods for the Examination of Water and Wastewater, 21st Edition (APHA 2005).

Macroinvertebrate Sampling

For nine of the ten stream reaches we collected six replicate macroinvertebrate samples. Only three

replicates were collected at the Tapto West site due to low stream flows. The macroinvertebrates were collected using a Surber sampler (0.09 m², 500-μm mesh). All benthic samples were fixed with 95% non-denatured ethanol and kept cold until they were transported to a laboratory. In the laboratory, all macroinvertebrates from each sample were handpicked, counted, and identified to the lowest possible taxonomic level using a dissecting microscope. All Chironomidae larvae were identified to the species or genus level by Rhithron Associates Inc. (Missoula MT). Voucher

TABLE 1. Location and general physical characteristics for five kryal and five rhithral lake outlet streams sampled between 31 August and 20 September 2007. Distance from glacier measured in ESRI ArcGIS using U. S. Department of Agriculture National Agriculture Imagery Program (NAIP) 2013 aerial imagery. Site codes for lake outlets are used in Figure 3.

Site	Site Code	Type	Sampling Date	Elevation (m)	Latitude (UTM)	Longitude (UTM)	Lake Area (Hectares)	Distance from Glacier (m)	Dis-charge (CMS)	Pfankuch Index
EP-11-01	EP-11-01	Kryal	31 Aug.	1209	636832	5382068	4.3	795	3.77	23
Lousy	Lousy	Kryal	11 Sept.	1117	624383	5410182	8.5	740	0.81	33
M-25-01	M-25-01	Kryal	20 Sept.	1602	610362	5390356	15.6	450	0.19	18
Ouzel	Ouzel	Kryal	12 Sept.	1728	627097	5424803	1.1	680	0.88	50
Price	Price	Kryal	2 Sept.	1193	602078	5412477	21.3	795	1.12	33
Middle, Lower	MidLow	Rhithral	9 Sept.	1707	620947	5415997	1.2	-	0.07	17
Middle, Upper	MidUp	Rhithral	9 Sept.	1740	620657	5416104	1.8	-	0.04	15
Tapto, Upper	TapUp	Rhithral	10 Sept.	1756	619540	5415758	4.1	-	0.01	17
Tapto, West	TapWest	Rhithral	9 Sept.	1725	619168	5415773	0.9	-	0.02	17
Thornton, Upper	UpThorn	Rhithral	15 Sept.	1536	622059	5394358	12.7	-	0.06	18

TABLE 2. Methods and summary statistics (median, minimum, maximum) for physical and chemical water quality parameters for five kryal and five rhithral lake outlet streams sampled between 31 August and 20 September 2007. Site-specific results presented in Turner 2009. Water chemistry methods reference specific methodology outlined in the Standard Methods for the Examination of Water and Wastewater, 21st edition (APHA 2005).

Parameter	Method	Detection limit or sensitivity	Kryal median (min – max)	Rhithral median (min – max)
Alkalinity	SM2320 (APHA 2004)	$\pm 0.6 \text{ mg L}^{-1}$	2.8 (< 0.6–5.5)	0.6 (< 0.6 – 2.4)
Conductivity	SM2510 (APHA 2005)	$\pm 0.8 \mu\text{S cm}^{-1}$	16.8 (3.8 – 24.2)	9.3 (4.3 – 76.6)
Dissolved oxygen	SM4500-O G (APHA 2005)	$\pm 0.2 \text{ mg L}^{-1}$	12.0 (10.0 – 13.0) ^a	10.0 (9.0 – 10.0) ^a
pH	SM4500-H+ (APHA 2005)	± 0.1 units	6.5 (5.0 – 6.7)	5.7 (4.8 – 6.2)
Temperature	SM2550 (APHA 2005)	± 0.1 °C	4.8 (2.2 – 7.2) ^a	10.2 (9.5 – 12.0) ^a
Discharge	Neutral buoyant object (EPA 2004)	$0.01 \text{ m}^3 \text{ s}^{-1}$	0.88 (0.19 – 3.77) ^b	0.04 (0.01 – 0.07) ^b
Total susp solids	SM2540 D (APHA 2005)	2.6 mg L^{-1}	all values < 2.6	all values < 2.6
Turbidity	SM2139 (APHA 2005)	± 0.2 NTU	12.6 (0.9 – 51.1) ^a	0.4 (0.2 – 3.2) ^a
Pfankuch stability index	Visual estimate (Pfankuch 1975)	na	33 (18 – 50) ^a	17 (15 – 18) ^a
Pct. fine sediment	Visual estimate	na	7 (0 – 60)	0 (0 – 6)
Pct. bedrock/boulder	Visual estimate	na	20 (0 – 66)	18 (10 – 45)
N - ammonium	SM4500-NH ₃ , H (APHA 2005)	$10 \mu\text{g-N L}^{-1}$	all values < 10	all values < 10
N - nitrate/nitrite	SM4500-NO ₃ I (APHA 2005)	$10 \mu\text{g-N L}^{-1}$	20.0 (< 10 - 21.50)	all values < 10
N - total persulfate	SM4500-N C (APHA 2005)	$20 \mu\text{g-N L}^{-1}$	< 20 (< 20 – 26.9)	< 20 (< 20 – 44.1)
P - orthophosphate	SM4500-P G (APHA 2005)	$3 \mu\text{g-P L}^{-1}$	all values < 3	< 3 (< 3 – 3.3)
P - total persulfate	SM4500-P H (APHA 2005)	$5 \mu\text{g-P L}^{-1}$	7.1 (< 5 – 20.2)	< 5 (< 5 – 17.7)
Chlorophyll	SM10200 H (APHA 2005)	$\pm 0.1 \mu\text{g L}^{-1}$	0.1 (< 0.1 – 0.6)	0.3 (< 0.1 – 2.1)

Kryal/rhithral stream groups significantly different at p-value $\leq 0.05^a$ or $\leq 0.01^b$ (Wilcoxon rank sum test; Crawley, 2007).

specimens were stored in permanent collection at the Institute for Watershed Studies, Huxley College of the Environment, Western Washington University, Bellingham, Washington.

Macroinvertebrate Functional Trait Groups and Indices

Taxa were placed into functional feeding groups (collector filterer, collector gatherer, omnivore, predator/parasite, scraper, shredder, macrophyte shredder, and unknown) and habit groups (attacher, burrower, clinger, climber, planktonic, skater, sprawler, swimmer, and unknown) based on Barbour et al. (1999), Merritt and Cummins (1996) with modifications by Wisseman and Doughty (2004). Taxa were also placed into thermal preference categories (cold stenothermal or cool eurythermal, cool/warm eurythermal, warm eurythermal, and unknown) based primarily on two North American studies (Poff et al. 2006, Vieira et al. 2006) and secondarily on two European studies (Rossaro 1991, Marziali and Rossaro 2013). The macroinvertebrate data were used to generate the following summary indices: total macroinvertebrate density; Ephemeroptera, Plecoptera, Trichoptera, and combined EPT densities; non-insect and Chironomidae densities; cold stenotherm or cool eurythermal taxa density; total and EPT taxa richness; cold stenotherm or cool eurythermal taxa richness; and the number of unique taxa collected in either kryal or rhithral streams, but not both.

Shannon's diversity index (H) and Pielou's evenness (J) were calculated for each lake outlet site using vegan 2.3-0 in the R software package (R Development Core Team 2014, Oksanen et al. 2015). Shannon's diversity index (H) was calculated using the formula

$$H = - \sum_{i=1}^S p_i \log_b p_i$$

where p_i is the proportion of individuals found in species i (Shannon 1948, Hill 1973). The Shannon index (H) increases as both the richness and evenness of the community increase. Typical values are generally between 1.5 and 3.5 for most ecological studies, and the index is rarely greater

than 4. Pielou's Evenness (J) was calculated using the formula

$$J = H' / \log(S)$$

where H is derived from Shannon's Diversity Index and S is the number of species (Pielou 1966, Hill 1973). Pielou evenness index is the ratio of the observed value of Shannon index to the maximum value. Values are constrained between 0 and 1. The closer the value gets to 1, the more even the quantities of the different species are (Pielou 1966).

Statistical Analyses

All statistical analyses were conducted using the R software package (R Development Core Team 2014). The water quality and macroinvertebrate data, (including traits and indices), were examined using univariate and bivariate summary statistics and graphical displays to determine basic patterns in the data. Macroinvertebrate density per square meter was calculated for each sample and averaged for the number of samples taken per sampling reach. Some of the macroinvertebrate and physical/chemical variables failed to meet the parametric assumptions of normality and homoscedasticity, so we used the Wilcoxon Rank Sum test (Mann-Whitney) to determine whether individual macroinvertebrate and physical/chemical variables were significantly different between stream types (Hollander and Wolfe 1999, Crawley 2007). To determine whether the data clustered by stream type, we used non-metric clustering and association analysis (NMCAA) based on RIFFLE software (Matthews and Hearne 1991).

Non-metric clustering is an uninformed, rank-based clustering procedure that identifies clusters based on variable similarity and then tests whether the clusters are associated with known groups (e.g., stream type). Non-metric clustering does not use distance metrics, but rather evaluates each variable independently and compares it to an evolving clustering scheme based on common properties. The method can be used to identify a subset of variables that contribute to good cluster formation, and, conversely, identify and ignore variables that are random. The method identifies within-group

similarity using proportional reduction in error (PRE), which is the improvement over random chance that you can predict the cluster if you know the variable rank. This process is computationally time consuming because of the huge number of possible combinations; as a result, the outcome is stochastic. To address this, we repeated the clustering routing 100x to measure cluster stability. Non-metric clustering is based on the ranking orders and median values of variables, not the actual concentrations, so unless more than half of the data are below detection, the median will not be affected.

For the non-metric clustering we used all of the water quality variables listed in Table 2 except ammonium, nitrate/nitrite, total persulfate nitrogen, orthophosphate, and total suspended solids, which were excluded because more than half of the values for these parameters were below detection. For the remaining water quality variables, below detection values were retained in uncensored form. We used all of the macroinvertebrate indices except Shannon's diversity index and Pielou's evenness and omitted the macroinvertebrate traits to avoid redundancy. To understand how water quality potentially affected macroinvertebrate communities, we used Kendall's non-parametric correlation analysis on all water quality variables and macroinvertebrate traits and indices.

Results

Physical and Chemical Characteristics

Geographic location, lake area, distance from glacier, and site elevation of each study site were determined using ESRI Geographic Information Systems (GIS) data from North Cascades National Park (NOCA), Western Washington University and U. S. Department of Agriculture National Agriculture Imagery Program (NAIP) 2013 aerial imagery (Table 1). All of the sites were characterized by very low alkalinities and conductivities, slightly acidic pH levels, and very low concentrations of nitrogen, phosphorus, and chlorophyll (Table 2). The only significant water quality differences between kryal and rhithral sites were for physical parameters (discharge, turbidity, PSI, temperature) and dissolved oxygen. Lake outlet discharge and

turbidity was significantly higher at kryal sites compared to rhithral sites. Kryal outlet streams had significantly lower channel stability with PSI scores ranging from poor to good (60–16 PSI units), whereas rhithral streams ranged from good to excellent (30 to ≤ 15 PSI units). We found significantly lower water temperatures in the kryal lake outlet streams. Dissolved oxygen concentrations were high at all sites (9.0–13.0 mg L⁻¹), though significantly higher in the kryal lake outlet streams.

Macroinvertebrate Density and Taxonomic Diversity

A total of 24 985 specimens representing 96 taxa were collected from the lake outlet sites. Of the 96 taxa, 25 were from the orders Ephemeroptera, Plecoptera, or Trichoptera (EPT); 53 were Diptera; and 19 were Collembola, Coleoptera, Hemiptera and non-insects (Table 3). The rhithral lake outlet streams had significantly higher invertebrate densities and supported more taxa than kryal sites (Table 4). A total of 82 macroinvertebrate taxa were collected from the rhithral lake outlet sites, with a mean density of 9049 individuals m⁻². In comparison, 38 taxa were collected from the kryal lake outlet sites, with a mean density of 821 individuals m⁻². Numerically, Chironomidae was the dominant taxon at all sites, although densities and taxon richness were much lower in the kryal sites compared to rhithral sites. Kryal lake outlets supported the chironomid subfamilies, Orthoclaadiinae and Diamesinae, which are common in cold-water environments, and are typically associated with glacial streams (Milner et al. 2001, Robinson 2010, Eggermont and Heiri 2011). These subfamilies were also present at rhithral sites, along with Podonominae (another cold-water subfamily), Tanypodinae, and Chironominae, which are generally found in wider temperature ranges (Eggermont and Heiri 2011). The rhithral lake outlet sites contained significantly higher densities and numbers of non-insect taxa such as Acari (mites), Oligochaeta (segmented worms), Nematelminthes (nematodes), Planariidae (planaria), and crustaceans (copepods). Crustaceans are common in lake outlet streams of all altitudes (Richardson and Mackay 1991, Kownacki et al.

TABLE 3. Summary statistics (median, minimum, maximum) and macroinvertebrate taxa list for five kryal and five rhithral lake outlet streams sampled between 31 August and 20 September 2007. Site-specific results presented in Turner 2009.

			Kryal median (min – max)	Rhithral median (min – max)
Arthropoda/Insecta				
Ephemeroptera	Ameletidae	<i>Ameletus</i> sp. Eaton ¹	2 (0 – 24) ^a	65 (2 – 415) ^a
	Ephemerellidae	<i>Drunella doddsi</i> Needham ²	0 (0 – 4)	-
	Heptageniidae	<i>Cinygmula</i> sp. McDunnough ¹	0 (0 – 13)	-
		<i>Epeorus deceptivus</i> McDunnough ¹	0 (0 – 24)	-
		<i>Epeorus grandis</i> McDunnough ^{1*}	0 (0 – 2)	-
		<i>Rhithrogena</i> sp. Eaton ¹	4 (0 – 37) ^a	-
Plecoptera	Capniidae	<i>Capnura</i> sp. Banks ²	0 (0 – 2)	0 (0 – 2)
		<i>Utacapnia</i> sp. Nebeker & Gaufin ¹	0 (0 – 31)	-
	Nemouridae	<i>Podmosta</i> sp. Ricker ¹	0 (0 – 2)	-
		<i>Zapada columbiana</i> Claassen ¹	-	194 (6 – 696) ^b
		<i>Zapada oregonensis</i> Gr. Claassen ¹	0 (0 – 241)	-
	Perlodidae	<i>Megarcys</i> sp. Klapálek ¹	9 (0 – 52) ^a	-
		<i>Setvena</i> sp. Illies ¹	-	7 (0 – 117) ^a
	Taeniopterygidae	<i>Taenionema</i> sp. Banks ¹	0 (0 – 1152)	-
Trichoptera	Apataniidae	<i>Apatania</i> sp. Kolenati ¹	-	0 (0 – 43)
	Brachycentridae	<i>Micrasema</i> sp. McLachlan ²	-	0 (0 – 2)
	Hydropsychidae	<i>Parapsyche elsis</i> Milne ¹	-	0 (0 – 6)
	Limnephilidae	<i>Desmona mono</i> Denning	-	0 (0 – 56)
		<i>Ecclisomyia</i> sp. Banks ¹	0 (0 – 2)	2 (0 – 28)
		<i>Ecclisocosmoecus scylla</i> Milne ¹	-	0 (0 – 2)
		<i>Psychoglypha</i> sp. Ross ¹	0 (0 – 2)	0 (0 – 7)
	Rhyacophilidae	<i>Rhyacophila brunnea</i> Gr. Banks ^{2*}	-	0 (0 – 2)
		<i>Rhyacophila rotunda</i> Gr. Banks ^{2*}	-	11 (0 – 185) ^a
		<i>Rhyacophila verrula</i> Gr. Milne ^{2*}	0 (0 – 11)	2 (0 – 85)
Diptera	Uenoidae	<i>Neothremma</i> sp. Dodds & Hisaw ¹	-	0 (0 – 2)
	Chironomidae/Chironominae ²	<i>Micropsectra</i> sp. Kieffer	-	22 (0 – 296) ^a
		<i>Paracladopelma</i> sp. Harnish	-	0 (0 – 2)
		<i>Paratanytarsus</i> sp. Bause ³	-	0 (0 – 11)
		<i>Polypedilum</i> sp. Kieffer ³	-	0 (0 – 2)
		<i>Tanytarsus</i> sp. Van Der Wulp ³	-	0 (0 – 11)
	Chironomidae/Diamesinae ¹	<i>Diamesa</i> sp. Meige	22 (0 – 467)	0 (0 – 4)
		<i>Pagastia</i> sp. Oliver	-	0 (0 – 13)
		<i>Pseudodiamesa</i> sp. Goetghe buer	2 (0 – 17)	26 (0 – 96)
	Chironomidae/Orthocladiinae ¹	<i>Chaetocladius dentiforceps</i> Gr. Edwards	0 (0 – 2)	0 (0 – 2)
		<i>Chaetocladius</i> sp. Kieffer ²	0 (0 – 37)	2 (0 – 6)
		<i>Corynoneura</i> sp. Winnertz ²	-	28 (0 – 481) ^a
		<i>Diplocladius</i> sp. Kieffer	0 (0 – 2)	0 (0 – 2)
		<i>Eukiefferiella brehmi</i> Gr. Gowin ²	-	7 (0 – 44) ^a
		<i>Eukiefferiella claripennis</i> Gr. Lundbeck ¹	-	35 (7 – 163) ^b
		<i>Eukiefferiella devonica</i> Gr. Edwards ²	-	0 (0 – 189)
		<i>Eukiefferiella gracei</i> Gr. Edwards	0 (0 – 63)	4 (0 – 217)
		<i>Heleniella</i> sp. Saether ²	-	0 (0 – 4)
		<i>Heterotrissocladius marcidus</i> Walker	-	0 (0 – 4)
		<i>Hydrobaenus</i> sp. Fries ²	0 (0 – 26)	0 (0 – 7)
		<i>Krenosmittia</i> sp. Thienemann	-	0 (0 – 6)
		<i>Limnophyes</i> sp. Eaton ¹	-	0 (0 – 4)
		<i>Nanocladius parvulus</i> Gr. Keiffer	-	0 (0 – 2)
		<i>Nanocladius</i> sp. Kieffer	-	0 (0 – 87)

		<i>Orthocladius</i> sp. Wulp ²	7 (0 – 694)	33 (15 – 550)
		<i>Orthocladius</i> (<i>Euorthocladius</i>) Thienemann	0 (0 – 43)	0 (0 – 4)
		<i>Orthocladius</i> (<i>Orthocladius</i>) Wulp	0 (0 – 4)	2 (0 – 9)
		<i>Parametriocnemus</i> sp. Thienemann	-	0 (0 – 6)
		<i>Parorthocladius</i> sp.	6 (0 – 72) ^a	-
		<i>Psectrocladius</i> sp. Kieffer	-	7 (0 – 493) ^a
		<i>Psectrocladius sordidellus</i> Gr. Zetterstedt	-	0 (0 – 7)
		<i>Pseudorthocladius</i> sp.	-	0 (0 – 2)
		<i>Psilometriocnemus</i> sp. Saether	-	0 (0 – 7)
		<i>Rheocricotopus</i> sp. Thienemann & Harnisch ²	-	52 (2 – 104) ^b
		<i>Rheocricotopus fuscipes</i> Gr.Kieffer ²	-	0 (0 – 507)
		<i>Synorthocladius</i> sp.	-	0 (0 – 81)
		<i>Thienemanniella</i> sp. Kieffer ³	0 (0 – 2)	4 (0 – 6)
		<i>Tvetenia</i> sp. Kieffer	0 (0 – 15) ^a	11 (7 – 159) ^a
		<i>Tvetenia bavarica</i> Gr. Goetghebuer ¹	0 (0 – 6) ^a	33 (4 – 1863) ^a
	Chironomidae/Podonominae			
		<i>Parochlus</i> sp. Edwards	-	0 (0 – 256)
	Chironomidae/Tanypodinae ²			
		<i>Krenopelopia</i> sp. Fittkan	-	0 (0 – 2)
		<i>Procladius</i> sp. Skuse ²	-	0 (0 – 2)
		<i>Thienemannimyia</i> Gr	-	0 (0 – 11)
		<i>Zavrelinyia</i> sp. Kittkau	-	6 (0 – 419) ^a
	Tipulidae ²			
		<i>Gonomyodes</i> sp.	0 (0 – 19)	-
		<i>Hesperoconopa</i> sp. Alexander ¹	0 (0 – 2)	-
		<i>Pedicia</i> sp. Latreille	-	0 (0 – 6)
		<i>Molophilus</i> sp. Curtis	0 (0 – 2)	-
	Ceratopogonidae ² /Ceratopogoninae			
		<i>Atrichopogen</i> sp.	-	0 (0 – 4)
	Empididae ²			
		<i>Clinocera</i> sp. Meigen	-	0 (0 – 6)
		<i>Oreogeton</i> sp. Schiner	-	0 (0 – 2)
	Simuliidae ²			
		<i>Simulium</i> sp. Latreille	-	0 (0 – 19)
		<i>Piezsimulium</i> sp.	-	0 (0 – 4)
		<i>Dicranota</i> sp.	-	0 (0 – 4)
Hemiptera	Heteroptera		-	0 (0 – 4)
	Homoptera		-	0 (0 – 4)
Coleoptera	Dytiscidae/Dytiscinae			
		<i>Agabus</i> sp. Leach ²	-	0 (0 – 2)
		<i>Hydrocolus</i> sp. Roughley & Larson in Larson, Alarie & Roughley	-	0 (0 – 4)
		<i>Hygrotus</i> sp. Stephens ³	-	0 (0 – 100)
		<i>Stictotarsus striatellus</i> LeConte	-	0 (0 – 106)
	Dytiscidae/Hydroporinae		-	0 (0 – 28)
	Hydrophilidae/Sphaeriinae		-	0 (0 – 2)
	Staphylinidae	<i>Stenus</i> sp. Latreille	-	0 (0 – 2)
Arachnida	Acari		0 (0 – 6) ^b	976 (9 – 5563) ^b
	Araneae		0 (0 – 2)	-
Entognatha	Collembola	Isotomidae	-	2 (0 – 6) ^a
		Poduridae	-	2 (0 – 11) ^a
Maxillopoda	Harpacticoida		-	402 (17 – 881) ^b
	Cyclopoida		1 (0 – 2)	13 (0 – 37)
	Calanoida		-	0 (0 – 4)
Annelida	Oligochaeta		4 (0 – 22)	13 (0 – 926)
Platyhelminthes/Turbellaria				
	Tricladida	Planariidae	<i>Polycelis coronata</i> Girard	2 (0 – 13)
Nematoda				235 (0 – 378)
			15 (0 – 33) ^a	293 (28 – 1128) ^a

Kryal/rhithral stream groups significantly different at p-value $\leq 0.05^a$ or $\leq 0.01^b$ (Wilcoxon rank sum test; Crawley, 2007). Thermal preference: cold stenotherm or cool eurythermal¹, cool/warm eurythermal², warm eurythermal³. *Based on genus classification.

TABLE 4. Summary statistics (median, minimum, maximum) for macroinvertebrate groups for five kryal and five rhithral lake outlet streams sampled between 31 August and 20 September 2007. Habit types are defined as follows: attachers use silk to attach retreats to bottom substrates, burrowers burrow into soft bottom substrates, clingers grasp hard bottom substrates in fast current, climbers use vegetation, wood or rocks to climb up into the water column, planktonic-in the water column, skaters on and above the water surface, sprawlers crawl on sediment surface, swimmers swim above the sediment surface, and unknown habit type (Wisseman and Doughty 2004).

	Kryal median (min – max)	Rhithral median (min – max)
<i>Macroinvertebrate index (# m²)</i>		
Total macroinvertebrate density	549 (29 – 1898) ^a	8349 (1897 – 33200) ^a
Non-insect density	34 (8 – 43) ^b	1764 (726 – 7985) ^b
Chironomidae density	334 (10 – 1073) ^a	4348 (1131 – 20243) ^a
EPT taxa density	207 (0 – 1262)	679 (16 – 3885)
Ephemeroptera density	26 (0 – 65)	89 (2 – 2208)
Plecoptera density	140 (0 – 1221)	498 (10 – 1485)
Trichoptera density	2 (0 – 18) ^a	75 (4 – 192) ^a
Cold stenotherm or cool eurythermal density	143 (0 – 1183)	802 (72 – 2993)
Total taxa richness	15 (5 – 22) ^b	36 (29 – 45) ^b
EPT taxa richness	8 (0 – 14)	8 (5 – 17)
Unique taxa richness	5 (0 – 7) ^a	14 (10 – 16) ^a
Cold stenotherm or cool eurythermal taxa richness	6 (0 – 10)	6 (5 – 10)
Shannon's Diversity Index (H)	1.65 (1.10 – 2.23)	0.65 (0.41 – 0.84)
Pielou's Evenness (J)	2.26 (1.41 – 2.49)	0.63 (0.42 – 0.67)
<i>Functional feeding group (# m²)</i>		
Collector filterer	0 (0 – 2) ^a	404 (18 – 1305) ^a
Collector gatherer	357 (12 – 1083) ^a	4908 (1002 – 20618) ^a
Scraper	58 (< 1 – 1301)	180 (3 – 710)
Shredder	23 (0 – 32)	76 (0 – 751)
Shredder - detritus	2 (0 – 188)	146 (5 – 526)
Shredder - macrophyte	0 (0 – 8)	4 (2 – 125)
Piercer - macrophyte	0 (0 – 0)	0 (0 – 1)
Omnivore	0 (0 – < 1) ^b	52 (2 – 613) ^b
Predator/Parasite	53 (15 – 92) ^a	1554 (725 – 8415) ^a
Unknown feeding group	0 (0 – 9)	2 (0 – 256)
<i>Habit types (# m²)</i>		
Attacher	0 (0 – 0)	11 (0 – 178)
Burrower	79 (14 – 412) ^b	1650 (637 – 7037) ^b
Clinger	151 (0 – 652)	884 (13 – 4334)
Climber	0 (0 – 1) ^b	257 (9 – 1441) ^b
Planktonic	2 (0 – 15) ^b	637 (17 – 1192) ^b
Skater	0 (0 – 0) ^b	7 (2 – 11) ^b
Sprawler	251 (13 – 1170) ^b	3999 (1196 – 16748) ^b
Swimmer	1 (0 – 6) ^b	280 (9 – 2000) ^b
Unknown habit type	0 (0 – 31)	4 (0 – 256)

Kryal/rhithral stream groups significantly different at p-value $\leq 0.05^a$ or $\leq 0.01^b$ (Wilcoxon rank sum test; Crawley, 2007).

1997, Donath and Robinson 2001, Hieber et al. 2005).

Shannon's index of diversity (H) was higher for rhithral lake outlet sites (median 2.26; range 1.41–2.49) and lower at kryal lake outlet sites

(median 1.65; range 1.10–2.23), though not statistically significant. Two lake outlet sites, Ouzel (kryal) and Lower Middle (rhithral), were below the typical range (1.5–3.5) for most ecosystems (MacDonald 2003). Pielou's evenness (J) was higher

for kryal lake outlet sites (median 0.65; range 0.41–0.84) than rhithral lake outlet sites (median 0.63; range 0.42–0.67), though not statistically significant. The kryal lake outlet sites with the lowest taxa richness, Price and M-25-01, also had the highest evenness values ($J \geq 0.8$).

Macroinvertebrate Functional Trait Groups—We were able to characterize the thermal preference for 44 of the 96 taxa detected at our study sites (Table 3). The thermal preference of the remaining 52 taxa was unknown. Of the 44 taxa characterized, 22 were cold stenotherm or cool eurythermal, 17 were cool/warm eurythermal and 5 were warm eurythermal. Kryal lake outlet streams were dominated by cold stenotherm or cool eurythermal taxa ($n = 14$), followed by cool/warm eurythermal taxa ($n = 6$). Only one warm eurythermal taxon, the Orthocladiinae chironomid, *Thienemanniella* sp. Kieffer, was found at one kryal lake outlet study site (Ouzel). Rhithral lake outlet sites were dominated by cool/warm eurythermal taxa ($n = 16$), followed by cold stenotherm or cool eurythermal taxa ($n = 13$), and warm eurythermal ($n = 5$) taxa.

Collector-gatherers were the dominant functional feeding group in both rhithral and kryal lake outlet streams (Table 4), reflecting the large number of collector-gatherer chironomid taxa found at these sites. Although both stream types were dominated by the same functional feeding group, there were significantly higher densities of collector-gatherers at the rhithral sites. Predator/parasite was the next most abundant functional group at the rhithral sites, and the third most abundant at kryal sites. This group was composed of Acari, Nematoda, Coleoptera, Diptera, Plecoptera, and Trichoptera and the densities of predator/parasites were significantly higher at the rhithral sites than the kryal sites. Collector-filterers were the third most abundant functional feeding group at rhithral sites, and nearly absent at kryal sites. This group was composed of crustaceans (copepods), Dipterans from the Simuliidae and Chironomidae (*Paratanytarsus* sp. Bause and *Tanytarsus* sp. Van Der Wulp) families, and Trichoptera from the Hydropsychidae family. The densities of collector-filterers were significantly higher at the rhithral sites than the kryal sites, primarily

due to the large number of Harpacticoida copepods found at rhithral sites (Table 3). Scrapers, primarily Ephemeroptera, were the second most abundant functional feeding group at the kryal sites, and fourth most abundant at rhithral sites. Although there were more Ephemeroptera taxa at the kryal sites than the rhithral sites (Table 3), the scraper densities were not significantly different between stream types. The only other significant difference among functional feeding groups was for omnivores, which were moderately abundant in the rhithral streams and nearly absent in the kryal streams.

Sprawlers were the dominant habit type in kryal and rhithral outlet streams, followed by burrowers and clingers. Many of the chironomid taxa collected at both kryal and rhithral sites were sprawlers. Although the habit types followed the same general abundance patterns in the kryal and rhithral streams, the rhithral streams had significantly higher densities of sprawlers and burrowers. The densities of clingers were highly variable at all sites, which resulted in a lack of statistical significance. In addition to sprawlers and burrowers, there were significantly more climbers, planktonic taxa, skaters, and swimmers in the rhithral sites compared to the kryal sites.

Unique Macroinvertebrate Taxa—The rhithral lake outlet streams had significantly more unique taxa (taxa found only in the rhithral sites) than the kryal streams (Table 3, Table 4). Overall, the rhithral sites contained 58 unique taxa, with each site having 10–16 unique taxa. Most of the taxa unique to rhithral sites were Diptera, reflecting the high diversity of Chironimidae, but the rhithral sites also contained 2 unique Plecoptera, and 8 unique Trichoptera. The chironomids *Eukiefferiella claripennis* Gr. Lundbeck and *Rheocricotopus* sp. were collected at all five rhithral sites; *Zavrelimyia* sp. and *Corynoneura* sp. were found at four sites and *Eukiefferella brehmi* Group Gowin, *Psectrocladius* sp., and *Micropsectra* sp. were found at three sites. The remaining 22 unique chironomid taxa were collected at only one or two rhithral sites. From the EPT taxa, *Zapada columbiana* Claassen was found at all rhithral lake outlets and *Setvena* sp. and *Rhyacophila rotunda* Gr. Banks were found

at four of the five rhithral outlets. Springtails from the Poduridae family were found at four rhithral sites and those from the Isotomidae family were found at three lake outlets. Thirty-seven of the 58 taxa were unique to an individual rhithral lake outlet site.

Although the kryal sites contained many fewer unique taxa (0–7 per site; 15 total), the taxa were quite different than those found only at the rhithral sites (Table 3, Table 4). Nearly all of the unique kryal taxa were Ephemeroptera and Plecoptera, and the unique Diptera were mostly Tipulidae, not Chironomidae. Of these 15 unique taxa, two taxa, the plecopteran *Megarcys* sp. and ephemeropteran *Rhithrogena* sp. were found at four of the five kryal lake outlets. The ephemeropteran *Epeorus* spp. (*E. deceptivus* McDunnough, *E. grandis* McDunnough or both) and the chironomid *Parothocladius* sp. were found at three of the five sites. The remaining nine taxa were collected at only one or two kryal outlet streams. Of these 15 taxa unique to kryal sites, six were unique to an individual lake outlet site.

Cluster and Correlation Analysis

Non-metric clustering revealed that the water quality and macroinvertebrate data could be clustered accurately by stream type using a subset of water temperature and four macroinvertebrate indices. Five variables out of 24 had PRE scores of 1.0 (water temperature, non-insect density, Chironomidae density, total taxa richness, and unique taxa richness). This means that there was a 100% improvement over random chance of predicting the cluster if you knew the rank of these variables. Clusters built using these five variables were very stable, producing identical results in 100 runs, with the samples split into groups that

were exactly aligned with kryal/rhithral stream types. Not surprisingly, the association analysis indicated that these clusters were significantly associated with stream type ($X = 6.4$; $p\text{-value} = 0.01141$). Because non-metric clustering does not create a multivariate similarity metric, the results need to be displayed using two or more of the high PRE score variables. We selected water temperature and total taxonomic richness to illustrate the relationship between stream type and the non-metric cluster groups (Figure 3), but similar cluster separation can be seen using any of the variables with high PRE scores. Three additional variables had PRE scores of 0.75 (dissolved oxygen, discharge, and PSI channel stability). When the clustering program was forced to use six, seven, or eight variables, thereby including at least one of the lower PRE-score variables, the association between stream type and cluster group was slightly lower (90–98% of the runs significantly associated with stream type).

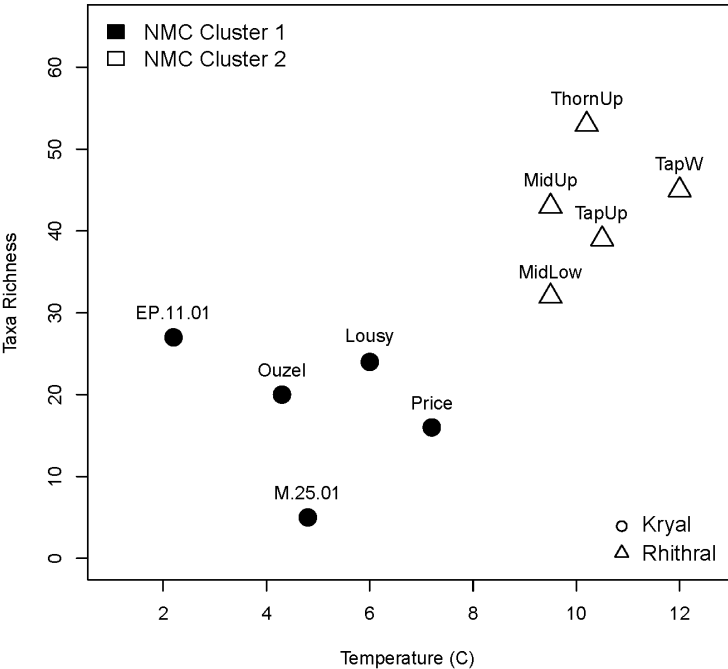


Figure 3. Non-metric clustering results plotted by two predictive variables (PRE scores = 1.0). Stream types are indicated using symbols; non-metric clustering group assignments are indicated using shading. The non-metric cluster group assignments were significantly associated with stream type ($X = 6.4$; $p\text{-value} = 0.01141$).

Kendall's tau rank-based correlation analysis revealed that the water quality parameters that were most different between kryal and rhithral sites, stream discharge, dissolved oxygen, water temperature, and turbidity, were correlated with many of the macroinvertebrate traits and indices

listed in Table 4. Water temperature was positively correlated with 65% of the macroinvertebrate groups, including all but one of the habit types (Table 5). Turbidity, discharge, and dissolved oxygen were negatively correlated with approximately 30% of the macroinvertebrate groups. Non-insect

TABLE 5. Correlations between macroinvertebrate groups and discharge, dissolved oxygen, temperature, and turbidity for five kryal and five rhithral lake outlet streams sampled between 31 August and 20 September 2007.

	Discharge	D. oxygen	Temperature	Turbidity
<i>Macroinvertebrate index</i>				
Total macroinvertebrate density	ns	ns	+0.584 ^a	-0.523 ^a
Non-insect density	-0.535 ^a	-0.716 ^b	+0.674 ^b	-0.614 ^a
Chironomidae density	-0.353 ^a	ns	+0.629 ^a	-0.523 ^a
EPT taxa density	ns	ns	ns	ns
Ephemeroptera density	ns	ns	+0.539 ^a	ns
Plecoptera density	ns	ns	ns	ns
Trichoptera density	ns	ns	+0.644 ^a	ns
Cold stenotherm or cool eurythermal density	ns	ns	ns	ns
Total taxa richness	ns	ns	+0.539 ^a	ns
EPT taxa richness	ns	ns	ns	ns
Unique taxa richness	ns	ns	+0.568 ^a	-0.506 ^a
Cold stenotherm or cool eurythermal taxa richness	ns	ns	ns	ns
Shannon's Diversity Index (H)	ns	ns	+0.539 ^a	ns
Pielou's Evenness (J)	ns	ns	ns	ns
<i>Functional feeding group</i>				
Collector filterer	-0.595 ^a	-0.628 ^a	+0.828 ^b	-0.535 ^a
Collector gatherer	ns	ns	+0.584 ^a	ns
Scraper	ns	ns	ns	ns
Shredder	ns	ns	+0.614 ^a	ns
Shredder - detritus	ns	ns	ns	ns
Shredder - macrophyte	ns	ns	ns	ns
Piercer - macrophyte	ns	ns	ns	-0.592 ^a
Omnivore	-0.575 ^a	-0.741 ^b	+0.772 ^b	-0.562 ^a
Parasite	ns	-0.665 ^a	+0.494 ^a	-0.568 ^a
Predator	-0.582 ^a	ns	+0.539 ^a	ns
Unknown feeding group	ns	ns	ns	ns
<i>Habit types</i>				
Attacher	ns	-0.595 ^a	+0.585 ^a	ns
Burrower	ns	ns	+0.674 ^b	ns
Clinger	ns	ns	ns	ns
Climber	-0.625 ^a	-0.659 ^a	+0.579 ^a	-0.513 ^a
Planktonic	-0.565 ^a	-0.646 ^a	+0.795 ^b	-0.552 ^a
Skater	-0.750 ^b	-0.735 ^b	+0.750 ^b	ns
Sprawler	-0.582 ^a	ns	+0.674 ^b	-0.568 ^a
Swimmer	-0.582 ^a	-0.614 ^a	+0.764 ^b	ns
Unknown habit type	ns	ns	+0.587 ^a	ns

Parameters significantly correlated at p-value $\leq 0.05^a$ or $\leq 0.01^b$ (Kendall's tau correlation analysis; Hollander and Wolfe 1999).

taxa densities decreased with increased discharge, dissolved oxygen and turbidity. Unique taxa richness also decreased with increased turbidity.

Discussion

Macroinvertebrate Assemblages of Alpine Lake Outlet Streams

In general, alpine streams are located on the declining limb of the harshness-diversity curve, where environmental harshness is high and taxonomic diversity is low (Tockner et al. 1997). The harshness-diversity curve states that species diversity peaks at intermediate environmental disturbance levels when conditions favor the coexistence of competitive and disturbance-tolerant species (Mackey and Currie 2001). Within this characterization, however, the range of environmental harshness and its effect on macroinvertebrate diversity is also dependent on the primary water source. Our results were similar to studies from Europe that found non-kryal lake outlets to have more diverse and abundant macroinvertebrate communities than kryal lake outlets (Füreder et al. 2001, Hieber et al. 2005, Maiolini 2006).

Certain macroinvertebrate taxa have been shown to have greater tolerance to glacial influence (i.e. low water temperature and electrical conductivity, unstable channels, and high suspended sediment), than other taxa (Ilg and Castella 2006, Brown et al. 2007, Milner et al. 2009). The chironomid *Diamesa*, in particular, has been found to dominate macroinvertebrate communities in kryal streams where maximum summer water temperatures do not exceed 2 °C and channel stability is low (Milner et al. 2001). Due to the moderating effect of an upstream lake on channel stability and water temperature at our kryal lake outlet stream sites, we would not expect *Diamesa* to be the dominant taxa, although it was one of the most abundant organisms at these sites. Other high tolerance taxa unique to our kryal sites included the mayfly *Rhithrogena* sp. and chironomid *Parorthocladius* sp., whereas others, such as the chironomids *Microspectra* sp., and *Corynoneura* sp., were unique to rhithral sites. Although not considered a glacial specialist, the stonefly *Zapada oregonensis* Gr., was unique to our kryal lake outlet sites. *Zapada oregonensis*

Gr. is only distinguished from *Zapada glacier*, a glacial specialist endemic to Glacier National Park, Montana, by characteristics of adult genitalia (Kubo et al. 2013). We did not examine the genitalia of the *Zapada oregonensis* Gr. specimens collected, but their close taxonomic relation to *Zapada glacier* and presence only at kryal sites may indicate that there is a kryal specialist in the North Cascades. Further taxonomic examination is required to test this hypothesis.

Macroinvertebrate Functional Trait Groups—As expected for alpine streams, cold stenotherm or cool eurythermal taxa were found in high densities at both kryal and rhithral lake outlet sites and were the dominant thermal tolerance group found at kryal sites. We were unable to find the thermal tolerance classification for over half of the 96 taxa found at our lake outlet sites, especially amongst chironomid taxa. Cold stenotherm or cool eurythermal taxa are particularly vulnerable to climate warming and glacier loss (Brown et al. 2007, Giersch et al. 2015), further emphasizing the need for a more comprehensive thermal tolerance list for North American alpine taxa.

Filter feeder taxa typically dominate low to mid-elevation lake outlets (Richardson and Mackay 1991). In alpine lake outlets, however, this pattern does not always hold true. Some alpine studies have found filter-feeders to be the dominant taxa (Kownacki et al. 1997, Donath and Robinson 2001), while others, such as this study, found collectors and collector-gatherers to be the dominant functional feeding groups (Hieber et al. 2005, Hamerlík et al. 2006). High concentrations of seston (suspended particles) flowing from the upstream lake is the factor most often attributed to high densities of filter feeders in outlet streams (Richardson and Mackay 1991). In oligotrophic alpine lakes, however, the lake vegetation is often less dense and diverse compared to lower elevation lakes, resulting in low concentrations of seston flowing out of alpine lakes (Hamerlík et al. 2006, Danks 2007). Although not the dominant functional feeding group, rhithral lake outlets still supported a large density of collector-filterers at significantly higher numbers than kryal lake outlets. Filter feeding invertebrates are generally less

tolerant of high turbidity typical to kryal streams, as increased suspended sediment can clog their filter apparatus and digestive organs (Kerr 1995). This may explain the lack of collector-filterer taxa found at our kryal lake outlet stream sites.

Partitioning the macroinvertebrate data by habit type produced more statistically significant differences than functional feeding group categories, with significantly more sprawlers, burrowers, climbers, planktonic taxa, skaters, and swimmers in the rhithral lake outlets compared to the kryal lake outlets. Sprawlers were the dominant habit type in kryal and rhithral lake outlet streams. Sprawlers crawl on substrates such as rocks, fine sediments, woody debris, and leaf packs. Chironomid sprawlers often reside in porous areas of rocks or debris and may become partially covered with sediment. Clingers were the second dominant habit type for kryal lake outlet streams and are the habit type typically associated with kryal streams. Clingers are specialized to grasp hard bottom substrates in fast current. Kryal sites were more turbid, with faster discharge rates and less stable substrate. This environment would be less suitable for macroinvertebrates that are more exposed to the current or rely on a stable substrate (e.g., climbers, planktonic taxa, skaters, and swimmers). Burrowers were the second and third most dominant habit type in rhithral and kryal lake outlet sites, respectively. Burrowers, such as oligochaetes and nematodes, burrow into the soft bottom substrates of slower moving sections or bank areas of streams and may be adversely affected by frequent disturbance (Merritt and Cummins 1996). This may explain the significantly higher densities of burrowers in rhithral lake outlets (median 1650; range 637–7037) when compared to kryal lake outlet sites (median 79; range 14–412).

Macroinvertebrate Dispersal in Alpine Environments—In the alpine environment, migration via larval drift or adult flight is difficult due to the low connectivity between mountainous watersheds (Monaghan et al. 2005) and the short ice-free season. Four of the five rhithral sites we sampled are located within the Little Beaver Creek drainage, and two of these sites, Upper Middle and Lower Middle, form a chain of lakes (Figure 2).

Close geographic proximity, however, does not necessarily result in dispersal amongst streams, especially for alpine and headwater streams. Due to the architecture of drainage basins, headwater streams are often disconnected and isolated from each other (Gomi et al. 2002, Clarke et al. 2008, Hughes et al. 2009), especially in elevated, mountainous terrain (Bush et al. 2012). Dispersal capabilities of aquatic insects are highly variable and for those species lacking an aerial dispersal stage, streams that are close spatially, may be effectively distant (Clarke et al. 2008, Hughes et al. 2009). Using genetic data from a range of freshwater species in upland streams, Hughes (2007) found that five out of six invertebrate species showed negligible dispersal among streams within catchments. In fact, the physical isolation of high-altitude headwater streams typically increases population genetic structure among basins (Finn et al. 2006, 2007, 2011, 2014). Each of our four rhithral lake outlet sites in the Little Beaver Creek drainage contained 5–9 unique taxa, and of these, Upper Middle and Lower Middle, forming a chain of lakes, had 5 and 7 unique taxa, respectively. These results emphasize the limited dispersal amongst these spatially ‘close’ streams, the α -diversity within these streams and the β -diversity within the catchment.

Macroinvertebrate Assemblages and Habitat Characteristics

The presence of a glacier was a major determinant driving several key physical, chemical, and biological characteristics of the lake outlet streams sampled for our study. Water temperature has long been recognized as one of the leading physical characteristics distinguishing kryal from rhithral streams and one of the primary factors influencing macroinvertebrate distribution and diversity (Vannote and Sweeney 1980, Vannote et al. 1980, Ward 1985, Milner and Petts 1994). Water temperature was significantly lower in kryal outlet stream sites, was one of the top NMCAA variables predicting stream type clustering, and was positively correlated with several invertebrate indices and traits, suggesting that lake outlet water temperature may be one of the most important

factors influencing macroinvertebrate assemblages between kryal and rhithral sites.

Discharge also has a strong influence over the physical and biological characteristics of lotic environments. The volume and velocity of water work to form stream channels and influence the creation and maintenance of in-stream habitats. In an alpine environment, discharge is primarily affected by water source and seasonal changes in weather. In a kryal stream, discharge slowly increases over the spring as first snow and then glacial meltwater enter the system. After the surrounding snow pack has melted away, glacial melt is the primary source of water into the stream and can maintain stream flow throughout the summer (Stahl et al. 2008, Hood and Berner 2009). Discharge reaches a peak by mid-summer, when the higher zones of the glacier also begin melting. In contrast, rhithral streams can have a peak in discharge as early as April and then decline over the summer as winter snow melts away (Milner and Petts 1994), although in North Cascades alpine streams this peak is closer to July, as April is still functionally winter at this elevation. The timing and intensity of these discharge peaks may be mitigated by the presence of a lake upstream, which can stabilize the discharge regime of outlet streams (Spence and Hynes 1971, Milner and Petts 1994). At our lake outlet sites, discharge was measured in late August and September, well past the predicted peaks for both stream types. By this time, the rhithral streams appeared to have returned to base flow, with the Upper Middle, Upper Tapto, and Tapto West Lake outlets barely flowing. The higher discharge and lower water temperatures measured at the kryal sites in late summer indicated that glacial meltwater contributed to these streams throughout the entire summer.

The seasonal and diel changes in discharge from glacial meltwater may influence in-stream stability by shifting active channels and altering bedloads during pulses of high flow (Milner and Petts 1994, Brittain and Milner 2001). Our results support similar findings from studies in Europe that reported kryal streams to have higher discharge and less in-stream, channel bottom stability than rhithral streams (Milner and Petts 1994, Ward

1994, Hieber et al. 2001). The channel bottom of a stream is a completely aquatic environment and the location where macroinvertebrates feed, develop, and seek shelter. Low channel stability implies not only movement of substrate within the channel, but a low resistance to and recovery from the forces stream flow may exert on the channel (Pfankuch 1975). This frequent disturbance may reduce macroinvertebrate diversity to a few specialized taxa that are adapted to highly unstable disturbance environment (Milner and Petts 1994). Similar to European studies (Hieber et al. 2005), we found a paucity of non-insect taxa at our kryal sites, possibly due to the habit of many of these taxa, such as oligochaetes and nematodes, who burrow in the stream bottom and may be adversely affect by frequent disturbance. In addition, high discharge in the summer may make it difficult for macroinvertebrates to emerge (Milner and Petts 1994).

Turbidity is a measure of suspended solids in the water column (Wetzel 2001). Based on a review of kryal research, Milner and Petts (1994) found that kryal stream turbidity in the summer was generally greater than 30 NTU from the contribution of rock flour. Rock flour (aka. glacial flour) is finely ground, clay-sized particles of rock that are produced as glaciers cause rocks to grind beneath them during advance and retreat. When glacial ice melts during the summer these particles become suspended and distributed throughout streams and lakes downstream. Median turbidity at our Kryal lake outlets sites was 12.6 NTU, lower than the typical concentration of 30 NTU, although significantly higher than rhithral sites. The lower than typical value for turbidity at our kryal lake outlets was most likely due to rock flour settling out in the lake before discharging into the outlet stream. High turbidity can affect macroinvertebrate communities by reducing primary production through decreased light penetration (Milner and Petts 1994) and by clogging the filter apparatus and digestive organs of filter feeding invertebrates (Kerr 1995). Other taxa, such as the chironomid *Diamesa*, are adapted to high turbidity and cold water temperatures (Füreder et al. 2005), and were found in large numbers at our kryal lake outlet stream sites.

The combination of cold water temperatures and high discharge leads to saturation of dissolved oxygen. While the higher dissolved oxygen levels in our kryal outlet streams were likely related to the lower water temperature of these streams, we should note that oxygen levels at both kryal and rhithral lake outlets were close to saturation, and the differences between the two stream types would not usually be considered ecologically relevant. All of the significant correlations between dissolved oxygen and macroinvertebrate groups were matched with significant correlations between temperature and the same macroinvertebrate groups, and in most cases, the strength of the correlations (Kendall's tau) were lower for dissolved oxygen than for temperature. This indicates that dissolved oxygen was not providing new information about the macroinvertebrate assemblages and was a weaker predictive variable than temperature.

As with dissolved oxygen, almost all of the discharge and turbidity correlations were paired with similar or stronger correlations with temperature. This does not mean that turbidity and discharge were not influencing the macroinvertebrate community. It means that all four variables (temperature, dissolved oxygen, turbidity, and discharge) are related, and of these four variables, temperature was the best predictor of the macroinvertebrate assemblages, regardless of stream type.

Summary and Implications

From our study it was clear that the primary water source shaped the physical features of lake outlet streams in the North Cascades, which in turn influenced the macroinvertebrate assemblages in these streams. Similar to studies from Europe, the presence of a glacier was a major determinant driving several important habitat characteristics of lake outlet streams. As a glacier melts during the summer it contributes cold water and rock flour to streams and lakes downstream. Water temperatures decrease while discharge increases. Cold water temperatures and high discharge lead to saturation of dissolved oxygen. Diel and seasonal discharge fluctuations alter stream beds resulting in unstable channel conditions. Rock flour

increases turbidity in the water column reducing light penetration and the combination of frequently disturbed stream beds and reduced light penetration may lead to a decrease in primary production (Milner and Petts 1994). As rock flour settles out into lake and stream beds, the percentage of fine sediments within the substrate increases. These conditions create a harsh environment for benthic macroinvertebrate communities.

Alpine ecosystems in the Cascade Mountains are subject to cold temperatures and extended periods of deep snow cover exceeding 200 cm (Larrabee 2011). The combination of these conditions makes alpine environments one of the harshest on the earth and sensitive indicators to climate change (Brown et al. 2007, Füreder 2007). Glacial retreat has been recorded in the North Cascades (Pelto 2006) and is evident at one of our study sites, M-25-01, a newly formed lake that is a direct result of glacial retreat. Our study provides evidence that the macroinvertebrate communities in kryal lake outlet streams have unique macroinvertebrate taxa that differ from rhithral lake outlet streams within the North Cascades. As glaciers recede with warming, an initial increase in glacial meltwater may occur, followed by a reduction and shift from glacial to snowmelt/precipitation dominated hydrology (Milner et al. 2009). Macroinvertebrate communities may shift from those associated with kryal water source to those associated with rhithral water source. Based on the results of this study, this shift may initially result in an overall increase in macroinvertebrate abundance and local diversity. However, in a study of over 100 sites across three continents, Jacobsen et al. (2012) demonstrated that a loss of kryal-based aquatic habitats resulted in a reduction of taxon turnover in proglacial reaches, local richness downstream, and an overall loss of specialists and decreased regional diversity. The loss of regional species richness is of particular concern because it is the metric that most directly measures extinction risk (Jacobsen et al. 2010). Similarly, Finn et al. (2013, 2014) found greater genetic diversity of the mayfly *Baetis alpinus* in stream reaches that were highly influenced by glaciers as opposed to those reaches with mid- or low-glacial influence, and significantly lower genetic diversity in recently

deglaciated basins. They hypothesized that the unique environment created by glacier meltwater may increase regional genetic diversity by driving an interaction between reproductive barriers within basins and physical barriers among basins. The loss of glaciers, therefore, may result in the substantial loss of regional genetic diversity (Finn et al. 2013, 2014). Long-term macroinvertebrate studies of North Cascade kroyal and rhithral streams would help clarify the function and structure of these groups and their response to effects of climate change. But the main message that should be taken from our study is that the effects of climate change are far reaching, with the potential to alter entire alpine stream communities.

Acknowledgments

Special thanks to Heath Bohlmann, Carmen Welch, Dennis Feeney, Scott Turner, Brett Turner, Jennifer Wright, Rachel Zack, and Aneka Sweeney

for assistance in the field, and Joan Vandersypen for support in protocol development and chemical analyses in the laboratory. Nancy Bonnicksen supplied field and laboratory equipment. We thank Dr. Leo Bodensteiner and Dr. Merrill Peterson for providing thoughtful insight into study design and interpretation of results. Robert Wisseman provided taxonomic verification of Trichoptera specimens. We thank three anonymous reviewers for their constructive comments that significantly improved the quality of this manuscript. This study was conducted within the boundaries of United States Department of Interior North Cascades National Park Service Complex under the NPS Scientific Research Permit number NOCA-2007-SCI-0015. The study was funded by The Institute for Watershed Studies, North Cascades National Park, Huxley's College of the Environment, WWU's Graduate Department Fund for the Enhancement of Graduate Research and the Washington State Lake Protection Association.

Literature Cited

- Acker, S. A., A. Woodward, J. R. Boetsch, K. Hutten, M. Bivin, R. Rochefort, C. C. Thompson, and L. Whiteaker. 2010. Forest vegetation monitoring protocol for the North Coast and Cascades Network. Natural Resource Report NPS/NCCN/NRR_2010/242. National Park Service, Fort Collins, CO.
- APHA. 2005. Standard Methods for the Examination of Water and Wastewater, 21th edition. American Public Health Association, American Water Works Association, Water Environment Federation, Washington, DC.
- Barbour, M. T., J. Gerritsen, B. D. Synder, and J. B. Stribling. 1999. Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates, and fish, 2nd edition. EPA 841-B-99-002. U. S. Environmental Protection Agency, Office of Water, Washington, DC.
- Boggero, A., and V. Lencioni. 2006. Macroinvertebrates assemblages of high altitude lakes, inlets and outlets in the southern Alps. *Archiv für Hydrobiologie* 165:37-61.
- Brittann, J. E., H. Adalsteinsson, E. Castella, G. M. Gislason, V. Lencioni, B. Lods-Crozet, B. Maiolini, A. M. Milner, G. E. Petts, and S. J. Saltveit. 2000. Towards a conceptual understanding of arctic and alpine streams. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* 27:740-743.
- Brittann, J. E., and A. M. Milner. 2001. Ecology of glacier-fed rivers: current status and concepts. *Freshwater Biology* 46:1571-1578.
- Brown, L. E., D. M. Hannah, and A. M. Milner. 2007. Vulnerability of alpine stream biodiversity to shrinking glaciers and snowpacks. *Global Change Biology* 13:958-966.
- Brown, L. E., N. Dickson, J. Carrivick, and L. Füreder. 2015. Alpine river ecosystem response to glacial and anthropogenic flood pulses. *Freshwater Science* 34:1201-1215.
- Brunke, M. 2004. Stream typology and lake outlets—a perspective towards validation and assessment from northern Germany (Schleswig-Holstein). *Limnologica* 34:460-478.
- Burgherr, P., and J. V. Ward. 2000. Zoobenthos of kroyal and lake outlet biotopes in a glacial flood plain. *Verhandlungen der Internationale Vereinigung der Limnologie* 22:1986-1991.
- Bush, A., D. Nipperess, E. Turak, and L. Hughes. 2012. Determining vulnerability of stream communities to climate change at the landscape scale. *Freshwater Biology* 57:1689-1701.
- Clarke A., R. Macnally, N. Bond, and P. S. Lake. 2008. Macroinvertebrate diversity in headwater streams: a review. *Freshwater Biology* 53:1707-1721.
- Crawley, M. J. 2007. *The R Book*. John Wiley & Sons, West Sussex, England.
- Danks, H. V. 2007. How aquatic insects live in cold climates. *Canadian Entomologist* 139:443-471.

- Donath, U., and C. T. Robinson. 2001. Ecological characteristics of lake outlets in Alpine environments of the Swiss Alps. *Archiv für Hydrobiologie* 150:207-225.
- Eggermont, H., and O. Heiri. 2011. The chironomid-temperature relationship: expression in nature and palaeoenvironmental implications. *Biological Reviews* 87:430-456.
- EPA. 2004. Wadeable stream assessment: field operations manual. EPA 841-B-04-004. U.S. Environmental Protection Agency, Office of Water and Office of Research and Development, Washington, DC.
- Finn, D. S., D. M. Theobald, W. C. Black, and N. L. Poff. 2006. Spatial population genetic structure and limited dispersal in a Rocky Mountain alpine stream insect. *Molecular Ecology* 15:3553-3566.
- Finn, D. S., M. S. Blouin, and D. A. Lytle. 2007. Population genetic structure reveals terrestrial affinities for a headwater stream insect. *Freshwater Biology* 52:1881-1897.
- Finn, D. S., N. Bonada, C. Múrria, and J. M. Hughes. 2011. Small but mighty: headwaters are vital to stream network biodiversity at two levels of organization. *Journal of the North American Benthological Society* 30:963-980.
- Finn, D. S., K. Khamis, and A. M. Milner. 2013. Loss of small glaciers will diminish beta diversity in Pyrenean streams at two levels of biological organization. *Global Ecology and Biogeography* 22:40-51.
- Finn, D. S., C. Zamora-Muñoz, C. Múrria, M. Sáinz-Bariáin, and J. Alba-Tercedor. 2014. Evidence from recently deglaciated mountain ranges that *Baetis alpinus* (Ephemeroptera) could lose significant genetic diversity as alpine glaciers disappear. *Freshwater Science* 33: 207-216.
- Füreder, L. 2007. Life at the edge: habitat condition and bottom fauna of alpine running waters. *International Review of Hydrobiology* 92:491-513.
- Füreder, L., C. Schütz, R. Burger, and M. Wallinger. 2000. Seasonal abundance and community structure of Chironomidae in two contrasting high alpine streams. *Verhandlungen der Internationale Vereinigung der Limnologie* 27:1596-1601.
- Füreder, L., C. Schütz, M. Wallinger, and R. Burger. 2001. Physico-chemistry and aquatic insects of a glacier-fed and a spring-fed alpine stream. *Freshwater Biology* 46:1673-1690.
- Giersch J. J., S. Jordan, F. Luikart, L. A. Jones, F. R. Hauer, and C. C. Muhlfeld. 2015. Climate-induced range contraction of a rare alpine aquatic invertebrate. *Freshwater Science* 34:53-65.
- Gomi T., R. C. Sidle, and J. S. Richardson. 2002. Understanding processes and downstream linkages of headwater systems. *BioScience* 52:905-916.
- Hamerlík, L., F. Šporka, and Z. Zatořičová. 2006. Macroinvertebrates of inlets and outlets of the Tatra Mountain lakes (Slovakia). *Biologia* 61:167-179.
- Hughes J. M. 2007. Constraints on recovery: Using molecular methods to study connectivity of aquatic biota in rivers and streams. *Freshwater Biology* 52:616-631.
- Hughes J. M., D. J. Schmidt, and D. S. Finn. 2009. Genes in streams: using DNA to understand the movement of freshwater fauna and their riverine habitat. *BioScience* 59:573-583.
- Hieber, M., C. T. Robinson, S. R. Rushfort, and U. Uehlinger. 2001. Algal communities associated with different alpine stream types. *Arctic, Antarctic and Alpine Research* 33:447-456.
- Hieber, M., C. T. Robinson, U. Uehlinger, and J. V. Ward. 2002. Are alpine lake outlets less harsh than other alpine streams? *Archiv für Hydrobiologie* 154:199-223.
- Hieber, M., C. T. Robinson, U. Uehlinger, and J. V. Ward. 2005. A comparison of benthic macroinvertebrate assemblages among different types of alpine streams. *Freshwater Biology* 50:2087-2100.
- Hill, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology* 54:427-473.
- Hollander, M., and D. A. Wolfe. 1999. *Nonparametric Statistical Methods*, Second Edition. John Wiley & Sons, New York, NY.
- Hood, E., and L. Berner. 2009. Effects of changing glacial coverage on the physical and biogeochemical properties of coastal streams in southeastern Alaska. *Journal of Geophysical Research* 114:G03001.
- Ilg, C., and E. Castella. 2006. Patterns of macroinvertebrate traits along three glacial stream continuums. *Freshwater Biology* 51:840-853.
- Jacobsen, D., O. Dangles, P. Andino, R. Espinosa, L. Hamerlík, and E. Cadier. 2010. Longitudinal zonation of macroinvertebrates in an Ecuadorian glacier-fed stream: do tropical glacial systems fit the temperate model? *Freshwater Biology* 55:1234-1248.
- Jacobsen, D., A. M. Milner, L. E. Brown, and O. Dangles. 2012. Biodiversity under threat in glacier-fed river systems. *Nature Climate Change* 2:361-364.
- Kerr, S. J. 1995. Silt, turbidity and suspended sediments in the aquatic environment: an annotated bibliography and literature review. Ontario Ministry of Natural Resources, Southern Region Science & Technology Transfer Unit Technical Report TR-008. 277 pp.
- Kownacki, A., E. Dumnicka, J. Galas, B. Kawecka, and K. Wojtan. 1997. Ecological characteristics of a high mountain lake-outlet stream (Tatra Mts, Poland). *Archiv für Hydrobiologie* 139:113-128.
- Kubo, J. S., C. E. Torgersen, S. M. Bolton, A. A. Weekes, and R. I. Gara. 2013. Aquatic insect assemblages associated with subalpine stream segment types in relict glaciated headwaters. *Insect Conservation and Diversity* 6:422-434. doi: 10.1111/j.1752-4598.2012.00210.x
- Larrabee, M. A., B. Baccus, R. Lofgren, and M. Huff. 2011. North Coast and Cascades Network climate

- monitoring report: North Cascades National Park Complex; water year 2010. Natural Resource Data Series NPS/NCCN/NRDS—2012/261. National Park Service, Fort Collins, CO.
- Lods-Crozet, B., E. Castella, D. Cambin, C. Ilg, S. Knispel, and H. Mayor-Siméant. 2001. Macroinvertebrate community structure in relation to environmental variables in a Swiss glacial stream. *Freshwater Biology* 46:1641-1661.
- Maiolini, B., V. Lencioni, A. Boggero, B. Thaler, A. F. Lotter, and B. Rossaro. 2006. Zoobenthic communities of inlets and outlets of high altitude Alpine lakes. *Hydrobiologia* 562:217-229.
- Marziali, L., and B. Rossaro. 2013. Response of chironomid species (Diptera, Chironomidae) to water temperature: effects on species distribution in specific habitats. *Journal of the Entomological and Acarological Research* 45:73-89.
- Matthews, G.B., and J. Hearn. 1991. Clustering without a metric. *IEEE Transactions on Pattern Analysis and Machine Intelligence* 13:175-184.
- Merritt, R. W., and K. W. Cummins. 1996. *Aquatic insects of North America*, 3rd edition. Kendall/Hunt Publishing Company, Dubuque, IA.
- Milner, A. M., and G. E. Petts. 1994. Glacial rivers: physical habitat and ecology. *Freshwater Biology* 32:295-307.
- Milner, A. M., E. E. Knudsen, C. Soiseth, A. L. Robertson, D. Schell, I. T. Phillips, and K. Magnusson. 2000. Colonization and development of stream communities across a 200-year gradient in Glacier Bay National Park, Alaska, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences* 57:2319-2335.
- Milner, A. M., R. C. Taylor, and M. J. Winterbourn. 2001. Longitudinal distribution of macroinvertebrates in two glacier-fed New Zealand rivers. *Freshwater Biology* 46:1765-1775.
- Milner, A.M., L. E. Brown, and D. M. Hannah. 2009. Hydroecological effects of shrinking glaciers. *Hydrological Processes* 23:62-77.
- Monaghan, M. T., C. T. Robinson, P. T. Spaak, and J. V. Ward. 2005. Macroinvertebrate diversity in fragmented Alpine streams; implications for freshwater conservation. *Aquatic Sciences* 67:454-464.
- 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. *Hydrological Processes* 23:42-61.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2015. *vegan: Community Ecology Package*. R package version 2.3-0. Available online at <http://CRAN.R-project.org/package=vegan> (accessed 19 June 2015).
- Pelto, M. S. 2006. The current disequilibrium of North Cascade glaciers. *Hydrological Processes* 20:769-779.
- Pfankuch, D. J. 1975. Stream reach inventory and channel stability evaluation. USDA Forest Service, R1-75-002. Government Printing Office #696-260/200, Washington, DC.
- Pielou, E. 1966. The measurement of diversity in different types of biological collections. *Journal of Theoretical Biology* 13:131-144.
- Poff, N. L., J. D. Olden, N. K. M. Vieira, D. S. Finn, M. P. Simmons, and B.C. Kondratieff. 2006. Functional trait niches of North American lotic insects—traits-based ecological applications in light of phylogenetic relationships: *Journal of the North American Benthological Society* 25:730-755.
- Post, A., D. Richardson, W. V. Tangborn, and F. L. Rosselot. 1971. Inventory of glaciers in North Cascades, Washington. U.S. Geological Survey Professional Paper 705-A, Washington, DC.
- R Development Core Team. 2014. R: A Language and Environment for Statistical Computing, R. Foundation for Statistical Computing. Available online at: <http://www.R-project.org> (accessed 14 December 2014).
- Richardson, J. S., and R. J. Mackay. 1991. Lake outlets and the distribution of filter feeders: an assessment of hypotheses. *Oikos* 62:370-380.
- Robinson, C. 2010. Glacial recession: biological changes in new streams following rapid glacial recession. *Mountain Research Initiative Newsletter* 4:22-24.
- Rocheffort, R. M., M. M. Bivin, J. R. Boetsch, L. Grace, S. Howlin, S. A. Acker, C. C. Thompson, and L. Whiteaker. 2012. Alpine and subalpine vegetation monitoring protocol for the North Coast and Cascades Network. Natural Resource Report NPS/NCCN/NRR—2012/570. National Park Service, Fort Collins, CO.
- Rossaro, B. 1991. Chironomids and water temperature. *Aquatic Insects* 13:87-98.
- Rossaro, B., V. Lencioni, A. Boggero, and L. Marziali. 2006. Chironomids from Southern Alpine running waters: ecology, biogeography. *Hydrobiologia* 562:231-246.
- Snook, D. L., and A. M. Milner. 2001. The influence of glacial runoff on stream macroinvertebrates communities in the Taillon catchment, French Pyrénées. *Freshwater Biology* 46:1609-1623.
- Spence, J. A., and H. B. N. Hynes. 1971. Differences in benthos upstream and downstream of an impoundment. *Journal of the Fisheries Research Board of Canada* 28:35-43.
- Stahl, K., R. D. Moore, J. M. Shea, D. Hutchinson, and A. J. Cannon. 2008. Coupled modelling of glacier and streamflow response to future climate scenarios. *Water Resources Research* 44:W02422.
- Steffan, A. W. 1971. Chironomid (Diptera) biocoenoses in Scandinavian glacier brooks. *The Canadian Entomologist* 103:477-486.

- Tockner, K., F. Malard, P. Burgherr, C. T. Robinson, U. Uehlinger, R. Zah, and J. V. Ward. 1997. Physico-chemical characterization of channel types in a glacial floodplain ecosystem (Val Roseg, Switzerland). *Archiv für Hydrobiologie* 140:433-463.
- Turner, K. L. 2009. A comparison of benthic macroinvertebrate assemblages among kryal and rhithral lake outlets in the North Cascade Mountains. Western Washington University Masters Thesis Collection. Paper 22. Available online at <http://cedar.wvu.edu/wwuet/22> (accessed 14 December 2014).
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37:130-137.
- Vannote, R. L., and B. W. Sweeney. 1980. Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *The American Naturalist* 115:667-695.
- Vieira, N. K. M., N. L. Poff, N. LeRoy, D. M. Carlisle, S. R. Moulton II, M. L. Koski, and B. C. Kondratieff. 2006. A database of lotic invertebrate traits for North America: U.S. Geological Survey Data Series 187. Available online at: <http://pubs.water.usgs.gov/ds187> (accessed 14 December 2014).
- Ward, J. V., 1994. Ecology of alpine streams. *Freshwater Biology* 32:277-294.
- Ward, J. V. 1985. Thermal characteristics of running waters. *Hydrobiologia* 125:31-46.
- Wetzel, R. G. 2001. *Limnology: Lake and River Ecosystems*, Third Edition. Academic Press, San Diego, CA.
- Wisseman, R. W., and K. Doughty. 2004. Final: Characterization of benthic invertebrate communities in the Clackamas River watershed, Oregon. Submitted to Portland General Electric Company, Portland, Oregon, Relicensing of the Clackamas Hydroelectric Project on the Clackamas River, Clackamas County, OR (FERC no. 2195).
- Winterbourn, M. J., S. Cadbury, C. Ilg, and A. M. Milner. 2008. Mayfly production in a New Zealand glacial stream and the potential effect of climate change. *Hydrobiologia* 603:211-219.
- Wotton, R. S. 1995. Temperature and lake outlet communities. *Journal of Thermal Biology* 20:121-125.
- Zbinden, M., M. Hieber, C. T. Robinson, and U. Uehlinger. 2008. Short-term colonization patterns of macroinvertebrates in alpine streams. *Archiv für Hydrobiologie* 171:75-86.

Received 14 December 2014

Accepted for publication 25 January 2016