

Elevation gradients in aquatic invertebrate assemblages:
Gathering baseline information in Grand Teton National Park's high elevation streams and lakes



Lusha M. Tronstad
Invertebrate Zoologist

J. Cody Bish
Assistant Invertebrate Zoologist

Wyoming Natural Diversity Database
University of Wyoming
Laramie, Wyoming
Email: tronstad@uwyo.edu
Telephone: 307-766-3115
Website: <http://www.uwyo.edu/wyndd/>



Cover photo: Cascade Creek below Lake Solitude with Grand Teton and Mount Owen in the background. Photo by Lusha Tronstad

Above photo: Owl Creek meandering through its valley with Moose Basin Divide in the background. Photo by Lusha Tronstad.

Suggested citation: Tronstad, L.M. and J.C. Bish. 2014. Elevation gradients in aquatic invertebrate assemblages: gathering baseline information in Grand Teton National Park's high elevation streams and lakes. Report prepared for Grand Teton National Park, Moose, Wyoming by the Wyoming Natural Diversity Database, University of Wyoming, Laramie, Wyoming.

Abstract

High elevation ecosystems are predicted to be strongly impacted by climate change. Invertebrate residents of high elevation streams and lakes have little area to move to in response to increasing temperatures. We sampled 5 streams and 6 lakes in the Teton Mountains of Grand Teton National Park to assess current invertebrate assemblages. We collected 5 Surber samples at low, middle, and high elevation sites along each stream. We collected nearly 10,000 individuals/m² on average in the streams. The density and richness of invertebrates did not vary significantly by elevation, but we tended to collect the highest densities and richness at the middle and upper sites. Five taxa were collected only at the upper sites (*Ampumixis*, *Tipula*, *Isoperla*, *Perlinodes*, and *Dicosmoecus*), and 6 taxa were most abundant at the high elevation sites (*Clinocera*, *Hemerodromia*, *Oreogeton*, Tanypodinae, *Kogotus*, and *Perlomyia*). The total density of aquatic invertebrates from headwaters to valley floor was positively related to the amount of visible biofilm and oxidation-reduction potential, but the density of Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies) was positively related to % saturation of oxygen. Total richness and the richness of Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa were negatively related to specific conductivity. The insect assemblages were more similar at low elevation sites compared to high elevation sites. Two taxa (*Sweltsa* and *Zapada*) occurred at all the high elevation sites. We gathered littoral invertebrates using dip nets and hand collecting in high elevation lakes. Invertebrates were far less diverse in the littoral zone of lakes (at least 19 taxa) compared to streams (at least 68 taxa). Caddisflies in the family Limnephilidae were the most diverse group. Results from our study contribute to the understanding of what structures aquatic invertebrate assemblages along a gradient in elevation. Additionally, the study provides baseline information on aquatic invertebrate assemblages and indicates which invertebrates to monitor with increasing temperatures.

Introduction

Climate change is predicted to strongly affect high latitude and high elevation ecosystems because these ecosystems will likely warm the most (Malmqvist and Eriksson 1995, Brown et al. 2007, Hannah et al. 2007, Brown et al. 2009). Warmer temperatures cause species to shift their range to higher latitudes. For example, Parmesan and Yohe (2003) discovered that species shifted their ranges 6.1 km/decade poleward on average. Species also move to higher elevations to compensate for rising temperatures in mountainous regions (Parmesan and Yohe 2003, Chen et al. 2009). Moths moved between 10 and 16 m/decade upward in elevation on Mount Kinabalu in Borneo (Chen et al. 2009). Plants are also shifting their ranges as shown by treeline moving to higher elevations in the Green Mountains of Vermont (Beckage et al. 2008) and the Montseny Mountains of Spain (Penuelas and Boada 2003). For these reasons, species restricted to high elevation ecosystems are excellent candidates for monitoring the effects of climate change. They are also important conservation targets, because organisms restricted to the tops of mountains have little remaining area to which to move as temperatures rise.

High elevation streams and lakes may be highly impacted by a changing climate. Headwater streams can form $\geq 75\%$ of the stream length in a drainage basin (Leopold et al. 1964, Benda et al. 2004), and collectively these small streams account for a large fraction of the biodiversity in a given basin (Clarke et al. 2008; Finn et al. 2011). Headwater streams are sensitive to changes in adjacent riparian areas, because many small streams rely on terrestrial litter as a carbon source (e.g., Bilby and Likens 1980). High elevation lakes are often small and shallow making these ecosystems vulnerable to changes in climate (Thompson et al. 2009). Receding glaciers further threaten these ecosystems with warmer water temperatures and changing hydrologic regimes (Brown et al. 2007, Finn et al. 2010). Mountain lakes and streams together create a heterogeneous landscape with unique and diverse habitats that can support rare or endemic species that may be lost if climate continues to warm (Gomi et al. 2002, Meyer et al. 2007, Clarke et al. 2008).

Warmer water temperatures will probably have the single largest effect on invertebrates in aquatic ecosystems. Rising water temperatures may increase the metabolism and growth of invertebrates (Sweeney et al. 1992), but how this will impact the timing of adult emergence and life cycle phenology of invertebrates is largely unknown. Increased temperatures also reduce oxygen solubility in water. A 4°C increase in water temperature results in a 10% decrease in dissolved oxygen (Sweeney et al. 1992). Higher temperatures and lower oxygen concentrations will likely increase the stress on aquatic invertebrates resulting in lower fitness, reproduction, and growth (Sweeney et al. 1992, Jacobsen 2008). Sweeney et al. (1992) predicted that current aquatic conditions would be found 680 km north if air temperature increased 4°C in eastern North America. Gene flow may become more limited as species ranges shift. For example, the genetic diversity of mayflies decreased at higher latitudes, one of the areas predicted to be most affected by climate change (Sweeney et al. 1992).

Our objective was to collect baseline information on the aquatic invertebrate assemblages in the Teton Mountains of Grand Teton National Park. Our specific questions were: 1.) How does the density and richness of aquatic invertebrates vary by elevation, 2.) What aquatic

invertebrates are restricted to high elevation sites, 3.) What biotic and abiotic factors best describe the structure of aquatic invertebrates across elevations, and 4.) How similar are the invertebrate assemblages at each elevation? To answer these questions, we sampled 5 streams and 6 lakes in the Teton Mountains. We collected 5 quantitative invertebrate samples at low, middle, and high elevation sites along each stream. We gathered littoral invertebrates from lakes by dip netting and hand collecting. Working in Grand Teton National Park was ideal because the land is protected to minimize anthropogenic impacts. To our knowledge, our study is the only assessment of aquatic invertebrates from the Teton Mountains. This study provides baseline information of aquatic invertebrate assemblages and may indicate which invertebrates to monitor with increasing temperatures.

Study Sites

Grand Teton National Park sits in the Snake River valley in northwestern Wyoming. The spectacular Teton Range (Grand Teton elevation 4197 m) looms over Jackson, Leigh, Jenny and Phelps Lakes. Ecosystems change dramatically from the sagebrush dominated valley floor to the forested mountainsides to the barren peaks of the Tetons.

We sampled 5 streams in Grand Teton National Park (Fig. 1) to estimate the degree to which aquatic invertebrate assemblages changed along the gradient in elevation. Moose and Owl Creeks are located in the northwestern area of the park and range from ~3050 m (Moose Creek) and ~2800 m (Owl Creek) down to 2064 m where they flow into Jackson Lake. The geology of both streams is dominated by sedimentary rock. Much of Owl Creek meanders through a wide valley with only a few tributary streams and 1 intermittent lake (dry during our visit) based on 1:80,000 scale map. Conversely, Moose Creek has many tributary streams in remote areas of Grand Teton National Park and ~10 backcountry lakes in its watershed. The lower section of Moose Creek flows through a tight canyon and trips over many falls.

Cascade Creek is located centrally in the Tetons and the bed rock is dominated by granite. The North Fork of Cascade Creek flows below Paintbrush Divide from Lake Solitude, Mica Lake, 3 unnamed lakes and 6 other tributary streams. Several tributaries flow from snowfields including one that begins at ~3353 m. The South Fork of Cascade Creek also has 5 tributaries of which 2 begin in cirque lakes. Both Icefloe Lake (3247 m) and Schoolroom Glacier Lake are highly influenced by snowfields. These 2 forks join at ~2362 m and flow down a scenic canyon into Jenny Lake (2067 m).

Death and Granite Creeks flow in southwestern Grand Teton National Park. The geology of the canyons is mainly granite with some sedimentary areas. Death Creek has ~24 tributary streams of which several originate from springs on Death Shelf. Two tributaries originate from lakes (Forget-me-not Lakes at 2926 m and Rimrock Lake at 3022 m). The stream flows through dense forest for much of its length and enters a tight canyon ~1 mile before flowing into Phelps Lake (2022 m). Granite Creek has 3 branches in the Teton Range (North, Middle and South Forks). The stream has ~18 tributary streams and only 3 originate from lakes (Indian Lake at 2989 m, Marion Lake at 2835 m, and a small unnamed lake). The stream flows through a densely forested canyon and eventually flows into the Snake River.

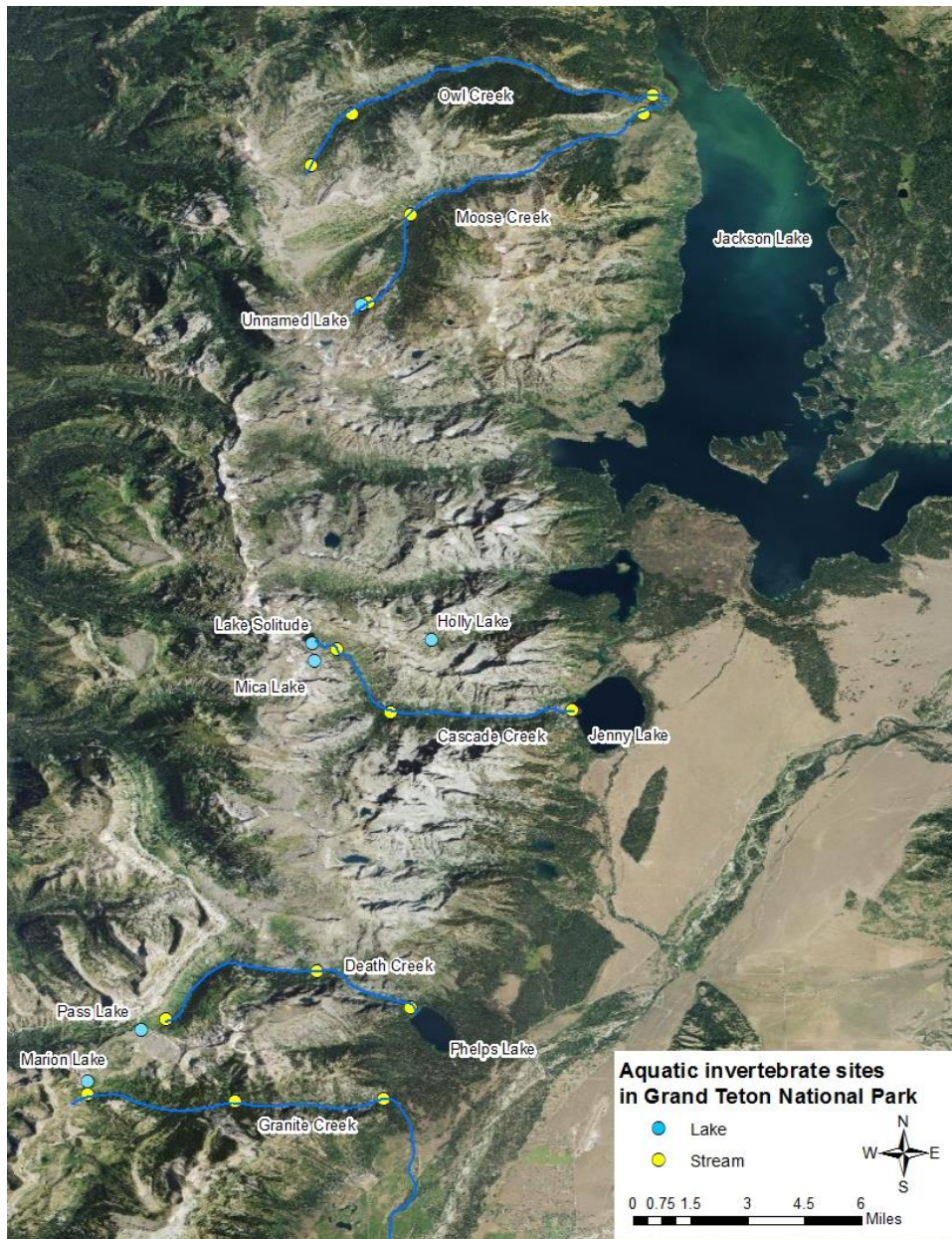


Figure 1. Map of the Teton Mountains in Grand Teton National Park showing the 6 lakes and 5 streams (blue lines) we sampled. We sampled each stream at 3 elevations (upper, middle, and lower elevations). All streams flow eastward.

Methods

We collected 5 replicate Surber samples at each of 3 different elevations (low, middle, and high) in each stream to estimate the density and diversity of aquatic invertebrates at each site. High elevation sites were sampled as close to the headwaters as possible where the stream was large enough to sample. We sampled low elevation sites near the valley floor or before flowing into a lake. Middle elevation sites were chosen by calculating the mean elevation between the upper and lower sites. The invertebrate samples were preserved in ~80% ethanol and returned

to the laboratory for sorting, identifying, and counting. We typically identified invertebrates to genus when mature specimens were captured using a dissecting microscope and identification keys (Merritt et al. 2008, Thorp and Covich 2010).

We collected additional variables to estimate the degree to which invertebrate density and richness varied with physical conditions at each site. Mean stream width and depth were calculated by estimating these variables at 3 locations at each elevation. We measured water temperature, dissolved oxygen concentration, specific conductivity, pH, and oxidation-reduction potential (ORP) using a YSI Professional Plus Multiprobe. Dissolved oxygen was calibrated at each site and specific conductivity, pH, and ORP were calibrated at the trailhead immediately before departing on our hike. Biofilm cover were ranked as either 1 (little growth), 2 (intermediate growth), or 3 (high growth) on the substrate (Finn and Poff 2005). Mean particle size of stream substrate were measured by recording the diameter of 20 arbitrarily selected rocks. We recorded the dominant riparian and landscape vegetation at each site. Slope and aspect were measured in the field using a clinometer. For analysis, we transformed the aspect (A') according to Beers et al. (1966) using $A' = \cos(45^\circ - A) + 1$ where A is the measured aspect in degrees. We recorded elevation and location with a GPS unit (datum NAD 83).

We used the AICcmodavg package in R (Mazerolle 2013) to select the best model to describe total density, density of Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies), total richness, and Ephemeroptera, Plecoptera, and Trichoptera (EPT) richness using the biotic and abiotic variables we measured from the valley floor to the headwaters. We used second-order Akaike information criterion (AICc) to rank models. AICc is used for datasets with a small sample size such as our dataset where we summarized the data for each stream and elevation ($n=15$; Appendix 1). We excluded one variable from any highly-correlated pair of variables in the candidate models. We created candidate models using information from exploring the data using correlation tables (Pearson's correlation), Random Forest models (Liaw and Wiener 2002), and best subsets (regsubsets; Lumley and Miller 2009) in R (R Core Development Team 2008). We also used knowledge of aquatic invertebrates, the field sites, and what variable might be most affected by changes in elevation.

We sampled the invertebrates of 6 high elevation lakes (Lake Solitude, Holly Lake, Marion Lake, Pass Lake, Mica Lake, and unnamed lake in the Moose Creek watershed; Fig. 1) using a D-frame dip net and hand-collecting. Basic water quality was measured using a YSI Professional Plus Multiprobe. Aspect, biofilm rank, mean particle size, location and elevation were measured as described for streams. We recorded the dominant riparian and landscape vegetation around each lake. We also noted whether or not we observed fish at each lake.

Results

Stream characteristics

The 5 streams sampled were cool mountain streams with cobble bottoms. Stream water temperature generally decreased with elevation; however, we observed some of the highest temperatures when we sampled below lakes at the upper sites (e.g., Moose and Cascade; Table

1). Dissolved oxygen was >100% saturation at most sites, and the concentration of dissolved oxygen was inversely related to elevation. The specific conductivity was lowest in Moose and Cascade Creeks and the pH of streams was basic. ORP indicated that oxidizing conditions occurred in most streams (>~200 mV). Streams were wider and deeper at lower elevations. Cascade Creek was the widest and deepest stream at the lower sites, and Granite and Owl Creeks were the narrowest and shallowest streams at the upper sites. The mean particle size in Granite (172 mm) and Cascade Creeks (180 mm) was larger than in Death, Owl, and Moose Creeks (~107 mm). Rocks had more visible biofilm at the upper sites compared to lower sites. Moose Creek had the highest biofilm rank (the greenest rocks) compared to the other streams. All streams were flowing in an easterly direction (mean aspect = 72°). The slope of the streams was generally steepest at the upper sites.

Table 1. Basic water quality and characteristics of 5 streams in the Teton Mountains, Grand Teton National Park. ORP stands for oxidation-reduction potential.

Stream Site	Units	Death			Granite			Owl			Moose			Cascade		
		Upper	Middle	Lower	Upper	Middle	Lower	Upper	Middle	Lower	Upper	Middle	Lower	Upper	Middle	Lower
Date		13-Aug-12	12-Aug-12	15-Aug-12	14-Aug-12	15-Aug-12	15-Aug	28-Jul-12	27-Jul-12	31-Jul-12	29-Jul-12	30-Jul-12	31-Jul-12	23-Jul-12	24-Jul-12	24-Jul-12
Elevation	meters	2697	2470	2038	2703	2389	2032	2586	2356	2082	2764	2379	2083	2726	2391	2003
Water temperature	°C	10.6	12.1	12.3	10.2	6.3	9.5	5.1	9	13.2	17.8	10.1	10.1	11	7.5	11
Dissolved oxygen	% saturation	109	124	123	130	124	134	106	96	133	126	109	129	115	114	121
Dissolved oxygen	mg O ₂ /L	10.8	12.2	12.4	13	14	14.4	12.1	10.2	13.1	10.6	11.3	13.7	11.3	12.5	12.6
Specific conductivity	µS/cm	190.8	123.1	103.5	174.3	176.2	169.7	147.5	160.5	185.4	7.8	50	99	9.3	44.8	25.5
pH		8.62	8.29	8.25	8.74	8.63	8.61	8.45	8.55	8.56	7.13	8.34	8.18	7.9	8.19	8.03
ORP	mV	217.8	172.5	195.4	216.2	208.7	209.2	211.4	192.2	257.7	300.9	299	276.3	169.2	177.9	224.5
Mean stream width	m	2	5	8	1	5	8	1	3	8	4	10	7	6	6	17
Mean stream depth	cm	14	24	28	10	38	29	7	16	51	15	27	30	28	33	60
Mean particle size	mm	103	73	152	74	160	282	105	97	110	152	128	44	174	165	202
Biofilm rank	1 to 3	2	1	1	2	2	1	2	1	1	3	3	2	1	1	3
Aspect	°	26	96	115	72	82	112	12	47	126	38	31	60	142	75	104
Slope	%	4	1.5	2	2	3	2	8	3	1	4	2	1	8	2	2

Lake characteristics

Most high elevation lakes in the Teton Range were glacially-formed cirques feed by streams and/or snowfields. Mica Lake was the highest elevation and coolest lake we sampled (Table 2). The water in all lakes was supersaturated with oxygen during the day and we measured the highest concentration of oxygen in Mica Lake. All lakes had low concentrations of dissolved ions and all lakes were basic. Water in most lakes appeared to favor reducing conditions (<200 mV). Most lakes had fairly large substrate in the littoral zone, and rocks had the most visible biofilm in Pass and Marion Lakes. All lakes had stream outlets, except for Pass Lake. Lake Solitude was the largest lake we sampled. We observed trout in Holly Lake and Lake Solitude.

Table 2. Basic water quality and characteristics of 6 lakes in the Teton Mountains of Grand Teton National Park.

Lake	Units	Holly	Mica	Solitude	Unnamed	Pass	Marion
Date		21-Jul-12	23-Jul-12	23-Jul-12	29-Jul-12	14-Aug-12	14-Aug-12
Elevation	m	2817	2912	2769	2777	2874	2820
Water temperature	°C	16.5	3.2	11.7	16.1	16.6	17.9
Dissolved oxygen	% saturation	109	113	122	133	119	118
Dissolved oxygen	mg O ₂ /L	9.3	13.1	11.8	11.6	10.2	9.9
Specific conductivity	µS/cm	10.2	9.3	9.3	7.8	70	136.4
pH		7.8	8.76	7.6	8.25	10.21	8.96
ORP	mV	180.1	99.9	174.2	281.2	155	188.5
Mean particle size	mm	22	258	286	165	82	100
Biofilm rank	1 to 3	1	1	2	2	3	3
Aspect	°	106	19	100	34	no outlet	131
Lake size	~hectares	2.6	3.8	14.9	6	0.3	2.3

Aquatic invertebrates in streams

Streams in the Teton Mountains were home to many aquatic invertebrates. We recorded an average of almost 10,000 individuals/m² on stream bottoms. We collected at least 68 taxa from 5 phyla and 8 classes (Appendix 2 and 3). Eighty-six percent of the taxa we collected were insects in 24 families and 6 orders. Similarly, 80% of the individuals we collected were insects. Diptera was the most abundant order of insects followed by Ephemeroptera, Plecoptera, and Trichoptera. Sphaeriidae were the most abundant non-insect invertebrates followed by Acari, Oligochaeta, and Crustacea.

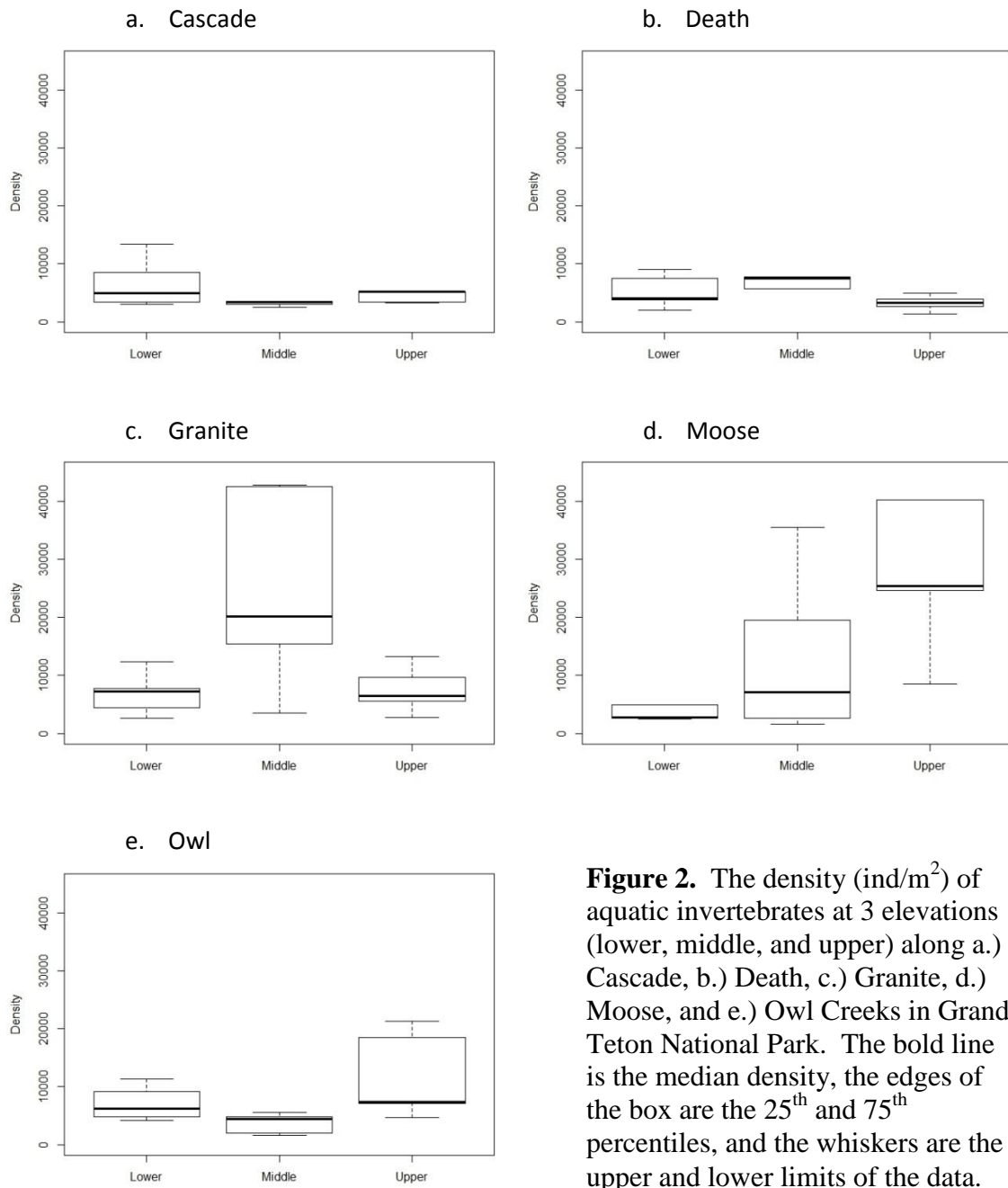


Figure 2. The density (ind/m²) of aquatic invertebrates at 3 elevations (lower, middle, and upper) along a.) Cascade, b.) Death, c.) Granite, d.) Moose, and e.) Owl Creeks in Grand Teton National Park. The bold line is the median density, the edges of the box are the 25th and 75th percentiles, and the whiskers are the upper and lower limits of the data.

The aquatic invertebrate assemblages differed among streams and elevations. The mean density of aquatic invertebrates in Moose Creek (17,550 ind/m²) was higher than Owl (7500 ind/m²), Cascade (5170 ind/m²), and Death Creeks (5140 ind/m²; ANOVA, *p*, Tukey's *p*<0.05; Appendix 1). We collected the most taxa in Moose Creek (50 taxa) and the fewest taxa in Granite (34 taxa) and Death Creeks (35 taxa; ANOVA, *p*=0.15). The density of aquatic invertebrates did not vary significantly by elevation (ANOVA, *F*=1.8, *p*=0.18). The highest

densities of invertebrates occurred at the upper elevations along Owl and Moose Creeks, and the middle elevatio on Granite Creek (Fig. 2). The density of invertebrates varied little along Cascade and Death Creeks. We measured the highest cumulative richness of invertebrates at the middle (61 taxa) and upper sites (59 taxa), and the lowest richness at the lower sites (49 taxa; ANOVA, $F=0.62$, $p=0.54$; Fig. 3). Overall, we collected the most taxa at the middle site of Cascade Creek and the fewest taxa at the upper site of Owl Creek.

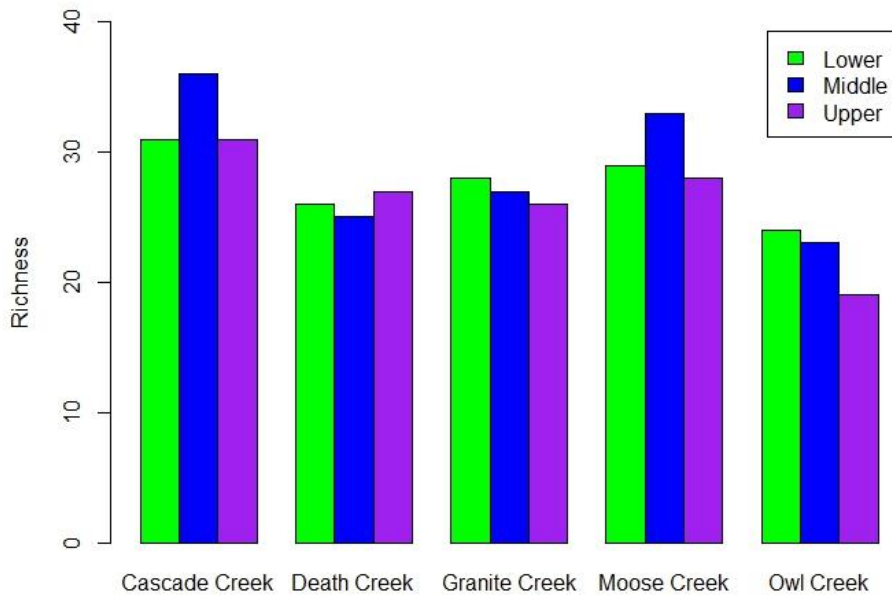


Figure 3. Cumulative richness at 3 sites along each stream in Grand Teton National Park.

Total density (ANOVA, $F=1.6$, $p=0.23$), the density of EPT taxa (ANOVA, $F=1.9$, $p=0.19$), total richness (ANOVA, $F=0.1$, $p=0.76$), and the richness of EPT taxa (ANOVA, $F=1.2$, $p=0.29$) were not related to elevation (Fig. 4). However, elevation was correlated with other parameters we measured in streams. Dissolved oxygen ($\rho=-0.56$), width ($\rho=-0.70$), and depth ($\rho=-0.70$) negatively correlated with elevation, and stream slope ($\rho=0.61$) positively correlated with elevation. Therefore, the effects of elevation may appear through other variables.

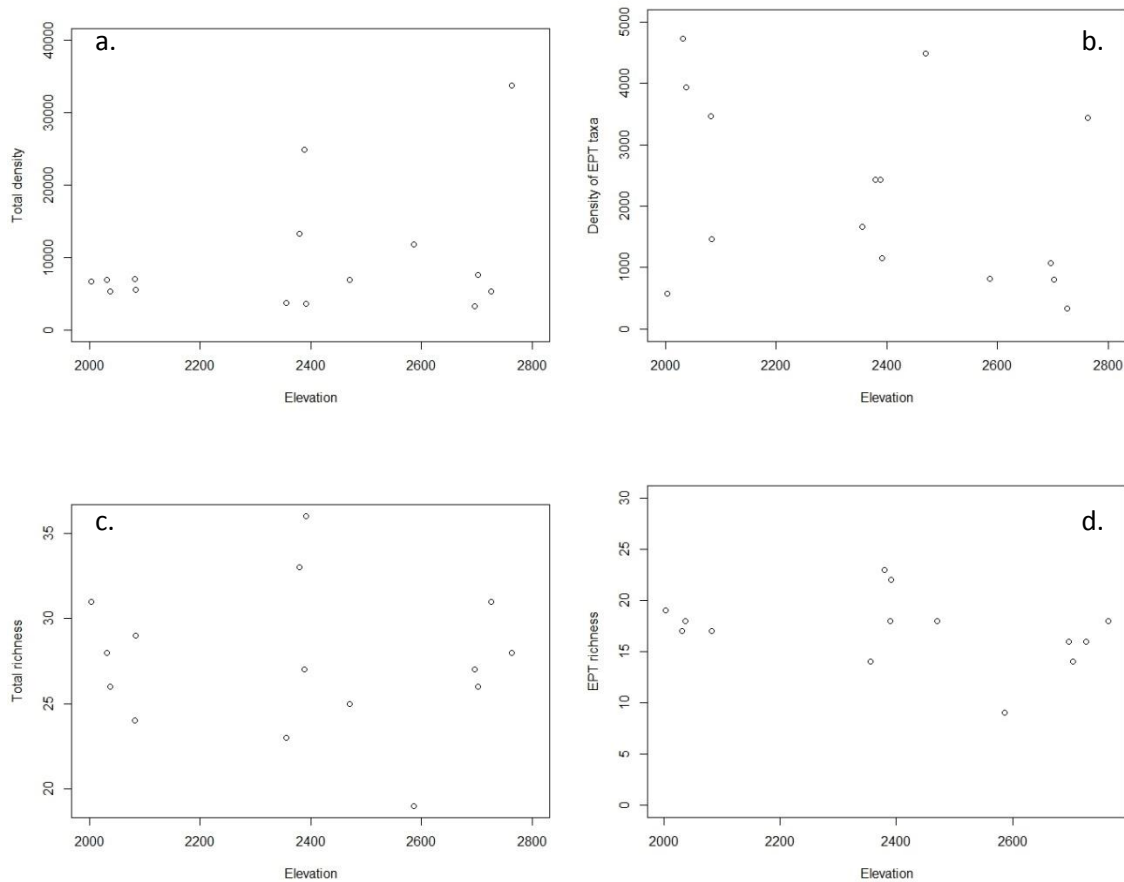


Figure 4. a.) Total density, b.) density of EPT taxa, c.) total richness, and d.) richness of EPT taxa were not related to elevation. EPT stands for Ephemeroptera (mayflies), Plecoptera (stoneflies) and Trichoptera (caddisfly) which are insect orders considered sensitive to ecosystem quality.

Larval insects are restricted to the aquatic habitat where they spend most of their life, but winged adults may disperse among habitats. We expected that larval stages may easily disperse downstream from the headwaters through drift. Between 4 and 16 insect taxa (7-30%) were collected at all three sites along a stream, and five taxa were only collected at the upper sites: *Ampumixis* (Coleoptera, Elmidae), *Tipula* (Diptera, Tipulidae), *Isoperla* (Plecoptera, Perlodidae), *Perlinodes* (Perlodidae), and *Dicosmoecus* (Trichoptera, Limnephilidae). *Clinocera*, *Hemerodromia*, *Oreogeton* (Diptera, Empididae), Tanypodinae (Diptera, Chironomidae), *Kogotus* (Plecoptera, Perlodidae), and *Perlomyia* (Plecoptera, Leuctridae) were most abundant at the upper sites. We expected fewer similarities among streams, especially those that were farther apart. Of 54 insect taxa (excluding Chironomidae), 37% were captured in only one stream. About a quarter of taxa were collected in two streams, and half of those taxa were in adjacent drainages. We collected 7.5% of taxa in three streams and 11% of taxa in four streams. Finally, 20.5% of taxa were collected in all 5 streams. We expected more similarities at lower elevation sites compared to the high elevation sites. Eight insect taxa (excluding

Chironomidae) were collected in all streams at the low elevation sites, and we collected 2 insect taxa at all high elevation sites (*Sweltsa* and *Zapada*).

The total density of aquatic invertebrates was best explained by 2 models. Biofilm rank ($t=2.4$, $p=0.03$) explained the most variance in density ($Density = -784 + 6042 \times Biofilm$, $AICc=315.9$, $AICc\ weight=0.63$; Fig. 5a) in Grand Teton National Park. Additionally, ORP ($Density = -13135 + 103 \times ORP$; $t=2.1$, $p=0.05$, $AICc=317.0$, $AICc\ weight=0.36$; Fig. 5b) also ranked high. Therefore, we collected more invertebrates at sites with greener rocks and higher ORP values. EPT taxa composed 28% of the individuals we collected and their densities appeared to be regulated by different variables than the entire assemblage. The highest ranked model indicated that higher densities of EPT taxa ($Density_{EPT}$) were collected at sites with higher % saturation of dissolved oxygen ($t=2.0$, $p=0.06$) and in stream reaches flowing in a northeasterly direction (transformed aspect; $t=2.0$, $p=0.07$; $Density_{EPT} = -6160 + 61 \times \%saturation + 994 \times Aspect$; $AICc=264.5$, $AICc\ weight=0.36$; Figs. 5c, d). Much of the variation in density of EPT taxa was explained by % saturation of oxygen alone ($Density_{EPT} = -5563 + 65 \times \%saturation$; $t=2.0$, $p=0.07$; $AICc=265.1$, $AICc\ weight=0.27$; Fig. 5c).

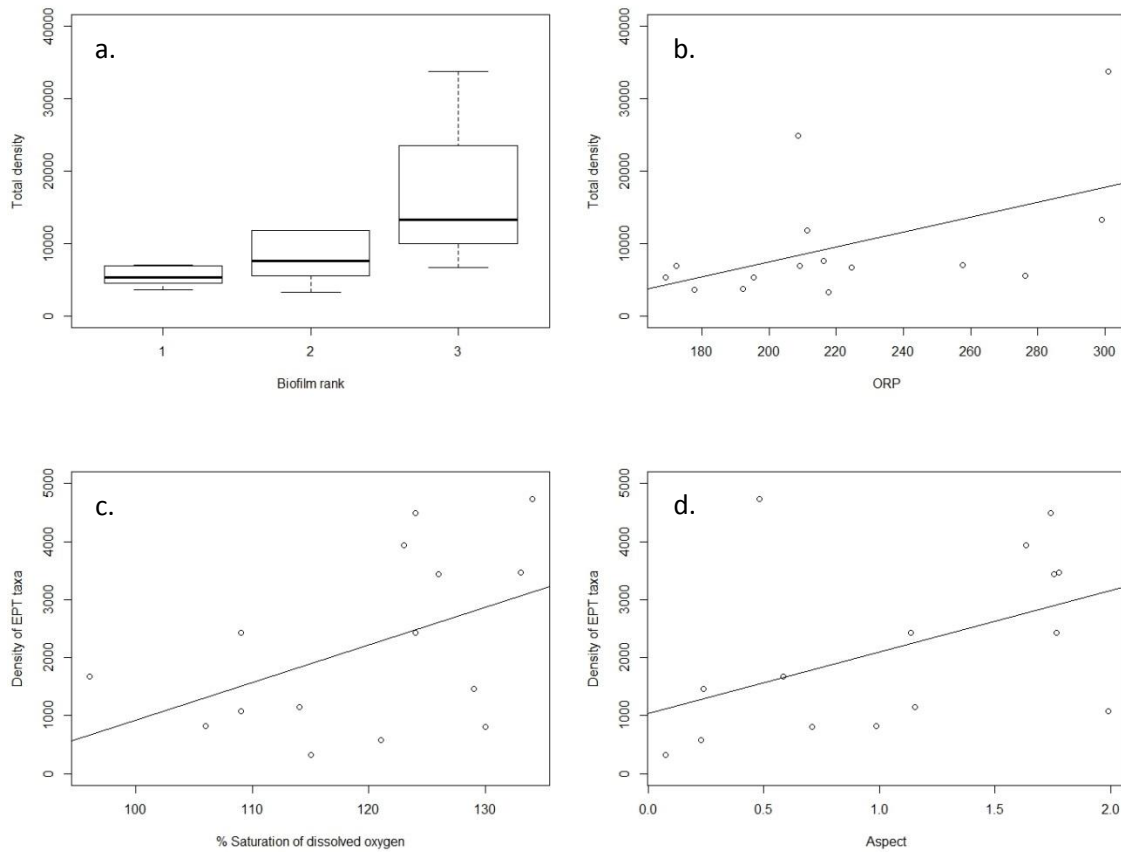


Figure 5. We collected higher densities of invertebrates at sites with a.) more visible biofilm on the substrate and b.) higher oxidation-reduction potential (ORP, mV) values in Grand Teton National Park. On the other hand, the density of the insect orders Ephemeroptera, Plecoptera, and Trichoptera (EPT) were higher at sites with higher c.) % saturation of dissolved oxygen, and d.) in stream reaches flowing in a northeasterly direction (transformed aspect).

Specific conductivity (SPC; $t=-3.1$, $p=0.009$) explained the most variation in total taxa richness ($Richness = 32 - 0.04 \times SPC$, $AICc=84.5$, $AICc$ weight=0.76; Fig. 6a). About 36% of the taxa collected were in the orders Ephemeroptera, Plecoptera, and Trichoptera. Similarly, specific conductivity ($t=-2.0$, $p<0.069$) was the highest ranked model to explain the variation in EPT richness ($Richness_{EPT} = 19.7 - 0.024 \times SPC$; $AICc=81.6$, $AICc$ weight=0.38; Fig. 6b). The model that included elevation ($t=-2.1$, $p=0.06$), specific conductivity ($t=3.0$, $p=0.01$), and transformed aspect ($t=2.1$, $p=0.06$) also ranked high ($Richness_{EPT} = 31 - 0.0054 \times Elevation - 0.033 \times SPC + 2.3 \times Aspect$; $AICc=82.8$, $AICc$ weight=0.21; Fig. 6c, Fig. 4d). The models indicate that the richness of EPT taxa is higher at sites with lower specific conductivity, at lower elevations, and in stream reaches flowing in a northeasterly direction.

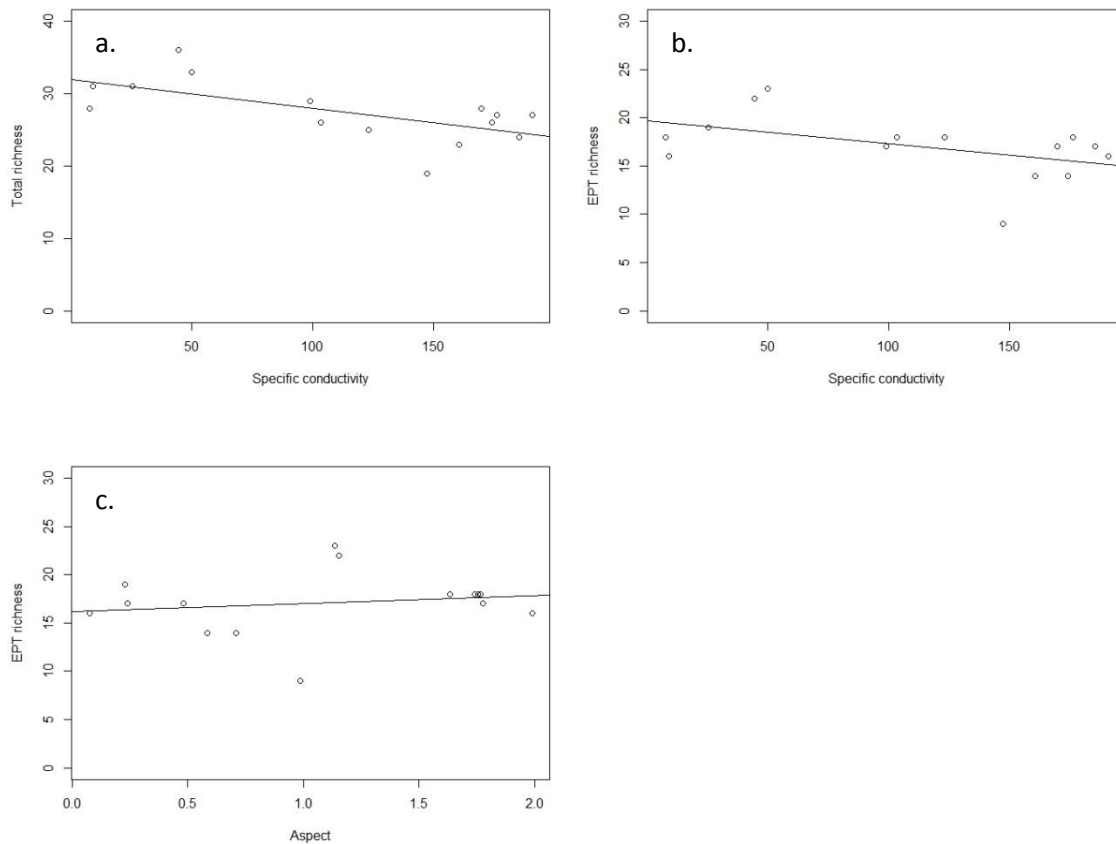


Figure 6. Total taxa richness was higher at sites with a.) lower specific conductivity ($\mu\text{S}/\text{cm}$). The richness of EPT taxa was higher at sites with b.) lower specific conductivity and c.) in streams flowing in a northeasterly direction (transformed aspect).

Invertebrates in lakes

We collected at least 19 taxa of benthic invertebrates in the littoral zone of high elevation lakes of Grand Teton National Park (Table 3; Appendix 2). We captured 5 taxa in each lake on average. Moose (8 taxa) and Holly Lakes (7 taxa) had the most taxa and Mica Lake (3 taxa) had the fewest taxa. Chironomidae were the most commonly collected invertebrates. *Agabus* (Coleoptera) was collected in half the lakes and 12 taxa were captured in only one of the lakes. Trichoptera, especially the family Limnephilidae, were the most diverse group of insects in these high elevation lakes. Limnephilids in half the lakes were pupating and preparing to emerge as adults.

Table 3. Aquatic invertebrates collected in 6 high elevation lakes in Grand Teton National Park.

Taxa	Lakes	Holly	Marion	Mica	Moose	Pass	Solitude
Coleoptera							
<i>Agabus</i>		X	X			X	
<i>Hygrotus</i>		X			X		
Diptera							
Non-Tanypodinae		X			X	X	X
Tanypodinae				X			X
Ephemeroptera							
<i>Parameletus</i>					X		
<i>Procloeon</i>		X		X			
Hemiptera							
Corixidae						X	
<i>Notonecta</i>					X		
Trichoptera							
<i>Apatania</i>					X		
<i>Desmona mono</i>		X					
<i>Hesperophylax</i>							X
Limnephilidae (pupae)		X			X		X
<i>Limnephilus</i>			X				
<i>Psychoglypha</i>					X		
Non-Insects							
Acari						X	
<i>Gammarus</i>			X				
<i>Helobdella stagnatilis</i>			X				
Oligochaeta		X					
Sphaeriidae			X		X		
Turbellaria		X		X			

Discussion

Few studies have investigated the aquatic invertebrates of Grand Teton National Park. Streams in the eastern portion of the park have been sampled for aquatic invertebrates including Kelly Warm Springs (Hotchkiss and Hall 2010), Two Ocean Lake Creek (Marshall and Hall 2004), the Snake River (Kroger 1970), and Pacific Creek (Freilich 1991), but we are not aware of any studies that have sampled aquatic invertebrates in the Teton Mountains within the park. Our study documented at least 76 taxa from 5 streams and 6 lakes in the Teton Mountains ranging from the northern to southern extents of the park.

The Teton Mountains rise steeply from the Snake River floodplain. Such an impressive mountain range protected as a national park is an ideal location to measure changes in aquatic invertebrates with elevation. Gradients in aquatic invertebrates across elevations are often obscured by anthropogenic factors (Rundle et al. 1993), but the streams in Grand Teton National Park have minimal human impacts. Many biotic and abiotic parameters structure

streams from headwaters to the valley floor. Studies from both hemispheres suggest that elevation strongly influences aquatic invertebrate assemblages (Ward 1986, Rundle et al. 1993, Suren 1994, Finn and Poff 2005). Suren (1994) noted that taxa richness was inversely related to elevation in Nepalese streams and this pattern has been observed around the world (Jacobsen et al. 1997, Jacobsen 2004). Jacobsen (2004) found that 50% of invertebrate families lived at 4000 m compared to sea level in the Andes Mountains, and the loss of most families occurred at >1800 m elevation. However, it is clear that elevation does not influence biota directly. Rather, it is a proximal measure that is correlated with several abiotic factors (e.g., temperature, stream gradient, dissolved oxygen, etc.) that more directly affect organisms.

Jacobsen (2008) argued that the loss in taxa richness of aquatic invertebrates at higher elevations was primarily driven by lower dissolved oxygen concentrations. Lower atmospheric pressure at higher elevations reduced the availability of oxygen to organisms. Conversely, water can hold more oxygen at cooler temperatures, and streams are generally colder at the headwaters. Jacobsen (2008) argued that the decrease in oxygen concentration due to atmospheric pressure negated any increase in oxygen due to temperature. Our results from Teton streams support Jacobsen's (2008) hypothesis. The concentration of oxygen and % saturation of oxygen were negatively correlated with elevation. Furthermore, percent saturation of dissolved oxygen best explained the density of EPT taxa. EPT taxa, especially, Plecoptera (stoneflies), are sensitive to oxygen concentrations, while other aquatic invertebrates (e.g., blood midges) have adaptations to survive with low oxygen availability. Lower oxygen concentrations may reduce the metabolism, feeding, growth, emergence, and fecundity of sensitive aquatic invertebrates over time (Jacobsen 2008).

Our models suggested that specific conductivity, elevation, and aspect best explained the richness of aquatic invertebrates in Teton Mountain streams. The streams we sampled in Grand Teton National Park differed in geology, with the northern watersheds primarily composed of sedimentary bedrock and the central and southern watersheds composed mostly of granite. As a result, specific conductivity varied among watersheds with Cascade Creek (granite bedrock) having the lowest specific conductivity. Specific conductivity varied less at the 3 elevations along a stream (standard error ranged from 2 to 26) compared to across streams at each elevation (e.g., all high elevation sites; standard error ranged from 27 to 40). Our results differed from Himalayan streams where conductivity was inversely related to elevation (Rundle et al. 1993), but these values likely depend on the local geology.

Streams flowing to the northeast had higher densities and richness of EPT taxa in the Teton Mountains. Southwest facing slopes are generally warmest and driest with sparser forest cover, and northeast facing slopes are coolest and wettest with denser forest cover (Stage 1976). Streams flowing southeast or northwest may have dense forest growing on the south side (northeast-facing slope). The dense forest would contribute terrestrial organic matter to the stream and shade the channel (more heterotrophic). On the other hand, streams flowing to the northeast or southwest would have sparser forest growing on the southern side (northwest facing slope) and they may have less terrestrial organic matter inputs and more light reaching the stream (more autotrophic). We are only aware of one study that described how streams

change depending on aspect. Perdril et al. (2014) measured higher soil carbon in streams with north-facing watersheds compared to south-facing watershed due to higher soil flushing rates. Much more work is needed to understand how stream aspect may affect the structure and function of streams.

Headwater streams are hotspots for biodiversity. Lotic ecosystems have traditionally been viewed as longitudinal continuums from small headwaters streams to large order rivers. The river continuum concept used such a view to describe streams along their length (Vannote et al. 1980) and this model has been used extensively in stream ecology. In this context, many studies reported that high elevation streams have the lowest invertebrate diversity (Ward and Dufford 1979, Ward 1986, Suren 1994, Jacobsen 2004, Finn and Poff 2005, Jacobsen 2008). Three of the 5 streams in our study had the lowest diversity of invertebrates at the highest elevation sites. However, comparing individual stream segments longitudinally refers to alpha or site diversity. When streams are viewed from a basin-wide perspective their dendritic nature is evident; >75% of stream length in a given basin can be in the headwaters (1-2 order streams; Leopold et al. 1964, Benda et al. 2004). Comparing headwater segments collectively to larger order segments occurring downstream suggests that headwater streams have high β or regional diversity (Clarke et al. 2008, Finn et al. 2011). That is, the diversity of invertebrates in all headwater streams within a basin is higher compared to larger rivers downstream. The idea that headwater streams collectively contain the highest diversity of invertebrates is relatively new, and Grand Teton National Park would be an ideal place to test this hypothesis.

The invertebrate assemblages in high elevation streams can vary greatly from one stream to another within a watershed. Basic geographic differences may be a main cause (Kubo et al. 2013). For example, headwater streams may obtain their water from different sources (e.g., glacier meltwater, groundwater, lakes or snowmelt) catering to invertebrates with different tolerances. Additionally, invertebrate assemblages may differ because of isolation. Non-insect invertebrates do not have an aerial stage and their predominant mode of dispersal is likely within the stream channel. Conversely, insects emerge as winged adults and may move across the terrestrial landscape. The distance that adult insects disperse likely depends on how well they can fly. For example, mayflies and stoneflies appear to be poor dispersers, because less than 50% of adults were captured ≥ 10 m from a stream in the Colorado Rocky Mountains (Finn and Poff 2008). Caddisflies seem to be better fliers as 30-100% of caddisflies were captured up to 30 m from the stream. Genetic analysis further supports the idea that populations of some aquatic insects are isolated at high elevations (Finn and Poff 2011). The degree to which aquatic invertebrates are isolated at high elevations in the Teton Mountains has not been investigated, but our analysis showed that streams at high elevation sites shared few similar taxa compared to lower elevation sites.

Lakes and streams may be affected differently by climate change. Rising air temperatures can increase lake water temperatures and melt ice cover earlier (Catalan et al. 2009). Earlier ice-off can cause a mis-match between phytoplankton blooms and maximum zooplankton densities as discovered in Lake Washington (Winder and Schindler 2004). Changes in water temperature, precipitation, and stream discharge are thought to have the largest effect on streams (Poff et

al. 2010). Using aquatic invertebrate species traits, physical variables, hydrologic metrics, and climate drivers, Poff et al. (2010) predicted that the Upper Colorado River and Great Basins were at greatest risk to climate change in the western United States. Aquatic invertebrates who are cold stenotherms (require cool water temperatures) and obligate rheophiles (live in erosional areas in streams) were reported to be taxa at the greatest risk.

Collecting baseline information is critical to assess how ecosystems are changing, and also to identify species at higher risk of extirpation because of those changes. Climate change poses the greatest risk to taxa restricted to or most abundant at high elevation sites. Five taxa were collected only at the upper sites of the Teton Mountains (*Ampumixis*, *Tipula*, *Isoperla*, *Perlinodes*, and *Dicosmoecus*) and 6 taxa were most abundant at the high elevation sites (*Clinocera*, *Hemerodromia*, *Oreogeton*, Tanypodinae, *Kogotus*, and *Perlomyia*). We recommend that high elevation sites be sampled every 5 to 10 years to monitor how climate change may be affecting invertebrates in high elevation headwater streams. Comparing future samples to the current study will advance our knowledge of how these streams are responding to increasing temperatures.

Acknowledgements

Thanks to Kyle Hack, Morgan Ford, Oliver Wilmot, and Phil Branigan for sorting samples. Bryan Tronstad was instrumental in data entry. Don and Lusha Alzner graciously provided meals and a roof between backpacking trips.

Literature Cited

- Beckage, B., B. Osborne, D. G. Gavin, C. Pucko, T. Siccama, and T. Perkins. 2008. A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. *Proceedings of the National Academy of Sciences of the United States of America* 105:4197-4202.
- Beers, T. W., P. E. Dress, and L. C. Wensel. 1966. Aspect transformation in site productivity research. *Journal of Forestry* 64:691-&.
- Benda, L., N. L. Poff, D. Miller, T. Dunne, G. Reeves, G. Pess, and M. Pollock. 2004. The network dynamics hypothesis: how channel networks structure riverine habitats. *Bioscience* 54:413-427.
- Bilby, R. E., and G. E. Likens. 1980. Importance of organic debris dams in the structure and function of stream ecosystems. *Ecology* 61:1107-1113.
- Brown, L. E., R. Cereghino, and A. Compin. 2009. Endemic freshwater invertebrates from southern France: diversity, distribution and conservation implications. *Biological Conservation* 142:2613-2619.
- 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.
- Catalan, J., C. J. Curtis, and M. Kernan. 2009. Remote European mountain lake ecosystems: regionalisation and ecological status. *Freshwater Biology* 54:2419-2432.
- Chen, I. C., H.-J. Shiu, S. Benedick, J. D. Holloway, V. K. Cheye, H. S. Barlow, J. K. Hill, and C. D. Thomas. 2009. Elevation increases in moth assemblages over 42 years on a tropical

- mountain. Proceedings of the National Academy of Sciences of the United States of America 106:1479-1483.
- Clarke, A., R. Mac Nally, N. Bond, and P. S. Lake. 2008. Macroinvertebrate diversity in headwater streams: a review. *Freshwater Biology* 53:1707-1721.
- Finn, D. S., N. Bonada, C. Murria, 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., and N. L. Poff. 2005. Variability and convergence in benthic communities along the longitudinal gradients of four physically similar Rocky Mountain streams. *Freshwater Biology* 50:243-261.
- Finn, D. S., and N. L. Poff. 2008. Emergence and flight activity of alpine stream insects in two years with contrasting winter snowpack. *Arctic Antarctic and Alpine Research* 40:638-646.
- Finn, D. S., and N. L. Poff. 2011. Examining spatial concordance of genetic and species diversity patterns to evaluate the role of dispersal limitation in structuring headwater metacommunities. *Journal of the North American Benthological Society* 30:273-283.
- Finn, D. S., K. Rasanen, and C. T. Robinson. 2010. Physical and biological changes to a lengthening stream gradient following a decade of rapid glacial recession. *Global Change Biology* 16:3314-3326.
- Freilich, J. E. 1991. Movement patterns and ecology of *Pteronarcys* nymphs (Plecoptera): observations of marked individuals in a Rocky Mountain stream. *Freshwater Biology* 25:379-394.
- Gomi, T., R. C. Sidle, and J. S. Richardson. 2002. Understanding processes and downstream linkages of headwater systems. *Bioscience* 52:905-916.
- Hannah, D. M., L. E. Brown, A. M. Milner, A. M. Gurnell, G. R. McGregord, G. E. Petts, B. P. G. Smith, and D. L. Snook. 2007. Integrating climate-hydrology-ecology for alpine river systems. *Aquatic Conservation: Marine and Freshwater Ecosystems* 17:636-656.
- Hotchkiss, E. R., and R. O. Hall. 2010. Linking calcification by exotic snails to stream inorganic carbon cycling. *Oecologia* 163:235-244.
- Jacobsen, D. 2004. Contrasting patterns in local and zonal family richness of stream invertebrates along an Andean altitudinal gradient. *Freshwater Biology* 49:1293-1305.
- Jacobsen, D. 2008. Low oxygen pressure as a driving factor for the altitudinal decline in taxon richness of stream macroinvertebrates. *Oecologia* 154:795-807.
- Jacobsen, D., R. Schultz, and A. Encalada. 1997. Structure and diversity of stream invertebrate assemblages: the influence of temperature with altitude and latitude. *Freshwater Biology* 38:247-261.
- Kroger, R. L. 1970. An annotated list of stream invertebrates collected from Grand Teton National Park, Wyoming, Univ. Wyo. Pubis 36:1-14.
- 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.
- Leopold, L. B., M. G. Wolfman, and J. P. Miller. 1964. *Fluvial Processes in Geomorphology*. W. H. Freeman, San Francisco, California.

- Liaw, A., and M. Wiener. 2002. Classification and regression by randomForest. *in*, R News 2:18-22.
- Lumley, T., and A. Miller. 2009. leaps: regression subset selection, an R package.
- Malmqvist, B., and A. Eriksson. 1995. Benthic insects in Swedish lake-outlet streams: patterns in species richness and assemblage structure. *Freshwater Biology* 34:285-296.
- Marshall, M. C., and R. O. Hall. 2004. Hyporheic invertebrates affect N cycling and respiration in stream sediment microcosms. *Journal of the North American Benthological Society* 23:416-428.
- Mazerolle, M. J. 2013. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c), an R package.
- Merritt, R. W., K. W. Cummins, and M. B. Berg, editors. 2008. *An Introduction to the Aquatic Insects of North America*, 4th edition. Kendall Hunt Publishing, Dubuque, IA.
- Meyer, J. L., D. L. Strayer, J. B. Wallace, S. L. Eggert, G. S. Helfman, and N. E. Leonard. 2007. The contribution of headwater streams to biodiversity in river networks. *Journal of the American Water Resources Association* 43:86-103.
- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37-42.
- Penuelas, J., and M. Boada. 2003. A global change-induced biome shift in the Montseny mountains (NE Spain). *Global Change Biology* 9:131-140.
- Perdrial, J. N., J. McIntosh, A. Harpold, P. D. Brooks, X. Zapata-Rios, J. Ray, T. Meixner, T. Kanduc, M. Litvak, P. A. Troch, and J. Chorover. 2014. Stream water carbon controls in seasonally snow-covered mountain catchments: impacts of inter-annual variability of water fluxes, catchment aspect and seasonal processes. *Biogeochemistry* 118:273-290.
- Poff, N. L., M. I. Pyne, B. P. Bledsoe, C. C. Cuhacyan, and D. M. Carlisle. 2010. Developing linkages between species traits and multiscaled environmental variation to explore vulnerability of stream benthic communities to climate change. *Journal of the North American Benthological Society* 29:1441-1458.
- R Core Development Team. 2008. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rundle, S. D., A. Jenkins, and S. J. Ormerod. 1993. Macroinvertebrate communities in streams in the Himalaya, Nepal. *Freshwater Biology* 30:169-180.
- Stage, A. R. 1976. An expression for the effect of aspect, slope, and habitat type on tree growth. *Forest Science* 22:457-460.
- Suren, A. M. 1994. Macroinvertebrate communities of streams in western Nepal: effects of altitude and land-use. *Freshwater Biology* 32:323-336.
- Sweeney, B. W., J. K. Jackson, J. D. Newbold, and D. H. Funk. 1992. Climate change and the life histories and biogeography of aquatic insects in eastern North America. Pages 143-175 *in* P. Firth and S. G. Fisher, editors. *Global Climate Change and Freshwater Ecosystems*. Springer-Verlag, New York.
- Thompson, R., M. Ventura, and L. Camarero. 2009. On the climate and weather of mountain and sub-arctic lakes in Europe and their susceptibility to future climate change. *Freshwater Biology* 54:2433-2451.
- Thorp, J. H., and A. P. Covich, editors. 2010. *Ecology and Classification of North American Freshwater Invertebrates*, 3rd edition. Elsevier, New York.

- 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.
- Ward, J. V. 1986. Altitudinal zonation in a Rocky Mountain USA stream. *Archiv fuer Hydrobiologie Supplement* 74:133-199.
- Ward, J. V., and R. G. Dufford. 1979. Longitudinal and seasonal distribution of macroinvertebrates and epilithic algae in a Colorado springbrook-pond system. *Archiv fuer Hydrobiologie* 86:284-321.
- Winder, M., and D. E. Schindler. 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology* 85:2100-2106.

Appendix 1. Data used to model gradients in Grand Teton National Park streams.

Stream	Units	Cascade Creek			Death Creek			Granite Creek			Moose Creek			Owl Creek		
		Lower	Middle	Upper	Lower	Middle	Upper	Lower	Middle	Upper	Lower	Middle	Upper	Lower	Middle	Upper
Elevation	m	2003	2391	2726	2038	2470	2697	2032	2389	2703	2083	2379	2764	2082	2356	2586
Temperature	°C	11	7.5	11	12.3	12.1	10.6	9.5	6.3	10.2	10.1	10.1	17.8	13.2	9	5.1
Saturation DO	%	121	114	115	123	124	109	134	124	130	129	109	126	133	96	106
DO	mg O ₂ /L	12.6	12.5	11.3	12.4	12.2	10.8	14.4	14	13	13.7	11.3	10.6	13.1	10.2	12.1
Specific conductivity	µS/cm	25.5	44.8	9.3	103.5	123.1	190.8	169.7	176.2	174.3	99	50	7.8	185.4	160.5	147.5
pH		8.03	8.19	7.9	8.25	8.29	8.62	8.61	8.63	8.74	8.18	8.34	7.13	8.56	8.55	8.45
ORP	mV	224.5	177.9	169.2	195.4	172.5	217.8	209.2	208.7	216.2	276.3	299	300.9	257.7	192.2	211.4
Width	m	17	6	6	8	5	2	8	5	1	7	10	4	8	3	1
Depth	cm	60	33	28	28	24	14	29	38	10	30	27	15	51	16	7
MPS	mm	202	165	174	152	73	103	282	160	74	44	128	152	110	97	105
Biofilm	1 to 3	3	1	1	1	1	2	1	2	2	2	3	3	1	1	2
Slope	%	2	2	8	2	1.5	4	2	3	2	1	2	4	1	3	8
Aspect	transformed	0.229	1.154	0.075	1.633	1.742	1.989	0.482	1.765	0.708	0.240	1.137	1.754	1.777	0.584	0.987
Density	ind/m ²	6661.8	3536	5313.8	5295.2	6913	3208.8	6870.4	24919.8	7551	5537.2	13316.6	33804.4	6972.75	3661.4	11756.4
EPT density	ind/m ²	575.6	1151.6	326.8	3942.8	4493.2	1076	4736.8	2426.2	801.6	1460.8	2429	3442.6	3471.5	1669.8	823.2
Richness	number of taxa	31	36	31	26	25	27	28	27	26	29	33	28	24	23	19
EPT richness	number of taxa	19	22	16	18	18	16	17	18	14	17	23	18	17	14	9

Appendix 2. Photos of some aquatic invertebrates collected from the Teton Mountains in Grand Teton National Park.



Appendix 3. The density (ind/m²) of aquatic invertebrates at 3 elevations along each of 5 streams in Grand Teton National Park. Early instar insects that could not be identified to genus were not listed in the table, thus densities in the table do not equal totals.

Taxa	Site	Cascade Creek			Death Creek			Granite Creek			Moose Creek			Owl Creek		
		Lower	Middle	Upper	Lower	Middle	Upper	Lower	Middle	Upper	Lower	Middle	Upper	Lower	Middle	Upper
Insects																
Coleoptera																
<i>Ampumixis</i>		0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hygrotus</i>		0	0	2	0	0	0	0	0	0	2	0	0	0	0	0
Diptera																
<i>Agathon</i>		0	22	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Clinocera</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	15	121
<i>Dicranota</i>		4	4	34	0	0	4	2	2	0	2	0	0	0	45	0
<i>Gonomyodes</i>		0	0	0	0	0	0	0	0	17	0	0	0	0	7	0
<i>Helodon</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	1382	88
<i>Hemerodromia</i>		0	0	0	0	0	0	11	250	390	0	0	0	0	0	0
<i>Mallochohelea</i>		0	0	0	0	0	0	0	0	0	30	144	0	6	0	30
Non-Tanypodinae		4947	1464	3128	1042	1798	1524	1686	21322	5623	3587	8997	9135	2592	495	9167
<i>Oreogeton</i>		0	0	0	0	0	0	0	0	0	0	17	24	0	0	0
<i>Pericoma/Telmatoscopus</i>		0	0	0	11	0	0	26	2	4	0	0	0	0	0	0
<i>Probezzia</i>		0	125	4	0	22	108	0	0	0	0	0	0	0	0	0
<i>Prosimulium</i>		32	11	4	0	0	0	97	2	80	4	0	280	0	0	0
<i>Rhabdomastix</i>		2	7	0	0	0	0	0	0	0	2	0	0	0	0	0
<i>Simulium</i>		0	0	0	9	2	43	0	2	0	0	0	0	0	0	0
Tanypodinae		204	153	876	0	0	4	0	0	0	0	11	1074	0	0	0
<i>Tipula</i>		0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
Ephemeroptera																
<i>Baetis</i>		75	0	0	0	0	0	0	0	0	28	599	15	116	0	0
<i>Cinygmula</i>		122	112	4	103	407	215	41	428	157	192	252	0	229	403	45
<i>Drunella coloradensis</i>		17	7	7	1034	2500	0	303	306	0	129	32	0	159	0	0
<i>Drunella doddsi</i>		0	0	0	0	2	0	35	0	0	54	0	0	266	0	0
<i>Epeorus</i>		43	258	20	403	245	54	1059	327	73	166	796	0	415	551	0
<i>Ephemerella</i>		0	0	0	0	0	0	0	0	0	0	37	0	0	0	0
<i>Heterocloeon</i>		0	241	30	13	2	41	140	82	22	0	202	493	0	0	0
<i>Paracloeodes</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	310	116
<i>Procloeon</i>		22	60	69	37	329	31	52	224	13	0	0	0	0	0	0
<i>Rhithrogena</i>		0	0	0	19	2	45	43	95	246	4	35	17	38	73	0
Hemiptera																
Plecoptera																
<i>Acroneuria</i>		0	15	13	0	0	0	0	0	0	0	0	0	0	0	0
<i>Alloperla</i>		0	0	0	0	0	0	0	0	0	0	13	0	0	0	0
<i>Claassenia</i>		0	0	0	0	0	0	0	0	0	0	4	47	30	0	0
<i>Isoperla</i>		0	0	0	0	0	0	0	0	0	0	0	4	0	0	0
<i>Kogotus</i>		0	28	37	0	0	0	0	0	0	0	0	0	0	0	0
<i>Megarcys</i>		39	2	2	795	437	17	790	131	103	9	34	4	0	26	0
<i>Perlinodes</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
<i>Perlomyia</i>		0	13	4	0	17	129	9	52	65	0	0	0	0	0	125
<i>Rickera</i>		4	0	28	0	0	0	0	0	0	0	15	0	0	0	0
<i>Suwallia</i>		0	62	0	0	0	0	0	0	0	0	0	84	0	0	0
<i>Sweltsa</i>		63	0	26	62	179	82	67	48	4	80	62	312	94	0	108
<i>Zapada</i>		65	155	54	155	148	226	215	377	73	13	114	1647	100	145	233
Trichoptera																
<i>Arctopsyche</i>		0	4	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Dicosmoecus</i>		0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
<i>Glossosoma</i>		9	13	0	0	0	15	106	7	11	2	13	0	94	4	7
<i>Manophylax</i>		0	0	0	0	0	0	0	2	2	0	0	0	0	0	0
<i>Neothremma</i>		19	50	13	934	60	0	2	4	0	4	0	618	81	2	0
<i>Parapsyche</i>		4	4	0	4	7	0	43	4	0	4	4	37	11	0	0
<i>Polycentropodidae</i>		0	0	0	0	0	0	0	0	0	4	17	0	0	0	0
<i>Psychoglypha</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
<i>Rhyacophila alberta</i>		11	11	0	2	0	32	0	0	0	43	19	4	0	26	4
<i>Rhyacophila arnaudi</i>		4	0	0	0	2	39	0	0	0	0	7	0	0	0	0
<i>Rhyacophila brunnea/vemna</i>		0	0	0	0	0	0	0	0	0	0	0	32	6	2	9
<i>Rhyacophila hyalinata</i>		0	0	0	2	0	4	28	67	4	0	0	0	0	0	0
<i>Rhyacophila vaccua</i>		43	39	15	84	101	26	28	4	2	2	0	43	33	7	0
<i>Rhyacophila verrula</i>		11	2	0	0	0	0	0	0	0	7	11	0	0	0	0
<i>Rhyacophila vofixa</i>		0	4	0	2	15	41	26	17	4	0	2	0	0	0	0
<i>Thremmatinae</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	6	0
Non-Insects																
Crustacea																
Calanoida		0	0	0	0	0	0	0	0	0	0	0	17	0	0	0
Cyclopoida		17	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Harpacticoida		0	4	75	0	129	4	9	0	17	0	0	0	0	0	43
Ostracoda		86	54	177	0	9	7	0	69	0	4	0	0	81	2	47
Annelida																
Hirudinea		133	0	2	63	140	0	9	0	73	0	0	0	0	0	0
Oligochaeta		187	2	4	2	0	4	2	0	2	306	1014	60	43	2	41
Mollusca																
Sphaeriidae		0	2	77	0	0	0	0	0	0	0	0	15647	0	0	0
Other																
Acari		245	276	437	129	295	332	215	745	355	75	433	3694	498	30	700
Nematoda		4	11	22	2	0	9	4	9	75	0	0	0	0	0	226
Nematomorpha		0	0	0	0	0	0	0	0	0	6	2	75	3	0	0
Turbellaria		0	0	0	0	0	0	0	0	0	6	73	0	0	0	435
Total		6662	3536	5314	5295	6913	3210	6870	24920	7551	5537	13317	33804	6974	3661	11756