

Food web structure and function in two arctic streams with contrasting disturbance regimes

STEPHANIE M. PARKER*,† AND ALEXANDER D. HURYN†

*Department of Biological Sciences, University of Maine, Orono, ME, U.S.A.

†Aquatic Biology Program, University of Alabama, Tuscaloosa, AL, U.S.A.

SUMMARY

1. We studied the effect of substratum movement on the communities of adjacent mountain and spring tributaries of the Ivishak River in arctic Alaska (69°1'N, 147°43'W). We expected the mountain stream to have significant bed movement during summer because of storm flows and the spring stream to have negligible bed movement because of constant discharge.
2. We predicted that the mountain stream would be inhabited only by taxa able to cope with frequent bed movement. Therefore, we anticipated that the mountain stream would have lower macroinvertebrate species richness and biomass and a food web with fewer trophic levels and lower connectance than the spring stream.
3. Substrata marked *in situ* indicated that 57–66% of the bed moved during summer in the mountain stream and 4–20% moved in the spring stream.
4. Macroinvertebrate taxon richness was greater in the spring (25 taxa) than in the mountain stream (20 taxa). Mean macroinvertebrate biomass was also greater in the spring (4617 mg dry mass m⁻²) than in the mountain stream (635 mg dry mass m⁻²). Predators contributed 25% to this biomass in the spring stream, but only 7% in the mountain stream.
5. Bryophyte biomass was >1000 times greater in the spring stream (88.4 g ash-free dry mass m⁻²) than the mountain stream (0.08 g ash-free dry mass m⁻²). We attributed this to differences in substratum stability between streams. The difference in extent of bryophyte cover between streams probably explains the high macroinvertebrate biomass in the spring stream.
6. Mean food-web connectance was similar between streams, ranging from 0.18 in the spring stream to 0.20 in the mountain stream. Mean food chain length was 3.04 in the spring stream and 1.83 in the mountain stream. Dolly Varden char (*Salvelinus malma*) was the top predator in the mountain stream and the American dipper (*Cinclus mexicanus*) was the top predator in the spring stream. The difference in mean food chain length between streams was due largely to the presence of *C. mexicanus* at the spring stream.
7. Structural differences between the food webs of the spring and mountain streams were relatively minor. The difference in the proportion of macroinvertebrate biomass contributing to different trophic levels was major, however, indicating significant differences in the volume of material and energy flow between food-web nodes (i.e. food web function).

Keywords: Alaska, bryophytes, *Cinclus*, macroinvertebrates, *Salvelinus*, spring streams, substratum stability

Correspondence: Stephanie M. Parker, Aquatic Biology Program, A122 Bevell Bldg., University of Alabama, Tuscaloosa, AL 35487-0206, U.S.A.
E-mail: parke003@bama.ua.edu

Introduction

Disturbance is defined as a change in abiotic factors affecting the structure of a biological community and is a fundamental determinant of stream community

structure (White & Pickett, 1985; Biggs, Smith & Duncan, 1999; Lake, 2000). Stream communities are subject to many types of disturbance (Resh *et al.*, 1988; Wallace, 1990; Lake, 2000). Perhaps the most commonly studied is the disturbance of bed substrata during floods (Scarsbrook & Townsend, 1993; Townsend, Scarsbrook & Doleddec, 1997; Duncan, Suren & Brown, 1999), which has been shown to alter community structure because of variation in the vulnerability of different populations to substratum movement (Townsend *et al.*, 1997; Bond & Downes, 2000; Holomuzki & Biggs, 2000; Lake, 2000). Streams subject to frequent substratum movement tend to have communities of lower overall abundance and biomass and lower taxonomic richness than those with less frequent substratum movement (Power, Parker & Wootton, 1996; Townsend *et al.*, 1997). As the number of taxa in a community decreases, the proportional number of connections within its food web may also decrease, which simplifies food-web structure (Pimm, 2002).

Flooding and the associated movement of bed substrata affects stream communities worldwide (Englund, 1991; Dudgeon, 1993; Lancaster & Hildrew, 1993; Flecker & Feifarek, 1994; Rosser & Pearson, 1995; Wootton, Parker & Power, 1996; Matthaei, Uehlinger & Frutiger, 1997; Townsend *et al.*, 1997; Lake, 2000). Other forms of disturbance may be regional, however. The streams of arctic Alaska show great physical and hydrological variability (Craig & McCart, 1975; Craig, 1989), resulting in a wide range of disturbance regimes. At the extremes are the high-gradient mountain streams and the perennial springs. Mountain streams have peak flows during snowmelt in spring and spates that occur frequently during summer and they may freeze solid during the Arctic winter (Craig & McCart, 1975; Craig, 1989). In comparison, the discharge of perennial spring streams is primarily groundwater flowing from sources below the permafrost layer, which results in relatively constant temperature and discharge throughout the year although winter temperatures may be less than -30°C for extended periods (Hopkins *et al.*, 1955; Williams, 1970). Consequently, the disturbance of spring communities by spates is minimal. Differences in disturbance regime between mountain streams and perennial spring streams are likely to result in large contrasts in the attributes of their biological communities.

Our study attempted to determine the effect of substratum movement on the communities of adjacent mountain and spring streams in the Ivishak River drainage on the North Slope of Alaska. We anticipated that the mountain stream would be subject to more variable flows and greater bed movement during summer, whereas the spring stream would have consistent perennial flow with little annual variability and negligible bed movement. Because of these physical contrasts, we predicted that the mountain stream would have lower species richness and biomass and a food web with fewer trophic levels and lower connectance (Briand, 1983; Thompson & Townsend, 1999; Pimm, 2002) than the spring stream.

Methods

Study site

This study was conducted in a headwater catchment of the Ivishak River, a braided river in the Arctic National Wildlife Refuge on the North Slope of Alaska ($69^{\circ}1'N$, $147^{\circ}43'W$). The Ivishak River originates in the Brooks Range and flows northwest into the Sagavanirktok River, which flows into the Beaufort Sea. The study catchment is underlain by permafrost and contains a mountain stream and a spring stream, as defined by Craig & McCart (1975). The catchments of both streams receive <150 mm of precipitation annually, with average air temperatures of -29°C in January and 10°C in July (Oswood, Irons & Milner, 1995). A 100-m study reach was established in each stream. The lateral distance between the two study reaches was approximately 50 m. Riparian vegetation at both study reaches consists of willows (*Salix* spp.) 1–2 m in height. There is a grove of balsam poplar (*Populus balsamifera* L.) trees 3–4 m in height along one bank of the spring stream at the downstream end of the study reach.

Potential substratum movement

Potential substratum movement was assessed using estimates of tractive force and particle size-distribution (Giberson & Caissie, 1998). Tractive forces were calculated using the following equation (Newbury, 1996):

$$T_c = \rho RS,$$

where T_c is tractive force (kg m^{-2}), ρ is the density of water (kg m^{-3}), R is the hydraulic radius (m), and S is the slope of the water's surface (m m^{-1}). Hydraulic radius was derived from measurements of bankfull perimeter and depth at transects placed every 10 m along the 100 m study reach in each stream. The slope of the water's surface was measured using a length of clear vinyl tubing as a water level between each transect. Particle size-distribution was quantified following Wolman (1954). Substrata were selected by walking across the stream at each transect and picking up the particle closest to the left foot at each of 10 steps. Ten particles were measured in each transect for a total of 100 particles measured in each stream.

Actual substratum movement

Actual substratum movement was assessed in the summer of 2002 and 2003 by quantifying movements of rocks marked *in situ* (Downes *et al.*, 1998). During 2002 we randomly selected 10 rocks along each of six transects using the same method by which particle size-distribution was assessed. The rocks were not removed from the streambed. Five holes were made on each rock with a star drill (total of 60 marked rocks). During 2003 we selected 10 rocks along each of five transects, and marked them with a battery-operated power drill fitted with a masonry bit (total of 50 marked rocks). In both 2002 and 2003, the position of each marked rock was noted using triangulation from permanent stakes placed along each bank. Approximate size and colour of each rock was also noted. Transects were revisited after approximately 1 month to determine the presence or absence of each rock in its original location. Rocks that were no longer in their original location or had been turned over were considered 'disturbed.'

Water temperature, discharge and nutrient chemistry

Water temperature was recorded hourly using digital temperature loggers (Onset Corporation, Pocasset, MA, U.S.A.). One logger was placed in a riffle in each stream from 9 July 2001 to 24 June 2002. Temperatures less than -1.0°C were assumed to indicate freezing of the water column. Stream stage-height was recorded at 15 min intervals using digital depth recorders

(Global Water, Gold River, CA, U.S.A.) in both streams from 24 June to 10 August 2002 and in the mountain stream from 20 June to 27 July 2003. A maximum stage recorder (Gordon, McMahon & Finlayson, 1992) was used to assess changes in stage height in the spring stream during 2003. Discharge was directly measured on nine dates in the mountain stream and five dates in the spring stream during 2002 but was not measured during 2003. These data were used to derive equations relating stage height and discharge. We defined spates as flows greater than twice the median discharge. Spates separated by more than 5 days were considered separate events (Biggs *et al.*, 1999). Concentrations of dissolved ammonium-N, nitrate-N, and soluble reactive phosphorus (SRP) were determined from samples taken from nine dates during 2002 and 2003.

Invertebrates and bryophytes

Invertebrates and bryophytes were sampled every 7–10 days throughout the summer (seven dates, five samples stream⁻¹ date⁻¹) using a Surber sampler (0.09 m², 243 μm mesh). Substrata were scrubbed with a nylon brush to remove invertebrates, bryophytes and detritus. Organic matter retained by the net was drained on a 250 μm mesh sieve, placed in plastic bags, and preserved in 4% formaldehyde. In the lab, each sample was separated into two size classes ($>1000 \mu\text{m}$, 1000–250 μm), and invertebrates were removed by hand under magnification, identified to genus or species, and measured for length. Their dry mass (DM) was estimated using family-level length-mass relationships provided by Benke *et al.* (1999). Bryophytes, an additional indicator of substratum stability (McAuliffe, 1983; Duncan *et al.*, 1999), were separated from other categories of organic matter, oven dried and weighed, ashed at 500°C and reweighed. The difference between dry weight and ash weight was used to estimate bryophyte ash-free dry mass (AFDM). Large samples were subsampled to 1/2 to 1/16 of the original volume using a Folsom plankton wheel.

Invertebrates from samples collected on 25 June and 4 August 2002 were used for gut analysis ($n = 10$ samples date⁻¹). We sought at least five individuals taxon⁻¹ sample⁻¹, although in some cases sufficient numbers of individuals were not present. This resulted in the analysis of 31–62 individuals sample⁻¹

(median 52). Gut contents from each individual were suspended in water and sonicated for 30 s to disperse food particles. The resulting slurry was filtered onto a 13-mm 1.2- μ m polycarbonate membrane filter and dried. The filter was then placed on a microscope slide and cleared with immersion oil.

Filters were observed at 400 \times magnification. Ten fields of view on each filter were chosen haphazardly and photographed using a digital camera (Nikon Coolpix 995; Nikon Inc., Melville, NY, U.S.A.) interfaced with a Zeiss Axiostar compound microscope using an Optem adapter (Avimo Precision Instruments, Fairport, NY, U.S.A.). ImagePro Express (Media Cybernetics, Inc., Silver Spring, MD, U.S.A.) was used to quantify particle type and abundance from the digital images. Particles were classified as diatoms, bryophytes, amorphous organic detritus, inorganic material or animal. Animals and diatoms were identified to genus.

Vertebrates

Dolly Varden char (*Salvelinus malma* Walbaum) were captured using unbaited minnow traps in late June and again in late July 2000. The stomachs of at least 10 fish from each stream on each date were irrigated with water in the field and the regurgitated contents drained onto a 250 μ m mesh sieve. Stomach contents were preserved in 4% formaldehyde and invertebrates were later removed by hand under magnification and identified to genus. Faeces of American dipper (*Cinclus mexicanus* Swainson), a passerine predator of aquatic invertebrates (primary prey) and fish, were collected from exposed boulders in the spring stream and prey remnants contained within them were identified to genus.

Food webs

Connectance food-webs were constructed using information from gut content analysis. This identifies the presence/absence of links between consumers and food sources, rather than the amount assimilated (e.g. Jaarsma *et al.*, 1998). Food-web statistics were calculated by creating symmetrical matrices of all possible consumers (columns) by all possible food sources (rows). Connections between consumers and food items were indicated by the number one in the matrix, whereas the lack of a connection was indicated as

zero. Connectance (C) was calculated using modifications of the formula from Jaarsma *et al.* (1998) and Warren (1994):

$$C = \frac{L}{S^2 - [(pp + ba) \times S]}$$

In this formula, L = the number of trophic links observed, S = the number of total possible trophic elements in the web, pp = the number of primary producers in the web and ba = the number of non-algal basal elements in the web. S^2 represents the number of possible links in the web. The portion of the equation $[(pp + ba) \times S]$ imposes the constraint that primary producers and non-algal basal elements do not feed. Mean food-chain length and connectance (C) were calculated using the procedures and software developed by Jaarsma *et al.* (1998).

Statistical analyses

Nonparametric methods were used for all analyses because assumptions of normality were not met with these data. Differences in invertebrate biomass for both functional feeding groups and individual taxa between the two streams were assessed using Wilcoxon pairwise Differences with a median of zero. Individual benthic samples were used as replicates. Differences in tractive force estimates ($n = 10$ per stream) as well as marked rock movement ($n = 60$ per stream 2002, $n = 50$ per stream 2003) between the two streams were analysed using the Mann-Whitney test. The difference in substratum particle size distribution between streams was determined using chi-square.

Results

Substratum movement

Particle size-distribution was significantly different between streams ($\chi^2 = 29.92$, $P = 0.002$, d.f. = 11). Mean particle size was 93 mm in the spring stream and 122 mm in the mountain stream (mean does not include bedrock; Fig. 1). Exposed bedrock occurred only in the mountain stream (3% of reach area). Tractive forces estimated for individual transects ranged from 8.3 to 33.7 kg m⁻² in the mountain stream and 2.0 to 12.7 kg m⁻² in the spring stream (Fig. 1). Mean tractive force at bankfull was greater in the mountain stream (22.8 kg m⁻²) than the spring stream (6.2 kg m⁻², Mann-Whitney $W = 68.0$, $P < 0.001$).

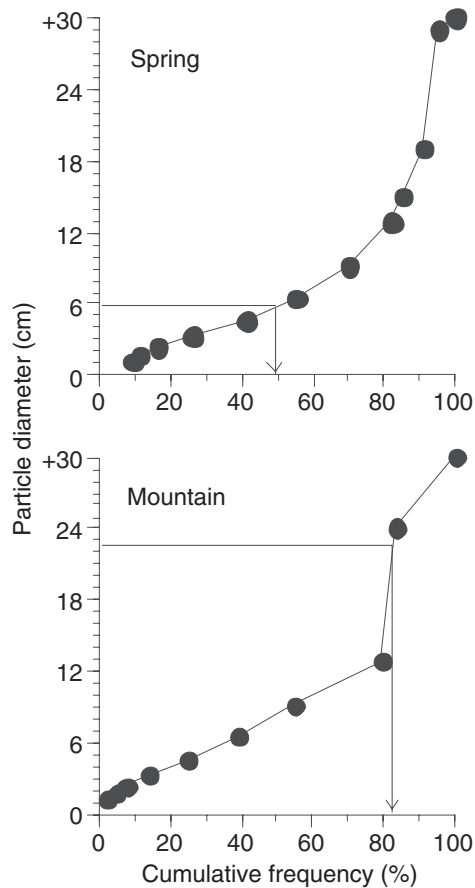


Fig. 1 Particle size-distribution of substrata sampled in Ivishak mountain and spring streams. Particle size-distribution is shown as cumulative frequency (%) from smallest to largest size categories. Maximum particle size and proportion of total stream-bed predicted to be moved by tractive forces estimated for bankfull flows is indicated by arrow.

As a rule of thumb, tractive forces expressed as kg m^{-2} will move spherical, non-cohesive particles with a numerically equivalent diameter expressed as centimetre (e.g. a tractive force of approximately 6 kg m^{-2} will move particles up to approximately 6 cm in diameter; Giberson & Caissie, 1998). When at bankfull discharge the spring stream should therefore be capable of moving particles up to approximately 6 cm in diameter and the mountain stream should be able to move particles up to approximately 23 cm in diameter. By combining estimates of tractive force with estimates of particle-size distribution, the proportion of stream substrata that should be mobilised during bankfull floods can be estimated (Fig. 1). In the mountain stream, 82% of substrata were predicted to be mobile at bankfull discharge, whereas in the spring stream 49% of substrata were predicted to be mobile.

Direct observations indicated that substratum mobility was indeed greater in the mountain than the spring stream (Fig. 2). Mean substratum movement measured during 2002 was 57% in the mountain stream, and 20% in the spring stream (Mann-Whitney $W = 26.0$, $P = 0.030$) and ranged from 40% to 73% in the mountain stream and from 7% to 27% in the spring stream, depending upon transect. Mean substratum movement during 2003 was 66% in the mountain stream and 4% in the spring stream (Mann-Whitney $W = 40.0$, $P = 0.011$). Substratum movement measured for individual transects in 2003 ranged from 50% to 80% in the mountain stream and from 0% to 10% in the spring stream. Particles moved by the spring stream were significantly smaller than those moved by the mountain stream in both years (Mann-Whitney $W = 113.5$, $P = 0.002$ in 2002, $W = 1646.0$, $P \leq 0.001$ in 2003). Differences between indirect estimates, based on the relationship between tractive force and particle size distribution and direct estimates, based on observation of particles marked *in situ* (i.e. 49% versus 4–20% in the spring stream and 82% versus 57–66% in the mountain stream), are attributed to the packing of particles into the stream bed, which will presumably reduce overall mobility and to deviations from the assumption that particles were spherical.

Water temperature, discharge and nutrient chemistry

Mean water temperature from 9 July 2001 to 24 June 2002 was 5.8°C in the spring stream and 1.6°C in the mountain stream (Fig. 3a). The minimum temperature of the spring stream was 1.0°C during snowmelt on 19 May 2002, and the maximum was 8.7°C on 16 July 2001. The temperature of the mountain stream was more variable, ranging from -0.4°C on 28 March 2002 to 9.5°C on 27 June and 16 July 2001. Contrary to expectations, the mountain stream apparently did not freeze as the temperature was reduced to -0.4°C for a maximum of 2 h. (Fig. 3a).

Mean discharge in the mountain stream during the summer of 2002 was 272 L s^{-1} (range = $69\text{--}3923 \text{ L s}^{-1}$) and 112 L s^{-1} (range = $96\text{ to }136 \text{ L s}^{-1}$) in the spring stream. During this period, changes in stage height ranged over 0.38 m in the mountain stream and 0.05 m in the spring stream (Fig. 3b). In 2003, changes in stage height ranged over 0.47 m in the mountain stream and 0.12 m in the spring stream

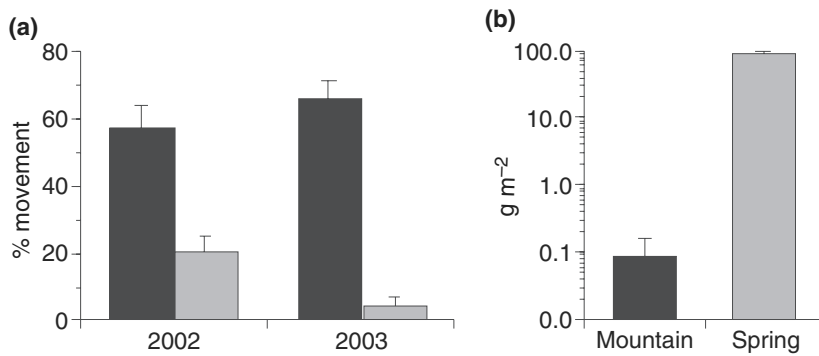


Fig. 2 (a) Percent of marked particles dislodged in Ivishak mountain (black) and spring (grey) streams during the summer of 2002 and 2003. (b) Bryophyte biomass measured in Ivishak mountain (black) and spring (grey) streams. Error bars = +1 SD.

(Fig. 3c). The discharge of the mountain stream was more variable than that of the spring. Three discrete storm flows were recorded in the mountain stream in 2002 (7 July, 3923 L s⁻¹; 28 June, 978 L s⁻¹; 5 August, 710 L s⁻¹). Changes in stage height indicate that four to five major storm flows occurred during 2003 (Fig. 3c).

Concentrations of ammonium-N ($t = 0.44$, $P = 0.669$), nitrate-N ($t = 1.44$, $P = 0.173$), and SRP ($t = 0.62$, $P = 0.549$) did not vary significantly between streams. Molar N : P ratios ranged from 214 in the mountain stream to 227 in the spring stream, indicating phosphorus limitation in both streams (A.C. Green, The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA, unpublished data; Table 1).

Invertebrates and bryophytes

Twenty-seven invertebrate taxa were collected from both the spring and mountain stream (Table 2); 25 occurred in the spring and 20 in the mountain stream. Seven taxa (*Ceratopogonidae*, *Dicranota*, *Dixa*, *Psychoda*, *Micropsectra*, *Thienemanniella*, *Ecclisiomyia*) were taken only from the spring stream and two (*Chloroperlidae*, *Gymnopais*) only from the mountain stream. Taxa restricted to a single stream were minor contributors to invertebrate biomass, however, contributing only 5.7% in the spring stream and 1.3% in the mountain stream.

Mean (\pm SE) invertebrate-biomass was an order of magnitude greater in the spring stream (4617 ± 416 mg DM m⁻²) than the mountain stream (635 ± 86 mg DM m⁻²; Table 2). Major contributors to biomass in the mountain stream were *Baetis bicaudatus* Dodds (32% of community biomass) and the Diam-esinae (*Diamesa* spp. + *Pagastia* sp., 33%). Major contributors to biomass in the spring stream were

B. bicaudatus (30%), *Isoperla sobria* (Hagen) (13%), *Eukieferiella* spp. (11%), and *Prosimulium* sp. (9%) (Table 2). Invertebrate biomass was significantly greater in the spring stream for all functional feeding-groups on all dates (Wilcoxon Paired Differences, $P < 0.001$ for all pairs). The distribution of biomass among predators and other feeding groups differed between streams. Predators contributed 25% (1135 mg DM m⁻²) to community biomass in the spring stream, but only 7% (43 mg DM m⁻²) in the mountain stream.

Bryophyte biomass [mainly *Cratoneuron filicinum* (Hedw.) Spruce] was three orders of magnitude greater in the spring stream (88.4 ± 6.9 g AFDM m⁻²) than the mountain stream (0.08 ± 0.06 g AFDM m⁻²; Fig. 2b).

Vertebrates

Dolly Varden char (*S. malma*) was the only fish species collected during the study. Total length averaged 13.6 ± 0.4 cm (± 1 SE) in the spring stream on 26–27 June 2002 ($n = 20$) and 11.6 ± 0.5 cm in the mountain stream on 28 June and 2 July 2002 ($n = 12$). On 30–31 July, mean total length (± 1 SE) of char was 13.1 ± 0.4 cm ($n = 10$) in the spring stream and 11.3 ± 0.7 cm ($n = 11$) in the mountain stream.

A pair of American dippers (*C. mexicanus*) nested along the spring stream in summer 2002 and reared two offspring. All four birds were observed foraging for aquatic invertebrates within the study reach of the spring stream. Dippers were never observed along the mountain stream.

Food webs

Connectance food-webs were created using benthic samples taken on 25 June and 4 August 2002, gut contents taken from fish collected 26 June to 2 July and

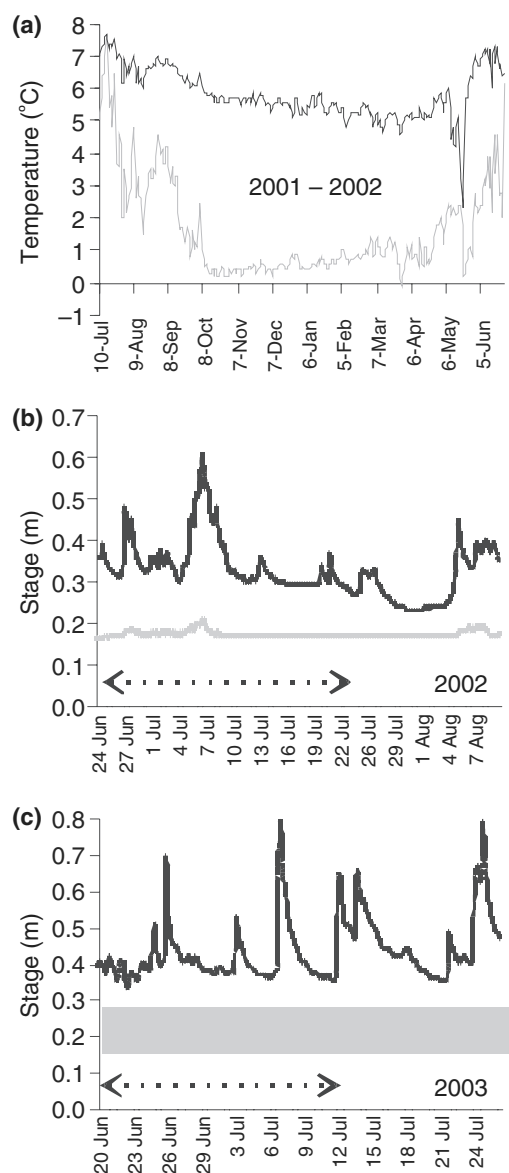


Fig. 3 (a) Daily mean temperature for Ivishak mountain (grey) and spring (black). Daily mean temperatures were calculated using data recorded at 1-h intervals from 9 July 2001 to 24 June 2002. (b) Stage height measured for Ivishak mountain (black) and spring (grey) streams during the summer of 2002 and (c) 2003. Both plots for the mountain stream and the plot for the spring stream in 2002 are based on data recorded at 15-min. intervals. The plot for the spring stream in 2003 shows the range of stage indicated by a peak stage recorder that was deployed over the entire field season. The dashed line indicates the period over which substratum movement was quantified (see Fig. 2).

30–31 July, and dipper faeces (Figs 4 & 5). *Prosimulium* from the spring stream consumed the greatest number of periphyton taxa (17 taxa; Table 3) and *Isoperla* from the spring stream consumed the greatest number of

Table 1 Nutrients (A.C. Green)

	Spring stream	Mountain stream
NH ₄ -N	0.11 (0.02)	3.93 (0.99)
NO ₃ -N	0.10 (0.02)	2.28 (0.59)
SRP	0.02 (0.01)	0.01 (0.01)
Molar N : P	227	214

Values are given as mean (SE).

invertebrate taxa (eight taxa; Table 3). Algae occurred in the guts of all predatory macroinvertebrates (Table 3). It is uncertain, however, whether these taxa were taken by directly feeding on biofilm or indirectly from their prey. *Salvelinus malma* had 12–14 (mountain stream) and 18 (spring stream) invertebrate taxa in their stomach contents (Table 3). Faeces of *C. mexicanus* from the spring stream indicated that its prey included four to five taxa of invertebrates and *S. malma* (Table 3; Fig. 5). Food web connectance in the spring stream foodweb ranged from 0.165 (Fig. 4) to 0.188 (Fig. 5) and 0.188 (Fig. 4) and 0.205 (Fig. 5) in the mountain stream. Mean food chain length ranged from 2.98 (Fig. 4) to 3.10 (Fig. 5) in the spring stream and 2.01 (Fig. 4) to 1.65 (Fig. 5) in the mountain stream.

The relationship between the number of consumers analysed and the rate of discovery of novel food types among their gut contents was assessed for *S. malma* and *Isoperla*. These taxa, as the major predators in the study streams, were chosen for analysis because of concerns about the number of samples required to obtain an accurate assessment of the range of prey types consumed by predators and thus food-web connectance (Woodward, Speirs & Hildrew, 2005). Plots of the rate of discovery of novel prey items against number of guts analysed for *S. malma* from both the spring and mountain streams indicated that prey richness began to approach an asymptote when the gut contents of approximately 10 individuals were analysed (16 of 25 potential animal prey taxa in the spring stream, 13 of 20 potential prey animals in the mountain stream). For *Isoperla*, however, the curve of prey richness against number of guts analysed did not reach an asymptote, but began an obvious decline in the rate of accumulation of new food types at approximately 20 individuals. The number of individuals of *S. malma* and *Isoperla* analysed on each date were thus probably sufficient to accurately account for the most frequent types of food items consumed, but

	Abundance (no. m ⁻²)		Biomass (mg m ⁻²)	
	Mountain stream	Spring stream	Mountain stream	Spring stream
<i>Baetis</i> (E)	23.88 (10.49)	308.02 (52.66)	201.83 (60.68)	1391.07 (136.00)
<i>Cinygmula</i> (E)	8.75 (4.37)	0.17 (0.12)	7.43 (1.86)	0.94 (0.92)
<i>Capnia</i> (P)	0.89 (0.38)	4.57 (4.57)	0.59 (0.24)	10.81 (10.81)
<i>Chloroperlidae</i> (P)	2.74 (0.64)	–	7.57 (2.93)	–
<i>Isoperla</i> (P)	0.09 (0.09)	147.47 (10.62)	3.32 (3.32)	614.10 (79.42)
<i>Zapada</i> (P)	20.19 (2.02)	39.71 (2.47)	14.38 (2.34)	67.25 (12.16)
<i>Ecclisiomyia</i> (T)	–	58.33 (19.36)	–	38.01 (14.13)
<i>Ceratopogonidae</i> (D)	–	4.44 (3.09)	–	3.98 (2.47)
<i>Chelifera</i> (D)	0.11 (0.06)	103.25 (10.78)	0.12 (0.11)	356.11 (47.16)
<i>Dicranota</i> (D)	–	0.14 (0.14)	–	1.10 (1.10)
<i>Dixa</i> (D)	–	0.06 (0.06)	–	0.07 (0.07)
<i>Gymnops</i> (D)	0.26 (0.26)	–	0.67 (0.67)	–
<i>Oreogeton</i> (D)	5.78 (1.36)	36.82 (22.62)	27.60 (7.52)	89.37 (14.51)
<i>Prosimulium</i> (D)	6.89 (0.79)	137.34 (43.66)	7.93 (1.96)	407.27 (132.12)
<i>Psychoda</i> (D)	–	26.16 (10.38)	–	5.13 (2.30)
<i>Tipula</i> (D)	0.81 (0.81)	0.11 (0.06)	13.71 (13.71)	10.16 (6.90)
<i>Corynoneura</i> (D : C)	26.73 (18.61)	516.38 (161.74)	1.72 (1.01)	37.86 (13.20)
<i>Diamesa</i> (D : C)	315.02 (89.45)	37.82 (34.66)	87.45 (13.61)	5.61 (1.90)
<i>Eukieferiella</i> (D : C)	57.63 (11.79)	3630.59 (641.75)	8.37 (1.36)	514.21 (103.11)
<i>Microsectra</i> (D : C)	–	250.31 (107.44)	–	211.45 (93.38)
<i>Orthocladus</i> (D : C)	237.64 (75.75)	1016.08 (136.95)	48.65 (11.22)	190.58 (40.65)
<i>Pagastia</i> (D : C)	366.52 (157.54)	137.63 (31.16)	124.46 (38.95)	145.96 (57.71)
<i>Rheocricotopus</i> (D : C)	4.43 (2.17)	73.63 (25.86)	2.04 (0.69)	44.76 (17.31)
<i>Thienemanniella</i> (D : C)	–	58.78 (25.42)	–	4.77 (2.35)
Acarina	10.71 (1.67)	316.25 (39.90)	1.26 (0.28)	34.10 (4.35)
Oligochaeta	29.72 (11.22)	113.56 (15.97)	72.37 (21.21)	396.28 (62.19)
Turbellaria	2.48 (0.49)	36.44 (5.89)	3.08 (0.73)	35.84 (5.04)
Predators			39.87 (8.82)	1094.79 (97.62)
Total			634.57 (86.34)	4616.79 (416.04)

Values are given as mean (SE).

E, Ephemeroptera; P, Plecoptera; D, Diptera; D : C, Diptera : Chironomidae.

were likely not sufficient to account for rare food items; consequently food-web connectance was probably underestimated. Nevertheless, values for connectance estimated in this study are similar to published values for food webs for other stream communities with similar taxonomic richness.

Major taxonomic differences between the food webs of the spring and mountain streams were because of differences among the predators. *Isoperla*, *Chelifera*, *Ecclisiomyia*, *Oreogeton* and *Pagastia* were predators in the spring stream. *Chloroperlidae*, *Oreogeton*, *Eukieferiella* and *Zapada* were predators in the mountain stream. The Dolly Varden char was the top predator in the mountain stream, whereas Dolly Varden char and the American dipper were top predators in the spring stream (Figs 4 & 5). The difference in mean food chain length between streams was due primarily to the effect of *C. mexicanus*. When *C. mexicanus* was

Table 2 Mean summer abundance and biomass of macroinvertebrate taxa occurring in both Ivishak mountain and spring streams. Biomass is reported as dry mass.

removed from the interaction matrix for the spring stream, mean food-chain length decreased from 2.98 to 2.21 in early summer and from 3.10 to 2.39 in late summer. Even with the dipper removed, however, mean food-chain length for the spring stream remained higher than those estimated for the mountain stream (2.21 versus 2.01 in early summer; 2.39 versus 1.65 in late summer).

Discussion

We originally predicted that the mountain stream would have lower species richness and biomass, and a food web structure with lower trophic height and lower connectance than the spring stream. The communities of the mountain and spring streams did show the predicted contrasts in biomass and trophic height, but had similar taxonomic richness and

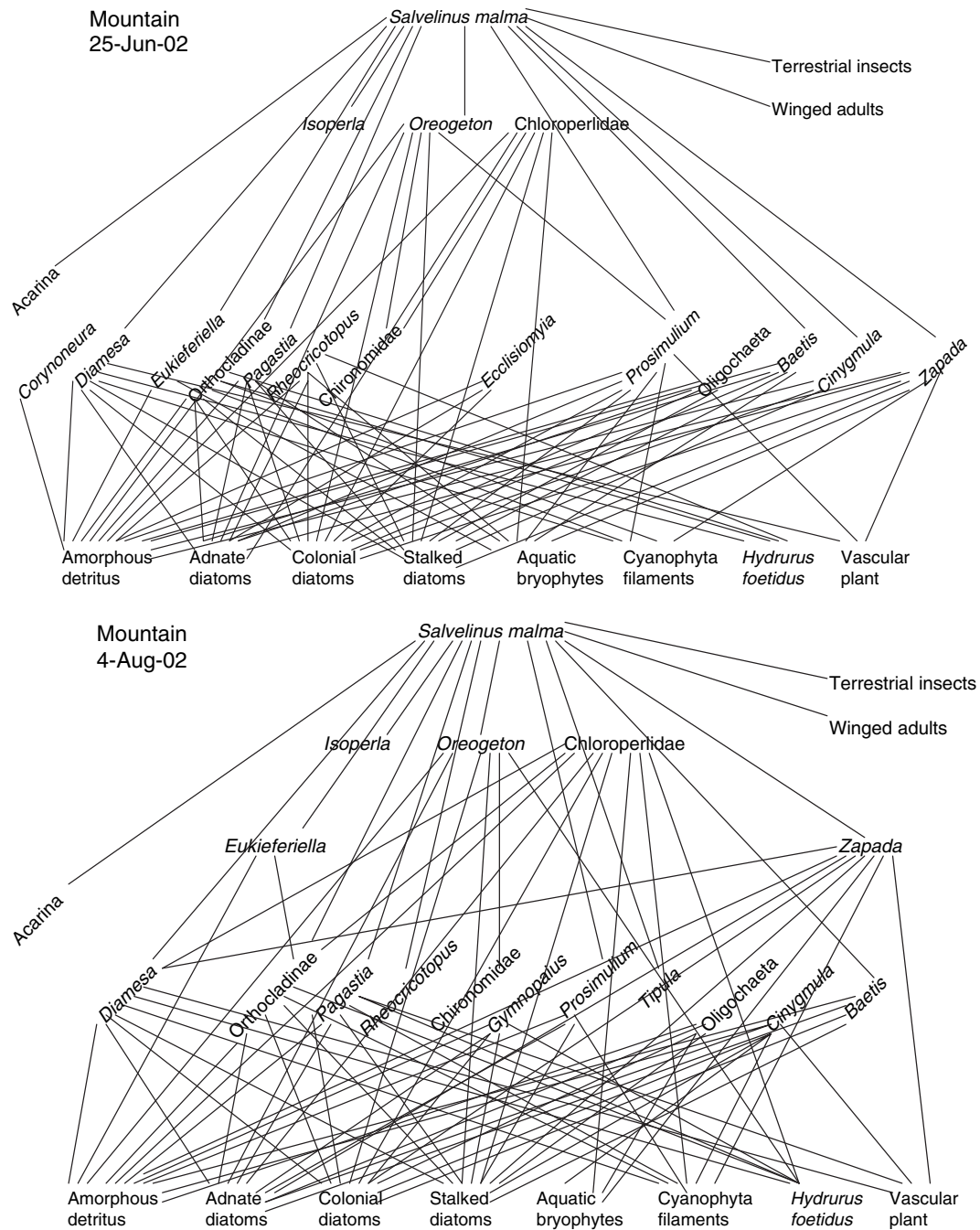


Fig. 4 Connectance food webs for two dates in the mountain stream. Algal taxa are summarised as functional groups to simplify the food web diagrams.

connectance. The most striking difference between streams was the greater total invertebrate biomass (seven to eight times) and predatory invertebrate biomass (26 times) in the spring stream.

We originally expected substantial differences between the communities of these streams, because of

both substratum movement and water-column freezing in the mountain stream. The water column of the mountain stream did not freeze solid, however. A parallel study of the biogeochemistry of the study streams (W.B. Bowden, personal communication) indicated that the study reach in the mountain stream

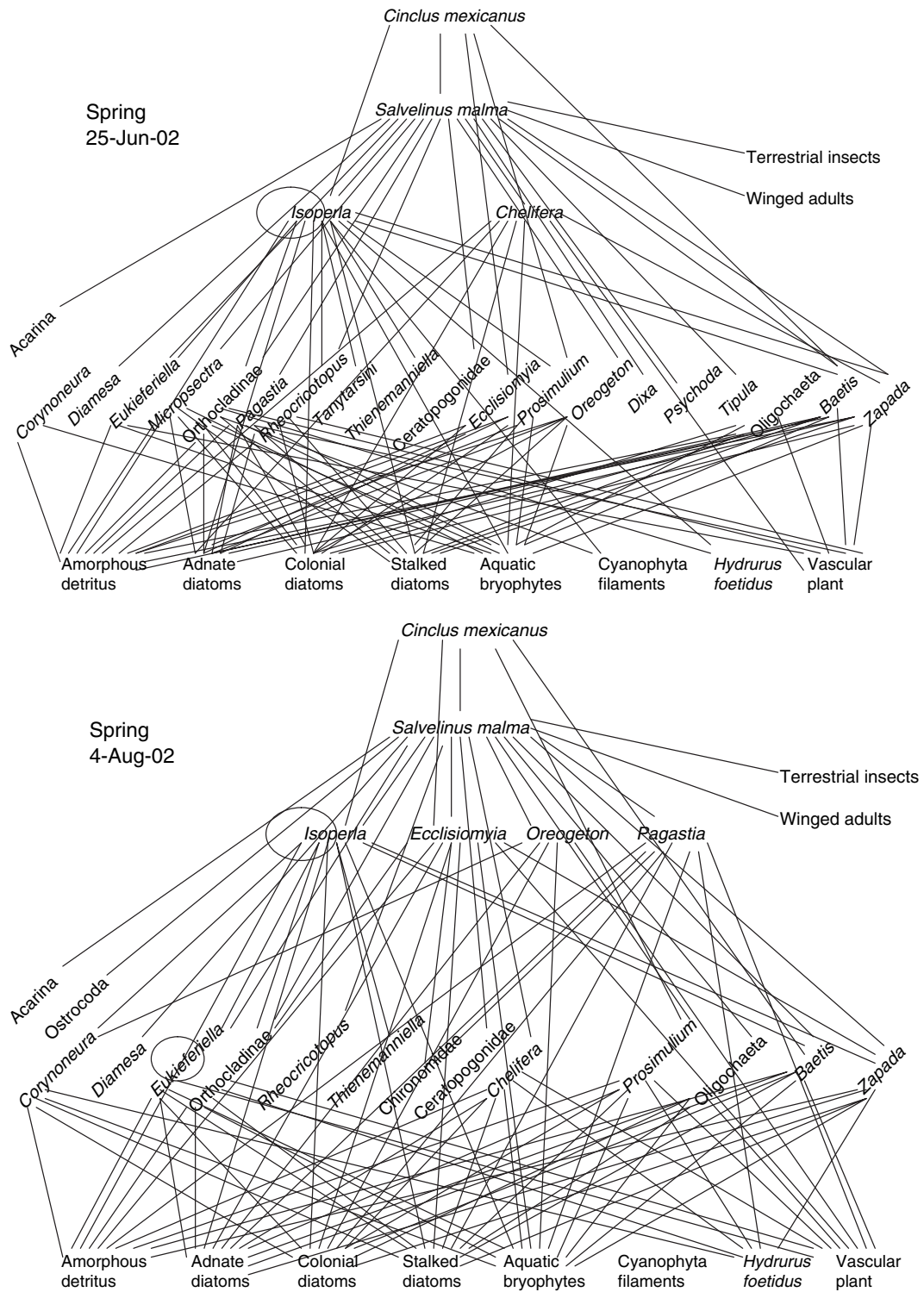


Fig. 5. Connectance food webs for the spring stream. Algal taxa are summarised as functional groups to simplify the food web diagrams. Circles indicate cannibalism.

Table 3 Summary of diet for primary (trophic level 2) and secondary (trophic levels 3, 4 and 5) consumers sampled on two dates in Ivishak spring and mountain streams. Values indicate total number of different taxa of primary producers, primary consumers and predatory macroinvertebrates consumed by each taxon.

	25 June 02				4 August 02		
	Primary producers	Primary consumers	Predators		Primary producers	Primary consumers	Predators
Spring							
Trophic level 2							
<i>Baetis</i> (E)	14	0	0	<i>Baetis</i> (E)	13	0	0
<i>Corynoneura</i> (D : C)	2	0	0	<i>Chelifera</i> (D)	11	0	0
<i>Ecclisiomyia</i> (T)	6	0	0	<i>Corynoneura</i> (D : C)	6	0	0
<i>Eukieferiella</i> (D : C)	3	0	0	<i>Eukieferiella</i> * (D : C)	12	1	0
<i>Micropsectra</i> (D : C)	13	0	0	<i>Oligochaeta</i>	16	0	0
<i>Oligochaeta</i>	16	0	0	<i>Orthocladinae</i> (D : C)	16	0	0
<i>Oreogeton</i> (D)	9	0	0	<i>Prosimulium</i> (D)	17	0	0
<i>Orthocladinae</i> (D : C)	18	0	0	<i>Zapada</i> (P)	13	0	0
<i>Pagastia</i> (D : C)	14	0	0				
<i>Prosimulium</i> (D)	11	0	0				
<i>Rheocricotopus</i> (D : C)	15	0	0				
<i>Zapada</i> (P)	11	0	0				
Trophic level 3							
<i>Chelifera</i> (D)	14	1	0	<i>Ecclisiomyia</i> (T)	12	4	0
<i>Isoperla</i> * (P)	14	8	1	<i>Isoperla</i> * (P)	13	6	1
				<i>Oreogeton</i> (D)	5	1	0
				<i>Pagastia</i> (D : C)	12	1	0
Trophic level 4							
<i>Salvelinus malma</i>	0	16	2	<i>Salvelinus malma</i>	0	15	3
Trophic level 5							
<i>Cinclus mexicanus</i>	0	3	2	<i>Cinclus mexicanus</i>	0	2	3
Mountain							
Trophic level 2							
<i>Baetis</i> (E)	14	0	0	<i>Baetis</i> (E)	11	0	0
<i>Cinygmula</i> (E)	5	0	0	<i>Cinygmula</i> (E)	14	0	0
<i>Corynoneura</i> (D : C)	1	0	0	<i>Gymnopauius</i> (D)	11	0	0
<i>Diamesa</i> (D : C)	15	0	0	<i>Oligochaeta</i>	12	0	0
<i>Ecclisiomyia</i> (T)	6	0	0	<i>Orthocladinae</i> (D : C)	12	0	0
<i>Eukieferiella</i> (D : C)	2	0	0	<i>Pagastia</i> (D : C)	13	0	0
<i>Oligochaeta</i>	11	0	0	<i>Prosimulium</i> (D)	7	0	0
<i>Orthocladinae</i> (D : C)	12	0	0				
<i>Pagastia</i> (D : C)	14	0	0				
<i>Prosimulium</i> (D)	13	0	0				
<i>Rheocricotopus</i> (D : C)	11	0	0				
<i>Zapada</i> (P)	12	0	0				
Trophic level 3							
<i>Chloroperlidae</i> (P)	11	1	0	<i>Chloroperlidae</i> (P)	11	2	0
<i>Oreogeton</i> (D)	12	2	0	<i>Eukieferiella</i> (D : C)	2	1	0
				<i>Oreogeton</i> (D)	11	1	0
				<i>Zapada</i> (P)	14	1	0
Trophic level 4							
<i>Salvelinus malma</i>	1	10	2	<i>Salvelinus malma</i>	0	12	2

*Indicated the occurrence of cannibalism.

E, Ephemeroptera; P, Plecoptera; T, Trichoptera; D, Diptera; D : C, Diptera : Chironomidae.

receives approximately 20% of its discharge as ground-water, which may prevent total freezing during winter. As neither the mountain nor the spring stream froze, we

conclude that substratum movement, which was significantly greater in the mountain stream, is probably the major abiotic factor underlying differences in

invertebrate biomass, energy and material flow, and thus food web function between streams.

Rather than directly affecting invertebrate communities, substratum movement may exert its most significant effect indirectly, by controlling bryophyte colonisation and persistence (McAuliffe, 1983; Englund, 1991; Suren & Duncan, 1999). Higher abundances of mayfly, stonefly and midge larvae in bryophyte-covered habitat compared with bryophyte-free habitat is expected, based on the findings of many studies worldwide (Stream Bryophyte Group, 1999). For example, the abundance of larval Chironomidae was 19 times greater on bryophyte-covered versus bryophyte-free substrata in an Alaskan tundra stream (Kuparuk River; Stream Bryophyte Group, 1999) and Brusven, Meehan & Biggam (1990) showed that insect biomass in bryophyte-covered reaches in an Idaho stream was 1.4–6.1 times greater than that in bryophyte-free reaches. On the basis of such findings, the seven to eight times greater invertebrate biomass in the spring stream, compared with the mountain stream, is almost certainly a consequence of its 1000-fold greater bryophyte biomass. The growth and accumulation of such a lush growth of bryophytes is probably facilitated by the high level of substratum stability shown for the spring stream (McAuliffe, 1983; Suren & Duncan, 1999).

The relatively high abundance of invertebrates among bryophytes is attributed to an architecturally complex habitat, providing a large surface area for the development of epiphytic food resources, and a refuge from high current velocity and predators (Brusven *et al.*, 1990; Suren, 1991; Stream Bryophyte Group, 1999). This last factor is of particular relevance to our study because it suggests that bryophyte-covered substrata may provide a refuge from predation by *S. malma*, and thus facilitate the accumulation of invertebrate biomass in the spring stream.

Given the large differences in habitat attributes between the study streams, both qualitative and quantitative differences in taxonomic richness seemed remarkably small. Only two taxa occurred in the mountain stream but not the spring stream, and seven occurred in the spring stream but not the mountain stream. These differences appear trivial when assessed in the context of community biomass. More than 98% of the invertebrate biomass in the mountain stream and >94% of the biomass in the spring stream were from taxa shared by both streams.

The most fundamental difference between the food webs was the presence of an additional top predator, *C. mexicanus*, in the spring stream (i.e. mean food-chain length approximately 2.7) compared with the mountain stream (i.e. mean food-chain length approximately 1.8). Given the high-energy requirements of birds, dippers can be quantitatively significant predators of stream invertebrates (Ormerod & Tyler, 1991; Harvey & Marti, 1993), and may have particularly significant effects on invertebrate communities of perennially flowing streams in the Arctic. *Cinclus mexicanus*, for example, has been observed along a number of perennial spring streams on the North Slope of the Brooks Range in Alaska, but is absent from similar aquatic habitats that freeze during winter (A.D. Huryn, S.M. Parker, personal observation). Presumably their presence on spring streams (Banerjee, 2003) is related to perennially flowing water, combined with high invertebrate productivity, which remains accessible through the Arctic winter.

In addition to invertebrate prey, which comprise the bulk of their diet, dippers also consume stream fishes (Armstrong & O'Clair, 1994) and their status as the top predator in the spring stream was confirmed by the presence of bones from young-of-the-year *S. malma* in their faeces. Because of their relatively small body size, dippers are probably unable to feed on *S. malma* of larger size classes. However, 1+ year *S. malma* also probably feed on young-of-the-year (Maekawa *et al.*, 1993; Klemetson *et al.*, 2003; Bystrom *et al.*, 2004). Although we found no evidence of such feeding behaviour, we assume that 1+ year *S. malma* occupy essentially the same trophic position as *C. mexicanus*. Because the spring stream provides the only suitable nursery habitat for *S. malma* in the study drainage (Craig, 1989) and because the population in the mountain stream has a relatively uniform size structure (i.e. young-of-the-year absent), we assume that cannibalism by *S. malma* is probable only in the spring stream.

Although structural contrasts between the food webs of the spring and mountain streams were subtle, differences in the biomass contributing to different trophic positions indicate that major differences in function may exist. Perhaps the most apparent is the difference in biomass of predatory invertebrates. The ratio of invertebrate predator to prey biomass was 4.5 times higher in the spring stream than the mountain stream, although predator biomass was 26 times

greater in the spring stream. The relative lack of predatory invertebrates in the mountain stream compared with the spring stream presumably reflects the harsh disturbance regime. This excludes long-lived and relatively large predators, resulting in a community dominated by short-lived and relatively small primary consumer. The effects of predation by Dolly Varden char on large predatory macroinvertebrates may also be relatively greater in the mountain stream, because of the lack of refuge provided by bryophytes in the spring stream.

We conclude that the contrast in frequency of substratum movement between the spring and mountain streams resulted in major differences in habitat structure and relatively subtle but important differences in the structure and function of their food webs. In particular, the mean food-chain length was shorter in the mountain stream (approximately 2) compared with the spring stream (approximately 3). The relatively long food chain, and the remarkably high proportion of consumer biomass contributed by the predators of the spring stream (including the energy-demanding American dipper), presumably resulted from the high biomass and probably high production, of basal consumers. In turn, the high biomass of consumers in the spring stream is attributable to the habitat structure provided by a lush cover of bryophytes. Although some of the differences in macroinvertebrate community structure between the study streams may be directly attributable to the effects of substratum movement (e.g. absence of long-lived and large-bodied predators from the mountain stream), most effects of substratum movement on community are probably indirect, being manifested through its control of patterns of bryophyte persistence and growth, with differences in the availability of bryophyte habitat between the spring and mountain streams controlling differences in their food web structure and function.

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