Research Article

Functional measures and food webs of high elevation springs in the Swiss alps

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Abstract. We examined the ecosystem functioning and food webs of high elevation springs in or near the Swiss National Park. Springs originated from silicate or carbonate geologies and were near or above treeline. One iron-sulphur and three temporary springs were also included in the study. Ecosystem function was assessed in four springs via measures of bacterial abundance, sediment respiration, nutrient uptake, and ecosystem metabolism. Food webs were assessed in all 20 springs using nutrient content (C, N, P) and stable isotopes of carbon and nitrogen. Bacteria counts ranged from 1.8 to 3.4×10^8 cells mL^{-1} sediment with no significant differences between sites. Sediment respiration rates ranged from 0.13 to 0.46 mg $O_2\,h^{-1}$ and did not differ between springs. Uptake lengths for N ranged from 11 to 63 m, and for phosphorus from 4 to 60 m. Nitrogen uptake rates (U) ranged from 57 to 266 $\mu g\,m^{-2}\,h^{-1}$ and those for P from 0.11 to 4.2 $\mu g\,m^{-2}\,h^{-1}$. Gross primary production (GPP) ranged from 0.7 to 7.1 g $O_2\,m^{-2}\,d^{-1}$, but reached values of 59.1–70.9 g $O_2\,m^{-2}\,d^{-1}$ in the iron-sulphur spring. Ecosystem respiration (ER) ranged from 1.3 to 10.3 g $O_2\,m^{-2}\,d^{-1}$, but was 91.1–101.8 g $O_2\,m^{-2}\,d^{-1}$ in the iron-sulphur spring. All four springs were net-heterotrophic with production to respiration ratios (P/R) ranging from 0.48 to 0.72. The percentage C, N, and P varied significantly among the different food web compartments. The molar ratios (C:P, C:N, N:P) of the different nutrients were consistent within compartments, although varying among the different compartments. Stable isotope signatures ($\delta^{13}C$, $\delta^{15}N$) were related to the specific spring types, although food webs were relatively simple with most benthic invertebrates showing omnivory. Riparian spiders partially used aquatic insects in the diet. The results suggest that these alpine springs are complex but functionally similar to forested headwater streams with simple food webs.

Key words. Stable isotopes; ecosystem metabolism; macroinvertebrates; Swiss National Park; temporary streams.

Introduction

Springs are the primary source of most running waters. They are distinctive running water habitats (Williams and Williams, 1998), often inhabited by a diverse but mostly stenotypic group of organisms (Cantonati et al., 2006; Collier and Smith, 2006). Springs are

physically stable habitats, but show high sensitivity to changes in land use and are considered endangered aquatic habitats due to direct and indirect human impacts (Zollhöfer et al., 2000). For instance, many springs in the Alps are subject to water abstraction or used for watering livestock. Many springs have also been converted into culverts with obvious consequences on the stenotypic fauna and flora. Intermittent springs also are common and show distinct biotic assemblages from those of permanent springs (Smith and Wood, 2002; Smith et al., 2003). The zoobenthos of springs have been relatively well documented with various groups predominating, such as water mites (Di Sabatino et al., 2003), turbellarians (Roca et al., 1992), chironomids (Mori and Brancelj, 2006), caddisflies, and hydrobioids (Cantonati et al., 2003). Readers are referred to Cantonati et al. (2003) for a detailed review of the literature on the biodiversity of springs in the Alps. One aspect that is noticeably absent are data on the ecosystem functioning and food web structure of springs.

In the Alps, a large number of springs surface above treeline where the potential for autochthonous production is high (Zah et al., 2001; Füreder et al., 2003). Whether these ecosystems act as detritus-based systems as would be expected for springs below treeline is unknown (sensu Cross et al., 2003). The grasses and herbs adjacent to alpine springs could be an important allochthonous source of organic matter and cause these systems to also rely strongly on detritus as a basal resource. In comparison, Zah et al. (2001) found invertebrate herbivores in glacier streams above treeline to be reliant on autochthonous resources such as diatoms and the common gold alga *Hydrurus foetidus*, whereas allochthonous organic matter was an important basal resource in a nearby groundwater-fed stream (also see Füreder et al., 2003). Measures of ecosystem metabolism and stable isotope analysis of the food web would provide important information on the heterotrophic nature of alpine springs. Bacterial activity is expected be high in alpine springs, causing them to be net-heterotrophic as found for other high elevation streams in the Alps (Logue et al., 2004).

Small headwater streams in temperate landscapes have been shown to be strong controllers of nitrogen export (Peterson et al., 2001), and exhibit high uptake rates for N and P (Mulholland et al., 2008). In high elevation streams in the Alps, phosphorus uptake was an order of magnitude higher than that of nitrogen (Robinson et al., 2002). Excess nitrogen is typically exported downstream as the efficiency of biotic uptake and denitrification decrease as nitrogen levels become excessive. Nitrogen concentrations are typically high in most streams and rivers throughout

Europe, including the Alps (Mallard et al., 2000). Although presently unknown, uptake rates of N and P in high elevation springs may show these systems to be strong controllers of N and P export to receiving waters, as found for temperate headwater streams.

This study examined the ecosystem function and food webs of alpine springs. Springs were stratified to encompass those above or near treeline, and draining silicate or carbonate geologies. A number of intermittent springs were included along with one iron-sulphur spring. Our objectives were to assess ecosystem function in four springs via measures of ecosystem metabolism, bacteria abundance, sediment respiration and uptake rates of N and P. Food webs of all 20 different springs were assessed using contents of carbon, nitrogen, and phosphorus in different food web compartments along with measures of carbon and nitrogen isotopes. We expected springs to be net-heterotrophic, have high nutrient uptake rates, and simple foods webs with omnivory predominating.

Study area description
The study took place from May to October 2004. Study springs were in the lower Engadine, in or near the Swiss National Park, southeast Switzerland. This selection allowed us to compare relatively pristine springs inside the Park with more human-influenced springs outside the Park. The area is relatively dry, with high solar radiation and low humidity, and lies in the southern Alps of Switzerland. Geology consists mainly of dolomite and other sedimentary rocks, except in the Laschadura region, which is influenced by Macun gneisses and amphibolites (Clausen, 2001). Forests consist mainly of *Pinus mugo*, *Larix decidua*, *Pinus cembra*, and *Picea abies*. Treeline in the lower Engadine is at ~2200 m a.s.l. Outside the park, the main disturbance is livestock grazing at altitudes up to 2600 m a.s.l. Wild game is the principal grazer inside the Park. We sampled 20 springs with around half of the springs above treeline (Table 1). Two forested springs were located along the Spöl River, at 1620 m a.s.l. The remaining springs were within forest or alpine meadows, partially covered by mountain pines. Spring names were taken from Schmassmann (1954) where available. Six categories of springs were sampled: (1) non-forested springs in carbonate dominated geology (n=5), (2) non-forested springs in silicate dominated geology (n=4), (3) forested springs in carbonate dominated geology (n=4), (4) forested springs in silicate dominated geology (n=3), (5) one iron-sulphur spring, and (6) temporary springs (n=3).

The springs were in four different areas. Val Laschadura lies outside the western edge of the park, and had the highest springs as well as two low elevation forested springs. Grazing by cattle is com-

Table 1. Physical chemical characteristics of the study springs. Values are means (SD) of 3–4 samples taken over the study period. NA=measure not recorded. PP=particulate P, DOC=dissolved organic carbon, TIC=total inorganic carbon, POC=particulate organic carbon. See text for methods.

Number	Spring	Locality	Altitude (m a.s.l.)	Aspect	Temperature (°C)	Conductivity (µS cm⁻²)	pH	Flow. (L s⁻¹)	Slope (°)	$NO_2\text{-}N*$ $NO_3\text{-}N$ [mg L⁻¹]	Dissolved N [mg L⁻¹]	Dissolved P [µg L⁻¹]	PP [µg L⁻¹]	DOC [mg L⁻¹]	TIC [mg L⁻¹]	POC [mg L⁻¹]
Non-forested carbonate springs																
1	Bu13a	Buffalora	2260	ENE	2.6	84	7.2	6.5 (4.9)	20	0.15 (0.05)	0.20 (0.01)	0.3 (0.6)	0.3 (0.1)	0.17 (0.12)	22.0 (1.8)	0.20 (0.12)
2	Bu13b	Buffalora	2260	ENE	NA	NA	NA	1.8	NA	NA	NA	NA	1.3	0.40	27.0	0.30
3	Bu13c	Buffalora	2260	ENE	3.8	187	7.8	1.3 (1.1)	NA	0.16 (0.01)	0.18 (0.0)	0.5 (0.7)	0.4 (0.1)	0.25 (0.07)	24.0 (0.4)	0.20 (0.04)
4	Juf15	Buffalora	2180	SE	4.2	217	7.9	0.5 (0.07)	17	0.13 (0.02)	0.19 (0.01)	1.7 (1.5)	0.6 (1.0)	0.50 (0.20)	29.0 (0.8)	0.20 (0.08)
5	JufX1b	Buffalora	2250	E	12	193	8	0.3 (0.11)	NA	0.19 (0.03)	0.22 (0.02)	1.3 (1.2)	1.8 (1.3)	0.43 (0.15)	24.0 (0.4)	0.60 (0.18)
Non-forested silicate springs																
6	Las10	Val Laschadura	2460	SSE	3.2	39	7.5	1	NA	0.11 (0.04)	0.18 (0.04)	2.5 (2.1)	0.5 (0.4)	0.40 (0.0)	2.0 (0.6)	0.10 (0.0)
7	Las11	Val Laschadura	2485	SSE	NA	NA	7.7	5	52	0.28	0.40	0.0	0.9	0.50	0.6	0.10
8	Las12	Val Laschadura	2435	SSE	2.3 (0.1)	22 (5)	7.4 (0.0)	7.5 (3.5)	NA	0.26 (0.03)	0.28 (0.03)	3.0 (0.0)	0.8 (0.0)	0.30 (0.14)	0.7 (0.4)	0.10 (0.03)
9	Liv22	Val dal Spöl	2320	ESE	7.2 (1.6)	175	8.1 (0.2)	1 (0)	NA	0.09 (0.05)	0.09 (0.06)	0.3 (0.6)	2.1 (2.8)	0.93 (1.29)	22.0 (0.9)	0.10 (0.01)
Forested carbonate springs																
10	Liv9	Val dal Spöl	1745	ESE	4.9 (0.1)	341 (9)	7.8 (0.1)	0.7 (0.2)	33	0.19 (0.01)	0.26 (0.04)	2.0 (1.0)	1.6 (2.1)	0.48 (0.13)	44.0 (1.4)	0.10 (0.07)
11	Pa1	Val dal Spöl	1710	E	5.1 (0.6)	242 (7)	8.4 (0.1)	1.5 (0.9)	38	0.30 (0.06)	0.34 (0.05)	1.0 (1.0)	2.5 (1.5)	0.70 (0.30)	23.0 (0.9)	3.10 (1.6)
12	PP10	Val dal Spöl	1620	NE	7.1 (0.2)	394 (34)	8.1 (0.2)	4.0 (1.4)	13	0.12 (0.01)	0.13 (0.04)	1.3 (1.2)	0.6 (0.2)	0.50 (0.30)	28.0 (0.7)	0.20 (0.11)
13	PP11	Val dal Spöl	1620	NE	7.2 (0.2)	414 (15)	8.1 (0.2)	9.5 (9.2)	1	0.11 (0.01)	0.12 (0.03)	1.0 (1.0)	0.1 (0.2)	0.50 (0.10)	27.0 (1.0)	0.10 (0.07)
Forested silicate springs																
14	Las1	Val Laschadura	1815	SSW	4.7 (0.3)	71 (1)	7.6 (0.5)	0.3 (0.12)	37	0.10 (0.02)	0.08 (0.07)	2.3 (2.1)	0.1 (0.2)	0.50 (0.10)	5.8 (0.3)	0.10 (0.09)
15	Las2	Val Laschadura	1855	SSW	4.4 (0.0)	49 (1)	7.7 (0.6)	0.9 (0.14)	40	0.13 (0.02)	0.13 (0.03)	2.7 (0.6)	0.5 (0.4)	0.47 (0.06)	3.9 (1.0)	0.10 (0.10)
16	Liv23b	Val dal Spöl	2110	ESE	4.2 (0.4)	257	8.2	0.1	NA	0.24 (0.12)	0.23 (0.10)	1.0 (1.4)	0.5 (0.4)	0.45 (0.21)	30.0 (0.2)	0.20 (0.0)
Iron sulphur spring																
17	GoFuO	Fuorn	1820	N	6.8 (0.2)	1967 (248)	7.2 (0.8)	2.8 (0.3)	20	NA	NA	3.3 (3.2)	0.6 (0.1)	0.47 (0.25)	26.0 (1.6)	0.10 (0.06)
Temporary springs																
18	Bu17	Buffalora	1990	E	6.2	289	5.1	0.2	28	0.16	0.20	2.0	5.0	1.30	33.0	3.70
19	BuX1	Buffalora	2150	NNE	NA	NA	NA	1.8	27	0.04	0.30	0.0	2.3	1.40	22.0	0.20
20	Liv11	Val dal Spöl	1755	WSW	5.7	NA	7.9 (0.1)	NA	38	0.07 (0.0)	0.11 (0.01)	1.0 (1.4)	2.2 (2.8)	0.75 (0.21)	37.0 (1.9)	2.20 (2.48)

mon here, even up to 2600 m a.s.l., in summer. Buffalora is outside the south-eastern edge of the park. To the south of Ova dal Fuorn is a large plain, Alp Buffalora, used as pasture for cattle. Most study springs here were about 200-m higher than Alp Buffalora. This area is carbonate-dominated and highly human-influenced by cattle ranching. The Bu13 spring group might be influenced by old mine shafts as the springs surface in what appears to be material from the mines. The canyon confined Val dal Spöl is inside the Park. A large hydroelectric dam (Punt dal Gall) is on its southern end and regulates flows in the Spöl River downstream. Two springs, PP10 and PP11, surface near the river. The other springs were in the forest on both valley side slopes, except Liv22 and Liv23b that were 500-m and 700-m higher, respectively, on Alp La Schera on the northern side. Last, God dal Fuorn (GoFuO), an iron-sulphur spring, originated from a 10-m diameter pond, ~2.5 m deep, near the valley bottom on the south side. Its bed sediments are anoxic. The chemistry of the spring has been described by Nadig (1942).

Methods

Physical chemical characteristics

Site coordinates and altitude data were obtained with a GPS receiver with a built-in barometric altimeter and magnetic compass (Garmin Geko 301, USA). The altimeter was calibrated several times a day at known altitudes. Each spring was visited three times during the summer at about 40 day intervals. On each visit, pH (WTW ph330i, Germany), conductivity (WTW LF323, Germany), temperature (spot measures) and discharge were measured. Dissolved oxygen (WTW Oxi340i, Germany) was also measured in some springs. Springs at higher altitudes were first sampled when physically accessible. In several springs (GoFuO, Las1, Las2, Las10, Liv22, Liv23b, PP10, PP11, and Pa1), temperature loggers (VEMCO Mini-log TR, Canada, and ONSET Stowaway Tidbit, USA) were installed. Water samples (1L) were collected each visit and analyzed for NO_2-N + NO_3-N, dissolved N, dissolved P, particulate P, DOC, TIC, and POC following methods in Tockner et al. (1997).

Ecosystem function of selected study springs

Measures of ecosystem function below were completed on four of the study springs (Liv23b, PA1, PP11, and GoFuO).

Bacterial abundance. Three sediment samples per site were collected using a modified 60 mL syringe (sanitex tube with the end cut off) and the material

transferred to a 50 mL Greiner tube (TPP, Switzerland). Samples were stored at 4 °C until analyzed in the laboratory. Homogenized sediment samples were first diluted 1:10 with 10x PBS buffer (0.58M Na_2HPO$_4$, 0.17M $NaH_2PO_4 \cdot H_2O$, 0.68M NaCl). Following vortexing for 4 min at intensity 8 (Vortex Genie 2TM, Switzerland), 10 mL of aliquot was further diluted 1:10 with 10x PBS buffer. Vortexing again for 2 min at intensity 8 and further diluting the aliquot 1:20 with sterile-filtered H_2O (0.4μm Millipore, MIL-LEX™GP, USA) diluted the sample at a ratio of 1:2000. Next, 10 mL of the sample was filtered through an ethanol-cleaned suction filter (PC MB 25 mm 0.2 μm B, Sterico AG, Switzerland) and the suction filter was carefully rinsed with 2 mL of sterile-filtered water. A microscope slide (Menzel Gläser, Switzerland) was cleaned with ethanol and mounted with the filter, and 50 μL of 4', 6-diamidino-2-phenylindole (DAPI) solution was added to the filter. The microscope slide was incubated in the dark at 37 °C for 30 min, before taking photos of 20 random fields through a fluorescence microscope (Olympus BX50F, Olympus Corporation, Japan). Ten photos were randomly selected for bacteria counting.

Hyporheic respiration. Respiration rates of hyporheic sediments (n = 5) were measured at all four springs. Sediment respiration was determined as the decrease in dissolved oxygen over time, after Jones et al. (1995). Sealed plexiglas chambers, filled about halfway with sediment and the rest with stream water, were buried in the stream channel, covered with sediment to exclude light, and incubated in situ for 3–7 hours. Dissolved oxygen concentrations before and after incubation were quantified with an Oxi340i oxygen meter calibrated in the field (WTW, Germany). Sediments were then frozen (-25 °C) and returned to the laboratory for analysis of organic matter content. In the laboratory, chamber sediments were analyzed for particulate organic matter (POM) in four fractions: <0.063 mm, 0.063–1 mm, >1 mm, and coarse sediment. Sediments were dried (60 °C for ≥48 hours) and then weighed. POM content was determined by loss of ignition at 500 °C for 4 hours.

Nutrient uptake. We conducted nutrient uptake experiments on two occasions at each site. After taking background water samples at each transect along a 100 m reach, nutrients in the form of dissolved PO_4-P and NO_3-N were released near the spring outflow using a 35 L Mariotte bottle at a rate of 8 mL s^{-1}. We added NaCl as a conservative tracer to monitor the dispersion of the amended solution. After a plateau had been reached, five 20 mL water samples were collected at each transect starting from the farthest

transect downstream. We measured conductivity to account for subsurface water inflow. All samples were analyzed within 24 h using a Digital Colorimeter (AutoAnalyzer 3, Bran+Luebbe, Norderstedt, Germany). All plateau nutrient concentrations were corrected for background levels and average values (for each transect) fit to an exponential uptake model to calculate uptake parameters (Stream Solute Workshop, 1990).

Open system metabolism. Open system metabolism was estimated at the four sites. Ecosystem respiration (ER) and gross primary production (GPP) were determined using the dual-station diel O_2 method refined by Marzolf et al. (1994). Dissolved oxygen concentrations were measured continuously over multiple days on 2–3 occasions. Stream temperature and DO were recorded at an upstream and downstream location using two oxygen meters (WTW Oxi340, Germany) at 30-min intervals. Both oxygen meters were calibrated regularly to ensure accuracy, both in absolute and relative measurements. The net oxygen production rate ß(t) in g $O_2 m^{-2}$ d^{-1} was calculated using: $ß(t) = [K_s(O_2 - O_{2sat}) + \Delta O_2/ \Delta t]z$ where $K_s(T, Q)$ is the reaeration rate coefficient (h^{-1}) as a function of temperature T (°C) and discharge Q (m^3/s); z represents the mean depth (m), $\Delta O_2/\Delta t$ is the change of oxygen concentration between the upstream and downstream station, and O_{2sat} is the saturation concentration of O_2 (mg O_2 L^{-1}).

To estimate K_s, the gas exchange of a volatile tracer (sulphur hexa-fluoride, SF_6) was measured. SF_6 (gas mixture of SF_6 and N_2, 1 % v/v SF_6) was continuously injected sufficiently above the upstream station to ensure complete lateral mixing when entering the study reach (Naegeli and Uehlinger, 1997). Following the collection of 7 water samples per station using gas tight 50 ml glass syringes, the syringes were transferred to the laboratory where they were analysed for SF_6 on a gas chromatograph. The K_s of sulphur hexa-fluoride was calculated as $K_s (T, Q) = ln(c_u/c_d) * (1/\tau)$ where τ is travel time of water (h) between the upstream and downstream station, and c_u and c_d are corresponding upstream (u) and downstream (d) steady state concentrations of SF_6. Water travel time was quantified by monitoring a NaCl tracer solution (1 kg NaCl per 5 L water) with a portable conductivity meter (WTW LF323, Germany). The reaeration rate coefficient of oxygen was calculated by multiplying the K_s of SF_6 by 1.4 (Cirpka et al., 1993). Thyssen and Erlandsen (1987) describe temperature dependence with an exponential temperature function: $K_s(T) = K_s (20 °C) * 1.024^{(T - 20 °C)}$ where K (20 °C) represents the reaeration rate coefficient at the reference temperature 20 °C. Based on net O_2 production rate, ß(t), ER,

GPP and the ratio of GPP to ER (P/R) were determined. To calculate ER, the average net oxygen production rate during the dark period was extrapolated to 24 hours. GPP was calculated as the sum of ß(t) and ER. The calculation of these metabolic parameters rested upon the assumption that day respiration equals night respiration (Bott and Kaplan, 1985).

Food web analysis of the study springs
Food web analysis was conducted on all 20 springs in the study.

Stable isotope analysis. In each spring, aquatic and terrestrial plants, and individual invertebrate samples were collected. Plant and invertebrate samples were frozen as soon as possible. Plant samples collected included grasses, herbs, conifer needles, moss, wood, algae, and periphyton. Terrestrial plants were sampled in the immediate vicinity of the springs. Periphyton was sampled from rocks by scraping with a metal brush, and transferring the loose material to a plastic storage bottle. Benthic macroinvertebrates were collected with a hand net (250-μm mesh), by disturbing the stream bottom directly upstream of the net. Care was taken to minimally disturb the system.

In the field, benthic invertebrate samples were examined for common species, and individuals separated from the remaining sample. Several individuals (10–20) were sampled per spring to achieve a mean isotope distribution for one species after homogenization. These invertebrates were left alive overnight to empty their guts, and then frozen for stable isotope analysis. Riparian spiders were sampled in late September to represent the terrestrial predator guild in food webs; at least 3 individuals were collected per spring and frozen immediately.

The frozen samples were freeze dried in a Leybold LYOVAC GT2 freeze drier, homogenized, and samples of 0.6–20 mg (depending on the type of sample) were placed into 4×6 mm tin cups and weighed to a precision of 0.001 mg for stable isotope analysis. Samples with carbonate content, mainly periphyton samples from carbonate springs in which minerals were scraped off the rocks together with periphyton, were decarbonated with concentrated hydrochloric acid. Nitrogen and carbon isotope composition for each sample, as well as P, N and C content for stoichiometric analysis, was determined using a Carlo-Erba elemental analyzer (NCS 2500) coupled in continuous flow to a Micromass-Optima isotope ratio mass spectrometer (IRMS). Sample material was combusted in the presence of O_2 at 1030 °C, combustion gases passed through a reduction column (650 °C), and produced N_2 and CO_2 gases were

Table 2. Bacteria abundance and organic matter concentrations in bed sediments (n = 3) along with hyporheic sediment respiration and associated organic matter concentrations as CPOM and FPOM of assessed sediments (n = 5). AFDM = Ash-free dry mass. Values are means and standard deviations.

Number	Spring		Bacteria	AFDM	Organic matter	Respiration	CPOM	FPOM
			(no. mL^{-1})	(g mL^{-1})	(%)	(mg O$_2$ h^{-1})	(g)	(g)
11	PA1	mean	1.87×10^8	0.041	9.23	0.13	0.51	5.76
		SD	1.30×10^8	0.022	10.52	0.01	0.16	0.36
13	PP11	mean	1.14×10^8	0.018	2.49	0.28	0.11	13.60
		SD	6.55×10^7	0.003	0.51	0.33	0.05	1.35
16	Liv23b	mean	3.35×10^8	0.019	3.04	0.46	0.15	4.48
		SD	4.37×10^8	0.010	1.24	0.11	0.08	0.42
17	GoFuO	mean	1.77×10^8	0.018	9.42	NA	7.97	7.22
		SD	6.94×10^7	0.006	6.11	NA	1.20	4.30

separated chromatographically and transferred to the IRMS via an open split for on-line isotope measurements. Isotope ratios are reported in the conventional ‰ -notation with respect to atmospheric N_2 (air) and V-PDB (Vienna Pee Dee Belemnite) standards, respectively. Methods were calibrated with IAEA-N1, IAEA-N2, IAEA N3 standards for ‰^{15}N values, and NBS22 for ‰^{13}C values. Reproducibility of the measurements is <0.2‰ for both nitrogen and carbon.

Results

Physical chemical characteristics of springs
Water temperature of the springs was relatively low, ranging from 2.3 to 7.2 °C for all springs except one (JufX1b) that averaged 12 °C (Table 1). Conductivity varied widely in relation to local geology. The silicate springs were typically <100 μS cm^{-1} (range 22–71 μS cm^{-1}), except for two silicate springs in Val dal Spöl (175 and 257 μS cm^{-1}). The carbonate springs had higher conductivities that ranged from 187 to 414 μS cm^{-1}, except for one buffalora spring (Bu13a) at 84 μS cm^{-1}. The iron-sulphur spring had a high conductivity of 1967 μS cm^{-1}. The pH ranged from 7.2 to 8.4 for all springs. Discharge of springs was relatively low, ranging from 0.2 to 9.5 L s^{-1} with most <5.0 L s^{-1}. Channel slope typically was >20° for the springs, except PP11 had a slope of 1°.

Nitrate-N ranged from 0.09 to 0.30 mg L^{-1}, except for two temporary springs with values of 0.04 and 0.07 mg L^{-1} (Table 1). Dissolved N showed similar values, ranging from 0.11 to 0.34 mg L^{-1}. Dissolved P ranged from 0.3 to 3.3 μg L^{-1}, and particulate P from 0.1 to 2.5 μg L^{-1}. Dissolved organic carbon ranged from 0.17 to 1.4 mg L^{-1} with most springs having values around 0.50 mg L^{-1}. Total inorganic carbon ranged from 0.7 to 44 mg L^{-1}, with non-forested silicate springs typically having low concentrations. Particulate organic carbon ranged from 0.10 to 0.30 mg L^{-1}, except for Pa1 (forested carbonate spring) at

3.1 mg L^{-1} and two temporary springs at 2.2 and 3.7 mg L^{-1}. The carbonate springs generally had higher POC levels than the silicate springs.

Functional assessment of springs
Bacteria counts in the four different springs ranged from 1.8 to 3.4×10^8 cells mL^{-1} sediment with no significant differences between sites (ANOVA, p > 0.05) (Table 2). The ash-free dry mass of organic matter associated with the sediments ranged from 0.02 to 0.04 g mL^{-1} and the relative amount of organic matter ranged from 2.5 to 9.2 %, and were non-significantly different between springs (ANOVA, p > 0.05). The correlation between bacteria counts and sediment organic matter was non-significant (p > 0.05).

Sediment respiration rates ranged from 0.13 to 0.46 mg O$_2$ h^{-1} and did not differ between springs (ANOVA, p > 0.05) (Table 2). Hyporheic respiration in the iron-sulphur spring GoFuO could not be assessed due to its low (<0.3 mg O$_2$ L^{-1}) initial dissolved oxygen concentration. The average coarse particulate organic matter (CPOM) per respiration chamber differed between sites and ranged from 0.11 to 1.2 g (ANOVA, p < 0.05). Fine particulate organic matter (FPOM) also differed between sites and ranged from 4.5 to 13.6 g (ANOVA, p < 0.05). Respiration rates did not correlate with CPOM, FPOM, or total organic matter content (p > 0.05).

All springs exhibited relatively short nutrient (N and P) uptake lengths (S_w) (Table 3). Uptake lengths for N ranged from 11 to 63 m, and for phosphorus from 4 to 60 m. Nitrogen uptake rates (U) ranged from 57 to 266 μg m^{-2} h^{-1} and those for P from 0.11 to 4.2 μg m^{-2} h^{-1}. The shortest uptake length (4 m at GuFuO) corresponded to the fastest P uptake rate (4.2 μg m^{-2} h^{-1}). Although discharge was relatively low in all springs, the spring with the highest discharge (PP11 at 13 L s^{-1}) showed the longest uptake lengths (S_w = 33–60 m for P, 62 m for N) and the lowest uptake rates (0.11–0.48 μg P m^{-2} h^{-1}, and 57 μg N m^{-2} h^{-1}).

Table 3. Discharge, nutrient uptake lengths (S_w) and rates (U), and ecosystem metabolism parameters for selected springs in summer and autumn. For logistic reasons the various measures were taken in different months. NA = data not available. Standard deviation in parentheses (n = 2 or 3, see methods).

Number	Spring	Date	Discharge	Phosphorus		Nitrogen		Ecosystem metabolism			
			(L s^{-1})	S_w (m)	U (μg m^{-2} h^{-1})	S_w (m)	U (μg m^{-2} h^{-1})	NPP (g O$_2$ m^{-2} d^{-1})	ER (g O$_2$ m^{-2} d^{-1})	GPP (g O$_2$ m^{-2} d^{-1})	P/R
11	PA1	July						−1.84 (0.45)	5.94 (0.41)	4.10	0.69
		September	1.3	10	2.16	63	130	−0.65 (0.78)	1.33 (0.84)	0.69	0.51
13	PP11	June						−3.20 (0.54)	10.33 (0.84)	7.14	0.69
		July	13	60	0.11	NA	NA				
		August						−1.57 (0.54)	3.02 (0.44)	1.45	0.48
		September	13.5	33	0.48	62	57				
16	Liv23b	July						−1.63 (0.32)	5.83 (0.23)	4.20	0.72
		August	0.45	NA	NA	11	266				
		September	0.35	8	1.12	29	89				
17	GoFuO	May						−30.92 (0.96)	101.79 (0.46)	70.87	0.70
		July	2.6	7	1.99	NA	NA				
		August						−31.99 (0.69)	91.13 (0.66)	59.14	0.65
		September	2.6	4	4.16	NA	NA				

Gross primary production (GPP) ranged from 0.7 to 7.1 g O$_2$ m^{-2} d^{-1}, but reached values of 59.1–70.9 g O$_2$ m^{-2} d^{-1} in the iron-sulphur spring GoFuO (Table 3). Ecosystem respiration (ER) ranged from 1.3 to 10.3 g O$_2$ m^{-2} d^{-1}, but was 91.1–101.8 g O$_2$ m^{-2} d^{-1} in GoFuO. All springs were net-heterotrophic with production to respiration ratios (P/R) ranging from 0.48 to 0.72. NPP generally increased from June to September, whereas ER, GPP and P/R decreased.

Food web analysis

Nutrient contents among different food web components. The percentage P, N, and C varied significantly among the different food web compartments (Fig. 1). Aquatic plants had relatively low %P content with average %P ranging from 0.05 for periphyton to 0.14 for algae. Terrestrial plants also had low %P values, ranging from 0.07 for conifer needles to 0.20 for herbaceous plants. The %P content of aquatic insects ranged from an average 0.62 for trichopterans to 1.06 for chironomids. The %P of the common lycosid riparian spider was the highest at 1.42.

The %N among these compartments also varied significantly (Fig. 1c). The average %N of aquatic plants ranged from 1.2 to 1.9%. For terrestrial plants, the %N ranged from 0.5% for wood to 2.5% for herbs. The %N of aquatic insects was higher than for plants, ranging from 6.2% for trichopterans to 9.2% for a predator stonefly. The average %N for the riparian spider was 11.1%.

The %C varied less among the different compartments, but was lowest for aquatic plants where it ranged from 9.7 to 35.0% (Fig. 1e). The %C of the other compartments was essentially the same with most groups having %C values between 45 and 50%.

The exceptions were aquatic coleopterans at 38.4% and 51.5% for the predator stonefly.

The ratios of the different nutrients were quite consistent within compartments, although varying among the different compartments (Fig. 1). The N:P ratio varied the least, being somewhat higher in the aquatic plant compartment than the other compartments (Fig. 1b). In the aquatic plants, the average N:P ratio ranged from 13.8 for algae to 33.1 for periphyton. The average N:P ratio for aquatic insects ranged from 7.8 (coleopterans) to 14.4 (predator stonefly), and for terrestrial plants from 7.8 (wood, needles) to 13.4 (grass). The riparian spider had an average N:P ratio of 7.4.

Average C:N ratio for aquatic plants ranged from 7.6 for periphyton to 29.9 for moss (Fig. 1d). The average C:N ratio for aquatic insects was similar among groups, ranging from 5.3 for the predator stonefly to 6.9 for trichopterans. The average C:N was highest for terrestrial plants, ranging from 19.4 for herbs to 63.8 for wood. The average C:N ratio for the riparian spider was 3.7.

The C:P ratios also varied among compartments (Fig. 1f). For aquatic plants, this ratio ranged from 170 for algae to 425 for moss. Terrestrial plants also had high C:P ratios, ranging from 229 for herbs to 763 for wood. The C:P ratio of aquatic insects ranged from 46 for chironomids to 73 for trichopterans, and the ratio for the riparian spider was 32.

Nutrient contents among spring types. The %C, %N, %P of algae was lowest in the iron-sulphur spring (9.2, 0.7, 0.08%, respectively) and highest in the non-forested silicate springs (41.6, 3.7, 0.28%, respectively) (Fig. 2a,b,c). Periphyton had similar %C, %N, and %P values for springs (ca. 7.9, 1.1, 0.04, respectively),
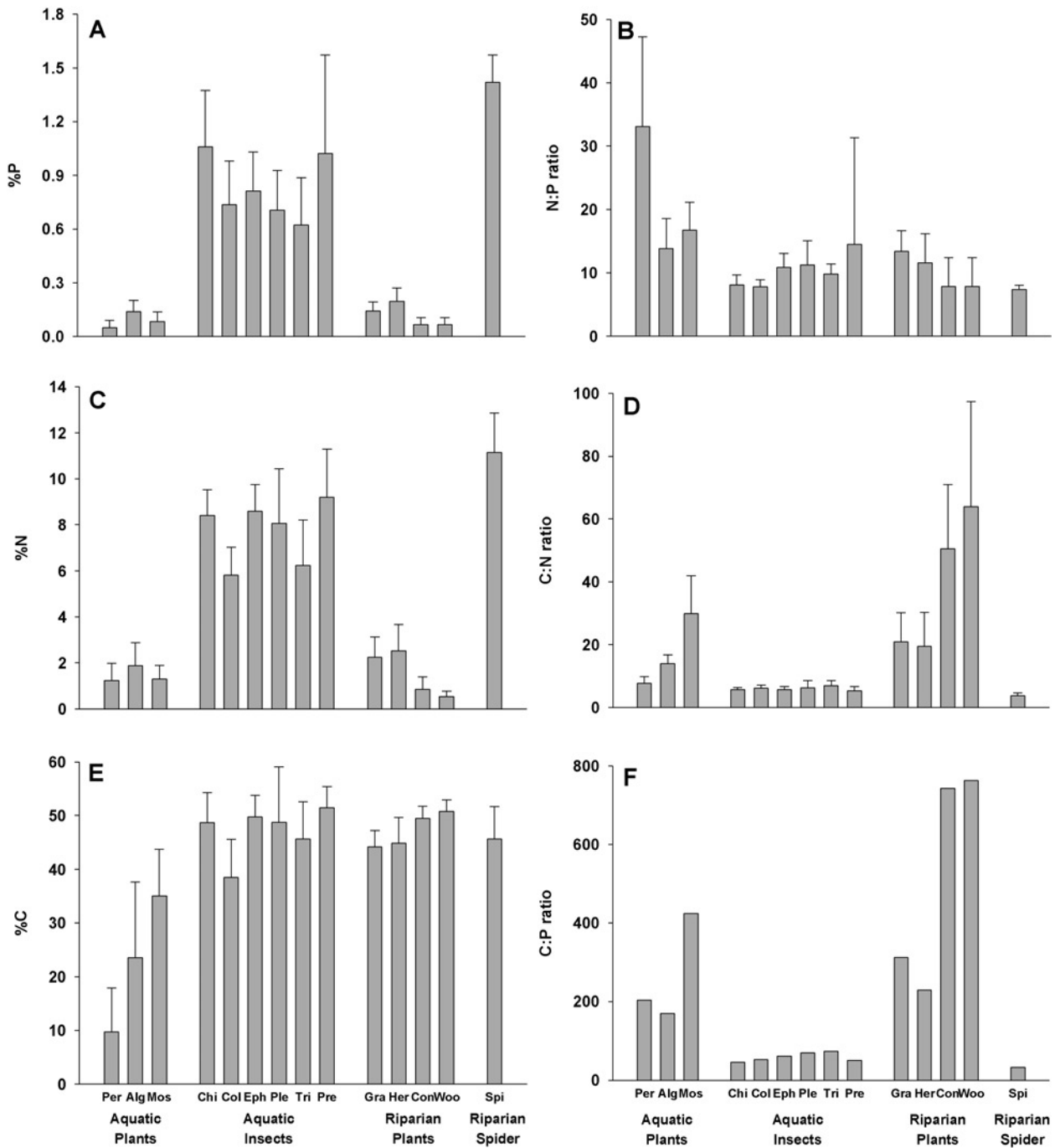
Figure 1. The mean (+1 SD) percentage P, N, C and ratios of N:P, C:N, C:P in the different food web compartments. Per = periphyton, Alg = algae, Mos = moss, Chi = chironomids, Col = coleopterans, Eph = ephemeropterans, Ple = plecopterans, Tri = trichopterans, Pre = predatory plecopterans, Gra = grass, Her = herbs, Con = conifer needles, Woo = wood, and Spi = spider.

although values were highest in silicate springs (19.8, 1.7, 0.16 %, respectively) (Fig. 2d,e,f). The %C of moss was lowest in the iron-sulphur spring (24.1 %), the %N was highest in the silicate springs (ca. 1.7 %), and the %P was highest in the non-forested silicate springs (0.17 %) (Fig. 2 g,h,i).

The %C of coleopterans was highest in silicate springs (ca. 44 %) and lowest in the carbonate spring

(31 %) (Fig. 2j). The %N and %P of coleopterans was similar among springs (ca. 6, 0.71 %, respectively) (Fig. 2k,l). The ephemeropterans had similar %C contents (ca. 50 %) and %N contents (ca. 8.3 %) between springs (Fig. 2 m,n). The %P content of ephemeropterans varied from 0.44–0.61 % in non-forested springs to 0.84–0.91 % in forested springs (Fig. 2o). The average %C of plecopterans was lowest
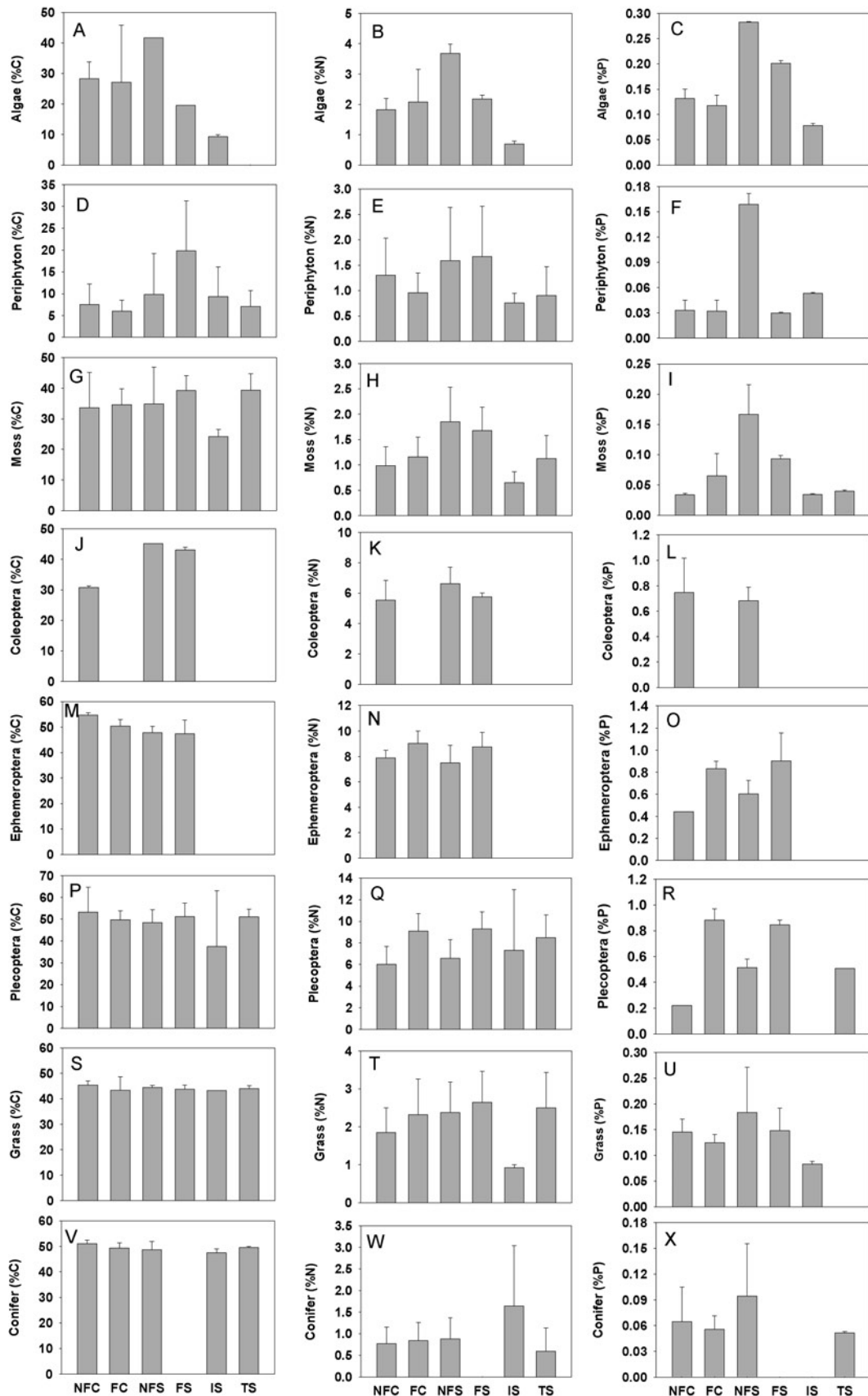
Figure 2. The mean (+1 SD) percentage C, N, and P for different food web groups in each of the different spring types examined. NFC = non-forested carbonate springs, FC = forested carbonate springs, NFS = non-forested silicate springs, FS = forested silicate springs, IS = iron-sulphur spring, and TS = temporary springs.

in the iron-sulphur spring (37%), but similar among the other spring types (ca. 50%) (Fig. 2p). The %N of plecopterans ranged from 6.0 to 9.3%, with average values being lower in forested springs (6.2%) than non-forested springs (9.2%) (Fig. 2q). The average %P content of plecopterans also was lowest in forested springs (0.36%) and highest in non-forested springs (0.86%) (Fig. 2r).

Grass had similar %C contents among springs (ca. 44%), but had the lowest %N content in the iron-sulphur spring (0.9%) relative to the other springs (ca. 2.4%) (Fig. 2 s,t). The %P content of grass also was lowest in the iron-sulphur spring (0.08%) compared to the other springs (ca. 0.15%) (Fig. 2u). Conifer needles had similar %C contents among springs (ca. 49%) (Fig. 2v). The %N content of conifer needles was highest in the iron-sulphur spring (1.6%), and averaged 0.8% in the other spring types (Fig. 2w). The %P content ranged from 0.05% to 0.09% between spring types (Fig. 2x).

Stable isotope analysis. In non-forested carbonate springs, terrestrial plant types were grouped together, and moss also occurred in this group (Fig. 3a). The $\delta^{13}C$ values ranged between -27 to -30, whereas $\delta^{15}N$ values ranged from -1.7 to -5.8. Algae and periphyton had lower $\delta^{13}C$ (-30 to -33) and higher $\delta^{15}N$ values (-0.4 to 1.8) than terrestrial plants. Aquatic insects had much lower $\delta^{13}C$ values (range -38 to -44), but similar $\delta^{15}N$ values as aquatic plants, indicating the aquatic insects used a different source for food. One stonefly group had similar $\delta^{13}C$ and $\delta^{15}N$ values as terrestrial plants. The riparian spider had a $\delta^{13}C$ of -26 and $\delta^{15}N$ of 3.2, suggesting some of its food resource came from aquatic insects. The predatory stonefly had isotope values that suggested it fed on ephemeropterans (mayflies).

In non-forested silicate springs, terrestrial plants also grouped together with $\delta^{13}C$ values from -27 to -29 and $\delta^{15}N$ values of -3.0 to -4.4 (Fig. 3b). Moss had values similar to terrestrial plants. Periphyton also showed similar values with $\delta^{13}C$ values around -28 and $\delta^{15}N$ values of 0.1 and 4.6. Isotope values for aquatic insects ranged from -33 to -38 for $\delta^{13}C$ and from -3.5 to 1.4 for $\delta^{15}N$, suggesting periphyton is not a food source for the examined organisms. The isotope values for chironomids suggest they may be food for other aquatic insects in these springs, plecopterans and coleopterans in particular. The riparian spider had isotope values of -24 for $\delta^{13}C$ and 5.2 for $\delta^{15}N$, similar to non-forested carbonate springs, and suggests aquatic insects only provide a minimal resource for these predators.

In forested carbonate springs, terrestrial plants had $\delta^{13}C$ values ranging from -26 to -30 and $\delta^{15}N$ values

from -7.9 to 1.8 (Fig. 3c). Moss had a somewhat lower $\delta^{13}C$ value at -33 and an intermediate $\delta^{15}N$ value at -2.7. Periphyton had similar $\delta^{13}C$ values as terrestrial plants, but algae had a higher $\delta^{13}C$ value at -24. Periphyton and algae had $\delta^{15}N$ values -0.8 to 5.2. Aquatic insects had isotope values ranging from -33 to -40 for $\delta^{13}C$ and from -4.2 to 0.2 for $\delta^{15}N$, suggesting algae and periphyton were not important as food resources in these springs. Isotope values suggest that the predator stonefly and coleopterans may prey on other aquatic insects. Other aquatic insects may use moss as a food source in these springs. Riparian spiders, with a $\delta^{13}C$ value of -27 and $\delta^{15}N$ value of 2.2 may use some aquatic insects such as mayflies and trichopterans as a food source.

In forested silicate springs, terrestrial plants along with aquatic plants had quite similar isotope values that ranged from -27 to -33 for $\delta^{13}C$ and from -4.1 to -0.8 for $\delta^{15}N$ (Fig. 3d). Aquatic insects showed a wide range in isotopic signatures, ranging from -25 to -38 for $\delta^{13}C$ and from -2.1 to 1.7 for $\delta^{15}N$. The ratios suggest that the predator stonefly and coleopterans use other aquatic insects as a food resource. Other plecopterans may be using periphyton as a resource in these springs. The isotope values for the riparian spider again suggest that aquatic insects are a potential resource.

In the iron-sulphur spring, conifer needles had similar isotopic signatures as the other springs but herbs had much higher $\delta^{15}N$ values at 3.1 (Fig. 3e). Aquatic plants in this spring had similar $\delta^{13}C$ values of -27 to -30 and $\delta^{15}N$ values from 3.1 to 4.1. The plecopteran in this spring had a $\delta^{13}C$ of -34 and $\delta^{15}N$ value of 5.7, suggesting plant material was used as a food resource. The riparian spider had an isotopic signature as found at the other springs and did not use the plecopteran as a food resource. The iron oxide precipitant in this spring likely influenced $\delta^{15}N$ values.

Temporary springs were all in forested carbonate areas, and terrestrial plants had isotope signatures as forested carbonate springs (Fig. 3c,f). Moss in these springs also had similar isotopic signatures as for forested carbonate springs. Periphyton had a $\delta^{13}C$ of -34 and $\delta^{15}N$ of 1.4, indicating it was not a food resource for the sampled aquatic insects. The plecopteran sampled in these springs had isotope values suggesting moss may be a food resource.

Discussion

Physical chemical characteristics

Local geology strongly influenced the physical chemical characteristics of the study springs. Springs flowing from silicate geology had lower conductivities and POC concentrations than those flowing from carbon-
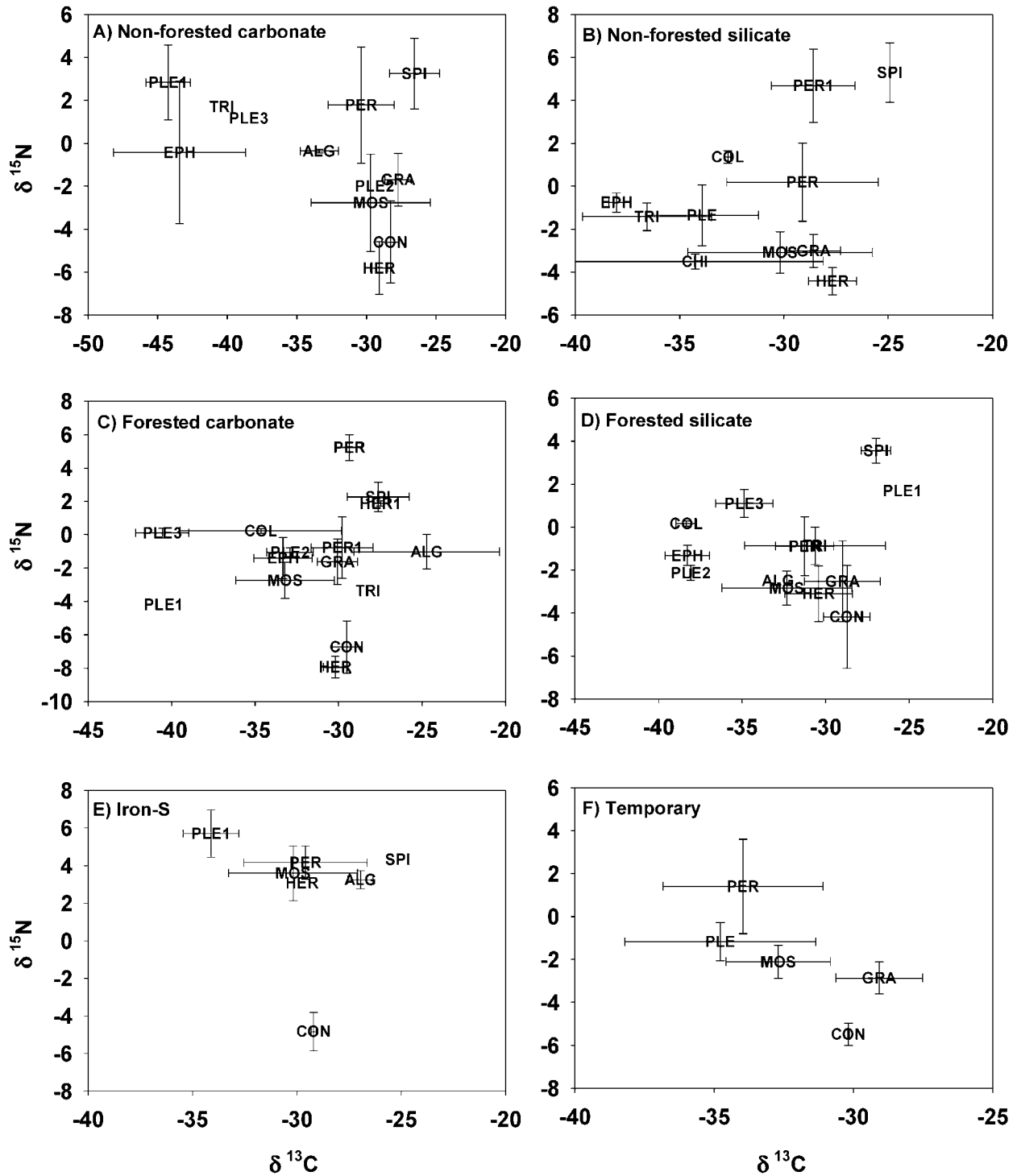
Figure 3. C and N isotopic ratios of different food web groups in each of the different spring types examined. Error bars are standard deviations from the mean. See figure 1 for notation explanations, except that PLE now stands for predatory plecopterans.

ate geology. All springs were relatively buffered with circumneutral pHs. As expected, springs displayed generally low water temperatures with higher elevation springs usually having lower temperatures than those at lower elevations. Factors of canopy cover, spring size, and water source caused exceptions to this

altitudinal pattern in temperature. For instance, temporary springs were typically snow-melt fed and became warmer as snowmelt waters receded over the summer season. These data support the summary of Cantonati et al (2006) suggesting conductivity and temperature in springs is related to local lithology and

altitude. Nitrate-N concentrations in the springs were less than those usually found in other alpine running waters (Tockner et al., 1997; Robinson and Matthaei, 2007), suggesting the influence of atmospheric N deposition is relatively low for these pristine springs. Further, most alpine springs are considered oligotrophic with generally low P levels (Cantonati et al., 2006), as was the case for our springs. Although local inputs from livestock and humans can increase nutrient concentrations in some impacted springs, most of our study springs were in the Swiss National Park and little influenced by humans or livestock.

Ecosytem function

All four examined study springs were found to be net-heterotrophic, even though some were above treeline. Gross primary production and ecosystem respiration values were in the range of that found in other alpine streams in the same geographic region (Logue et al., 2004). Bacterial abundances were at or above levels found in other alpine streams (Logue et al., 2004) or even lowland streams in temperate biomes (Bott et al., 1984). Sediment respiration values further indicate that microbial activity was relatively high for these springs. Logue et al. (2004) suggested microbial activity was a primary factor causing their alpine study streams to be net-heterotrophic. Herbs and grasses contributed a substantial amount of detrital organic matter to open-canopy streams in the study of Menniger and Palmer (2007), and our springs were also bordered by dense grasses and herbs. We suggest these grasses and herbs probably enhanced the detrital resources available in springs for heterotrophic consumption by microbes, as DOC and POC concentrations were generally low in the springs.

The small size and oligotrophic nature, i.e. low N and P concentrations, of the springs probably was a major factor in the short uptake lengths and high uptake rates of N and P in the different springs. These data suggest high elevation springs, in general, can retain much of the nutrient input into these systems and act as important sinks of N and P in alpine landscapes (sensu Peterson et al., 2001). The high density of springs in alpine landscapes suggest their role of retaining and incorporating N and P can be quite important and a significant ecosystem service. Many springs throughout the European landscape, and likely globally, are highly used by humans and for watering livestock (Cantonati et al., 2006), making it even more imperative for conserving and protecting these valuable ecosystems. Springs are highly stable but quite sensitive environments, often demonstrating little resistance or resilience to human perturbations. Besides hosting a distinct biodiversity (Cantonati et al., 2006), they also show a high degree of functional complexity. In general, there is at present a paucity of information on the functional attributes of springs, emphasizing the importance of additional research on these endangered freshwaters.

Spring food webs

The food webs of springs were relatively simple with omnivory predominating. In contrast to alpine glacial streams (Zah et al., 2001; Füreder et al., 2003), algae was little consumed by the examined zoobenthos and detritivores dominated spring food webs. Frost et al. (2005) found algal C was a minor component of periphyton in various aquatic systems, and this may explain the lack of association between zoobenthos and algae in this study. The predatory stonefly did feed on aquatic insects and the riparian spider partially incorporated aquatic insects in the diet. A number of recent studies have documented the subsidy linkage between riparian predators such as spiders and aquatic insects (Paetzhold et al., 2005; Marczak and Richardson, 2007; Burdon and Harding, 2008).

The various food web compartments showed the typical increase in nutrient contents (N, P) with an increase in trophic position regardless of spring type sampled (e.g. Cross et al., 2003; Bowman et al., 2005). For instance, the riparian spider showed a higher %N and %P than the examined aquatic insects that were detritivores. This pattern between trophic groups also held in respect to ratios of C:P and C:N with plants having much higher ratios than the consumers and the riparian spider having the lowest ratios. Evans-White et al. (2005) found %N to be highest in predators and N:P ratios reflected this value. The strong differences in ratios between food sources and aquatic insects may reflect the prevalence of omnivory in the springs and especially the dominance of detritivores. Cross et al. (2003) documented substantial differences in elemental ratios of shredders and their food source (also see Evans-White et al., 2005), suggesting elemental imbalances may be prevalent in detritus-based ecosystems, especially those with simple food webs (see Thompson et al., 2007).

The elemental imbalances observed between the aquatic insects and the food sources in these springs suggest they may be sensitive to changes in nutrient status. Nutrient enrichment could dramatically alter the pathways of material flows in springs and change the functional attributes of these systems. Nutrient enrichment changed the zoobenthic composition and its response to physical disturbance in a high alpine stream (Gafner and Robinson, 2007). The change in nutrient status also increased the %N and %P in food resources and that in the zoobenthos, and potentially reduced the elemental imbalances between trophic groups in the system. Cross et al. (2007) found a

similar response in elemental composition of zooben-thos following nutrient enrichment of a detritus-based temperate stream. Bowman et al. (2005) suggest measures of elemental imbalance could be important for predicting the magnitude of response due to nutrient enrichment in streams.

Springs are an inherent feature of natural land-scapes. The pressure to develop landscapes, especially in the Alps, poses a serious threat to these sensitive and endangered freshwater habitats and the diverse biota inhabiting them. Our data suggest that springs show a high degree of functional complexity as shown for other headwater detritus-based systems. Being net-heterotrophic, having high nutrient uptake and retention, and demonstrating clear elemental imbal-ances between resources and consumers, suggests these systems play an important functional role in limiting the quantity and quality of nutrients and carbon exported from alpine landscapes to down-stream receiving waters. The functional data suggest that microbes probably are important players in this role.

Acknowledgments

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