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SUBSURFACE FLOWPATHS IN A FORESTED HEADWATER STREAM HARBOR A DIVERSE MACROINVERTEBRATE COMMUNITY

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Abstract: Headwater streams and wetlands with a combination of surface and subsurface flows are common features of many upland-forested watersheds. Unlike headwater stream reaches with continuous surface flow, the hydrology and ecology of subsurface stream reaches are poorly studied and not factored into existing wetland legislation. We assessed subsurface habitats and associated biota in a 435-m reach of a first-order, intermittent stream draining a riparian zone dominated by eastern hemlock (*Tsuga canadensis*) in north central Massachusetts. Stream flow was found only in subsurface flowpaths beneath large boulders and surface root mats over approximately 70% of the total stream length at summer base flow. Temperature, specific conductivity, dissolved oxygen, and dissolved organic carbon concentrations of subsurface water were similar to surface water. Macroinvertebrates were found in subsurface habitats but at a lower abundance and richness per unit area compared to surface habitats. Collectors such as Chironomidae, Polycentropodidae, and Ephemerellidae were generally the most abundant families in both surface and subsurface habitats. Our findings indicate that in some glaciated watersheds, intermittent streams with no visual evidence of surface flow may contain subsurface flowpaths with water chemistry and biota comparable to coupled perennial surface flow reaches. The prevalence and importance of subsurface habitats in some headwater streams may warrant review or revision of existing state and local regulatory definitions of intermittent and headwater streams.

Key Words: hyporheic zone, intermittent streams, stream macroinvertebrates, wetland delineation

INTRODUCTION

Headwater streams make up greater than 80% of total channel length in the United States (Meyer 2003) and play important roles in regulating nutrient, organic matter, and sediment fluxes (Lowe and Likens 2005). In addition, headwater streams support diverse faunas that differ from those in larger downstream reaches (Williams and Hynes 1974, Vannote et al. 1980) and function as critical habitat or migration corridors for a multitude of amphibian, reptile, mammal, and bird species (e.g., Semlitsch and Bodie 2003). Intermittent headwater streams, or streams without surface flow at regular or irregular temporal intervals (Gordon et al. 1992, del Rosario and Resh 2000), are poorly studied compared to perennial headwater streams and are not explicitly included in some conceptual models of stream ecosystems (e.g., Vannote et al. 1980). In addition, intermittent streams receive limited regulatory protection compared to perennial streams (e.g., Massachusetts Department of Environmental Protection 2002).

In eastern North America, many small headwater streams or reaches within streams become intermittent for varying lengths of time during summer months when lower precipitation and higher evapotranspiration result in a lower water table (Feminella 1996). Other streams or reaches may retain low base flows continuously in response to discharges from local or regional ground-water systems (Freeze and Cherry 1979, Gordon et al. 1992). Temporal and spatial variation of flow creates a complex and heterogeneous environment that may account for the historical neglect of intermittent streams (Clinton et al. 1996). Among the factors regulating the biological community in headwater streams, flow patterns are one of the most important (Pepin and Hauer 2002, Poole et al. 2006). Macroinvertebrate populations in intermittent streams differ from those in perennial streams (Williams and Hynes 1974, Price et al. 2003), and drying disturbance has been posed as an important organizing mechanism in many stream communities (Resh et al. 1988, Bonada et al. 2006). Differences in the structure of an intermittent stream relative to nearby perennial streams depend on the duration of the drying event and the extent to which longitudinal connectivity and water quality decrease (Lake 2000). Increased competition, diversity lag effects (Lake 2000), use of refugia (Clinton et al. 1996, Lake 2000), and hydrological history (Boulton 2003) are other factors that affect community structure in intermittent streams.

Interacting physical, chemical, and biological factors account for added variation in benthic communities among intermittent streams (Feminella 1996, Williams 1996). In some intermittent headwaters, as well as in larger perennial streams, flow below the surface of the streambed provides important habitat for aquatic invertebrates during periods when the stream channel is dry (Hynes 1970, Stanford and Ward 1988). This hyporheic zone, in which stream water and ground-water mix and percolate, is also an important site of metabolism and nutrient cycling, which results in marked variation in dissolved oxygen concentrations and food resources (Findlay and Sobczak 2000, Pepin and Hauer 2002, Sobczak and Findlay 2002, Marshall and Hall 2004).

In the course of recent surveys of headwater streams in central Massachusetts, we observed numerous headwater streams with extended reaches that had no signs of surface flow yet were continuously flowing in relatively unimpeded subsurface flowpaths. Here we provide a preliminary report on the habitat structure, water chemistry, and macroinvertebrate community of subsurface flowpaths in a forested headwater stream in central Massachusetts.

METHODS

Study Site

We studied a headwater tributary of Bigelow Brook in north central Massachusetts, USA. Bigelow Brook drains into the east branch of the Swift River before entering the Quabbin Reservoir. Underlying geology is a monadnock of granitic bedrock (elevation 420 m) resting on a peneplain, located at the Prospect Hill tract (337 ha) of the Harvard Forest, an experimental forest in Petersham, Massachusetts (lat 42.5°N, long 72°W). The forest is located in the Transition Hardwoods-White Pine-Hemlock region and has well-drained soils with glacial till. Annual temperature at the Prospect Hill tract is 8.5°C, with an annual precipitation of 105 cm. Riparian vegetation is dominated by *Tsuga canadensis* (L.) Carr., a species associated with many of the region's streams and steep ravines. *T. canadensis* stands create a cool, dark microclimate with acidic litter (Rogers 1978, Kessell 1979) and can influence stream community structure (Snyder et al. 2002). Other common riparian and catchment tree species include *Betula alleghaniensis* (Britton), *Fagus grandifolia* (Ehrh.), *Acer pensylvanicum* (L.), and *Acer rubrum* (L.). Mosses appear to be the dominant stream autotroph and cover 60% of submerged boulders and cobble. Detailed records of past land use in the Harvard Forest archives indicate that much of the catchment had historically been kept as woodland, but some areas were clear cut in 1793 and 1895.

Stream Mapping

We mapped three reaches along the 435-m headwater stream: 1) continuous surface flow in a steeper upstream section in narrow runs, riffles, and pools; 2) a flatter region between surface flow sections dominated by subsurface flow, usually with no discernible stream channel; and 3) a downstream reach with continuous surface flow where channels widened before flowing into a beaver wetland (Figure 1). In areas with a clear stream channel, average channel width was approximately 1 m, maximum water depth in surface reaches ranged from approximately 3 cm in patchy pool areas to 15 cm in an upstream run, and substrate was composed of cobble and gravel with sand and silt deposits. Continuous flow has been observed since 2002 in both upstream and downstream surface flow reaches, and these reaches are thought to be perennial.

Stream Hydrology and Chemistry

We installed 16 shallow wells in four transects perpendicular to the stream channel in July 2004 to investigate the hydrology and chemistry of the subsurface flow reach. Wells were constructed using

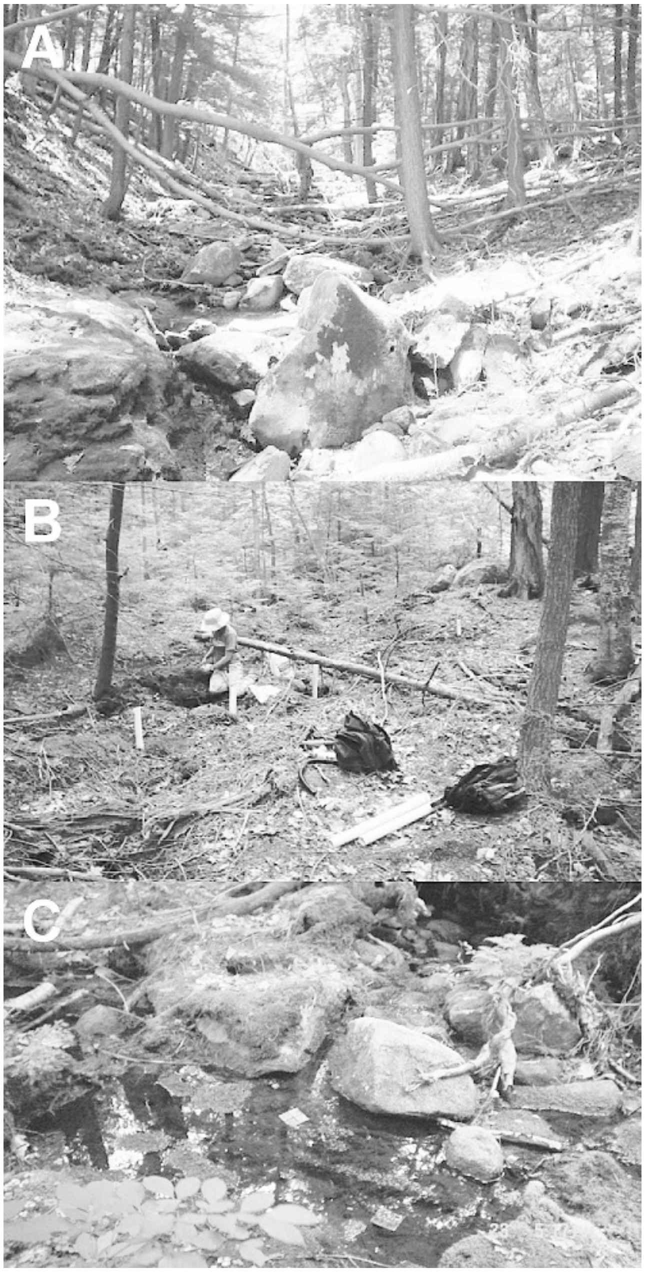

Figure 1. Photographs of the three study reaches: A) upstream surface flow, B) reach with subsurface flowpaths, and C) downstream surface flow.

6-cm diameter polyvinylchloride pipes with the bottommost 10 cm perforated and screened (Sobczak and Findlay 2002). Transects were placed at 148, 224, 305, and 373 m upstream from the beaver wetland in reaches without discernible stream channels or surface flow. Numerous wells were installed using a post-hole digger, but wells were only left in locations hydrologically connected to the stream (i.e., where wells quickly recharged after bailing with a bilge pump; *sensu* Sobczak and Findlay 2002). Dowels were used to measure water depth in wells in July, August, and September 2004. Data loggers (Thermochron i-buttons, Dallas Semiconductor Company, Dallas, Texas) were used to collect temperature of well water (n = 4, one per well transect), surface flow (n = 3, randomly placed), and ambient air temperature (n = 7, paired with well and surface flow sites) every 30 minutes from August 14 to September 14, 2004. Mean daily water temperature was compared between surface flow and wells using a one-way ANOVA. Water chemistry (pH, specific conductivity, and dissolved oxygen) was sampled four times in July 2004 at randomly selected sites in upstream surface flow (n = 3) and downstream surface flow (n = 3), and at 20 subsurface flow sites (n = 13 wells, 7 small naturally exposed pockets). Specific conductivity and pH were measured using a YSI Model 63 pH, conductivity, and temperature meter, and dissolved oxygen (DO) was monitored using a YSI Model 57 dissolved oxygen meter. Dissolved organic carbon (DOC) concentrations were measured via high-temperature combustion using a Shimadzu 5000 TIC/TOC analyzer for samples from upstream (n = 2) and downstream (n = 2) surface water and from well water samples (n = 8) collected in July 2004. Measurements for each parameter (conductivity, pH, DO, and DOC) were compared among reaches with a one-way ANOVA.

Macroinvertebrate Sampling

We sampled randomly selected locations (to the closest riffle) in upstream (n = 3) and downstream (n = 3) surface flow twice, once each in summer (June–July) and fall (October) 2004 for a total of 12 samples. Samples were collected in surface flow locations by kick netting a 0.5 m^2 quadrate and holding a D-net downstream from the riffle to collect macroinvertebrates and substrate. We sampled macroinvertebrates in the subsurface reach in summer (July) and fall (October) 2004 from 0.5-m^2 pits. Pits were dug in three of the four well transects at the nearest accessible subsurface flowpath, and separate pits were dug for each summer and fall sampling to yield a total of six samples. Once the appropriate sized pit was dug, we collected the thin layer of silt and sand substrate within the exposed flowpath for our sample. We were unable to dig pits at the fourth well transect due to an abundance of boulders. Both surface and subsurface samples were placed in bags in the field and returned to the lab for preservation in 70% ethanol and sorting. Samples were sorted in their entirety, and subsurface samples were screened through an 860-μm mesh to remove silt. Invertebrates were identified to at least family

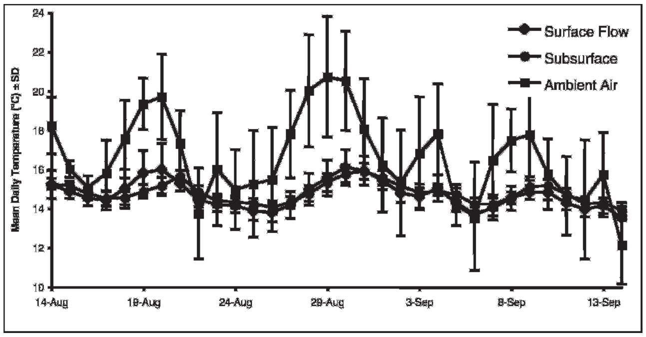

Figure 2. Mean daily temperature (± SD) as recorded by miniature data loggers placed in surface flow (n = 3) and well water (n = 4), and measuring ambient air temperature at these sites (n = 7) between August 14 and September 14, 2004.

(with the exception of mites and oligochaetes) using Merritt and Cummins (1996). Macroinvertebrate samples from the upstream surface, subsurface, and downstream surface reaches were compared in regards to total abundance, total taxa, Shannon index of diversity (H′), and evenness (E_H). Over- and under-represented taxa in the three reaches were identified according to binomial probabilities (Bertin 2002), where the observed frequency of a taxon in a given sample is compared with the taxon's overall frequency out of all pooled samples.

RESULTS

Subsurface flow accounted for approximately 70% of the total length of the 435-m study stream. Subsurface flow was found in continuous channels that functioned as pipe-like conduits in places, channeling flow around large boulders and beneath soil, surface root mats, and mosses. Subsurface flowpaths varied from approximately 10–50 cm in diameter and had a thin substrate of predominantly silt and sand layered over cobble and boulders. Flowpaths were not completely filled with stream water in summer and fall 2004, enabling contact with air. Water depth in wells ranged from 1.0–32.7 cm (mean = 17.7 cm) from July to September 2004.

Mean daily water temperature between August 14 and September 14 did not differ significantly between wells and surface flow ($F_{[1,86]} < 0.36$, $P > 0.55$; Figure 2), while air temperature was subject to large daily fluctuations. Conductivity, dissolved oxygen, and dissolved organic carbon did not differ significantly among upstream, downstream, and subsurface reaches (Table 1). All three reaches exhibited a low pH (range: 3.57–4.68), but there was a significant difference in pH among reaches (Table 1). Dissolved oxygen ranged from 8.8–10.2 mg/L (81%–101% saturation) along the study stream.

Overall, 2,678 macroinvertebrates in 31 taxa were found in our 18 samples. Macroinvertebrates were found in all subsurface samples but at lower abundances compared to surface flow reaches (Table 2). Abundances were greatest in the upstream surface flow reach. The upstream surface flow reach had the greatest number of taxa in summer, the downstream surface flow reach had the greatest number of taxa in fall, and the subsurface reach had the fewest taxa during fall and summer (Table 2). Shannon diversity and evenness values were highest in the downstream surface reach in fall 2004 and lowest in the summer samples of the upstream reach (Table 2).

Binomial probabilities were used to infer under- and overrepresented taxa among surface and subsurface reaches (Table 2). Chironomidae was significantly overrepresented in the upstream habitat in both summer and fall ($P < 0.001$, summer; $P < 0.05$, fall). Elmidae ($P < 0.001$, summer), Hydrophilidae ($P < 0.05$, summer), and Hydropsychidae *Homoplectra* ($P < 0.05$, fall) were overrepresented in the subsurface reach. Leuctridae ($P < 0.001$, summer), Nemouridae ($P < 0.001$, summer), and Tipulidae ($P < 0.001$, fall) were overrepresented in the downstream reach.

DISCUSSION

Subsurface flow of water has been described by hydrologists, ecologists, and geomorphologists as traveling through stream hyporheic zones (e.g., Stanford and Ward 1988, Hill and Lymburner 1998, Sobczak and Findlay 2002), through soil pipes or

Table 1. Mean values (± SD) for chemical parameters measured on four sampling dates in July 2004. Samples were collected at locations in upstream (n = 3), downstream (n = 3), and subsurface (n = 20) reaches; a single sample for dissolved oxygen was collected in the upstream and downstream reaches. Significance levels are $P < 0.05$* and $P < 0.001$** for one-way ANOVA comparisons among stream reach parameter measurements.

Chemical Parameter	Upstream Surface Flow	Subsurface Flow	Downstream Surface Flow
pH*	4.51 ± 0.43	4.05 ± 0.32	3.75 ± 0.21
Specific Conductivity (μS)	20.43 ± 0.50	20.24 ± 2.64	20.98 ± 0.94
Dissolved Oxygen (mg/L)	9.6	9.17 ± 0.70	9.0
Dissolved Organic Carbon (mg/L)	1.72 ± 0.04	1.75 ± 0.05	1.66 ± 0.01

Table 2. Number of individuals in each taxon and number of taxa in each sampling season, reach, and all samples pooled. The triplicate samples collected within each sampling season and reach are pooled. Shannon index of diversity (H′) and evenness (E_H) are reported per sampling season. Significance levels are $P < 0.05^*$ and $P < 0.001^{**}$ for binomial probabilities of over- and underrepresented taxa.

	Taxon		Upstream Surface Flow		Subsurface Flow		Downstream Surface Flow		
	Family	Genus	Summer	Fall	Summer	Fall	Summer	Fall	Totals
Coleoptera	Dytiscidae		1*	5	0	0	6	2	14
	Elmidae		0	0	3**	1	0	0	4
	Hydrophilidae		0	0	1*	0	0	0	1
Diptera	Ceratopogonidae		3	2	0	2	1	6**	14
	Chironomidae		836**	508*	59	96	218	89**	1,806
	Simulidae		0	0	0	0	6*	0	6
	Tabanidae		2	0	0	1	3*	3*	9
	Tipulidae		7**	3	3	10*	26	22**	71
Ephemeroptera	Ephemerellidae		14	21**	0	0	0**	0	35
Hemiptera	Gerridae		1	0	0	0	0	0	1
	Veliidae		2	9*	0	0	3	2	16
Hydracarina spp.			0**	2*	6**	4	17*	7*	36
Megaloptera	Sialidae		3	6	0	0	4	2	15
Odonata	Aeshnidae		0	1	0	0	1	0	2
	Gomphidae		1	0	0	0	0	0	1
Oligochaeta spp.			1	2	2	4*	2	2	13
Plecoptera	Leuctridae		2**	1**	0*	5	180**	1**	189
	Nemouridae		1**	1**	0*	0*	99**	8	109
	Perlodidae		0	0	1	0	0	1	2
Trichoptera	Hydropsychidae	*Homoplectra*	0	0	0	1*	0	0	1
	Hydropsychidae	*Potamyia*	0	0	0	0	0	2*	2
	Hydropsychidae	*Parapsyche*	0	0	0	0	0	1	1
	Lepidostomatidae	*Lepidostoma*	20*	43**	2	4	13	1*	83
	Lepidostomatidae	*Theliopsyche*	8*	0	0	0	0	0	8
	Molanidae	*Molanna*	10	28**	1	1	0**	0	40
	Odontoceridae	*Psilotreta*	19*	61**	0	0*	0**	0*	80
	Philopotamidae		0*	0*	5**	2	1	6**	14
	Phryganeidae	*Oligostomis*	3	1	0	0	1	1	6
	Polycentropodidae		2**	4**	0	8	42**	28**	84
	Psychomyiidae	*Lype*	2	0	0	0	0	0	2
	Rhyacophilidae	*Rhyacophila*	2	4	0	0	6	1	13
	Individuals per season		44	24	68	124	282	20	
	Seasonal richness		12	8	6	10	12	10	
	Seasonal H′		0.623	1.161	1.181	1.299	1.782	1.98	
	Seasonal E_H		0.205	0.394	0.513	0.507	0.617	0.66	Totals
	Individuals per reach		68		192		302		2,678
	Reach richness		14		10		15		31

macropores after storm events (e.g., Walsh and Howells 1988, Crouch 1990, Ghodrati and Jury 1990, Anderson et al. 1997, Bryan and Jones 1997, Uchida et al. 1999), and through underground cave systems (e.g., Jasinska et al. 1996). Subsurface flow in the headwater stream in this study had physical properties representative of hyporheic flow in which water moved through a matrix of roots, cobble, and boulders and macropore flow in which water moved through pipe-like conduits. Subsurface flow in our study stream was not physically impeded by a continuous matrix of sand and gravel, which is characteristic of many hyporheic zones (White

1990, Sobczak and Findlay 2002). Further, the near saturation of dissolved oxygen and relative stability of other chemical constituents along subsurface flowpaths indicates that subsurface-flow reaches have conservative transport of solutes (Table 1). These data indicate that Bigelow Brook's subsurface flowpaths have physical and chemical features conducive to macroinvertebrates. The significant trend in pH is likely more strongly influenced by the acidic litter of the hemlock-dominated riparian zone than by processes along subsurface flowpaths. Unlike many hyporheic zones (Sobczak and Findlay 2002, Storey and Williams 2004), the subsurface habitats in this study did not significantly impede flow or alter water chemistry.

Subsurface flow through soil macropores has been described in many regions and is associated with high-velocity transport of water during and following storm events (Bryan and Jones 1997). Uchida et al. (1999) described the macropores in their study as natural, round pipes in the soil that followed the longitudinal axis of a hollow and that were found interconnected to other pipes. The macropore description given by Uchida et al. (1999) and others is analogous to portions of Bigelow Brook's subsurface flowpaths, although flowpaths in this study were usually not more than 10 cm below the soil surface and were hydrologically connected to surface-stream segments. Further, flow was found continuously in the flowpaths during the entire study period (which included summer base flow) and not just during storm events.

Subsurface flowpaths support a surprisingly diverse macroinvertebrate community, albeit at lower abundance compared to surface flow reaches (Table 2) (*sensu* Storey and Williams 2004). Lower abundances in subsurface habitats may be the result of lower food resources. For example, exclusion of coarse organic matter inputs and low autochthonous production due to light limitation may limit food resources for macroinvertebrates within subsurface flowpaths. Subsurface flowpaths support a subset of species found in surface flow; however, Elmidae, Hydrophilidae, and Hydropsychidae (*Homoplectra*) were found only in subsurface habitats. Although it is unlikely that these taxa represent subsurface flow specialists in our stream, these findings do suggest that subsurface flowpaths serve as a critical habitat for a variety of macroinvertebrates.

Do subsurface flowpaths serve as an invertebrate refuge during low-flow events? The study period may represent a high summer and fall base flow. A long-term data set of weather information kept by Harvard Forest (1964 to present) indicated that summer precipitation was average (196.3-mm total for June and July 2004, compared with 196.4-mm mean total for June and July 1964–2003); however, temperatures were on the whole slightly cooler, often falling below the average for the summer months. Further study is needed during dry years to determine the relative importance of subsurface flowpaths during low-flow conditions.

Documentation of subsurface habitats that harbor a diverse stream macroinvertebrate community contributes to a growing body of literature suggesting that hyporheic zones may be a critical habitat for biota in intermittent streams (Feminella 1996, del Rosario and Resh 2000, Boulton 2003, Poole et al. 2006). In the case of Bigelow Brook, subsurface flowpaths kept the stream ecosystem hydrologically connected even when some surface flow reaches were dry. Further, subsurface flowpaths functioned similarly to surface flow habitats, conserving the chemical signature of the stream water and providing habitat for macroinvertebrates. These observations demonstrate that even the upper most reaches of Bigelow Brook are perennial in regards to flow, yet appear intermittent.

We observed similar streams during our regional stream surveys suggesting that Bigelow Brook's subsurface hydrologic regime may be fairly common, yet easily overlooked. Assuming that other streams have continuous subsurface flowpaths that harbor macroinvertebrates and connect perennial surface flow reaches, classifying these systems as intermittent might be inappropriate. Better recognition of perennial subsurface flowpaths may have important implications for conservation and legislative protection. In Massachusetts, for example, intermittent streams do not qualify for having protected associated riverfront areas, and protections for "land under water bodies and waterways" only extend to the land under the low water level in stream channels (MA Department of Environmental Protection 2002). Perennially flowing subsurface stream reaches would not likely qualify for either protection; hence, a review or revision of current state and local regulatory language may be justified.

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