Measuring adult insect emergence from streams: the influence of trap placement and a comparison with benthic sampling

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Abstract. Increased need to quantify adult insects emerging from streams as a part of foodweb and ecosystem studies has placed new demands on techniques used to sample adults. The population sampled must be better understood to establish the scope of inferences that may be drawn from emergence data. We used data from 2 different studies to compare the structure of insect assemblages represented by benthic samples and emergence-trap samples and to compare adult insect assemblages collected in emergence traps placed at mid-channel vs streambank locations. Nonmetric multidimensional scaling (NMDS) ordination showed that some components of the benthic assemblage were underrepresented in the emergence-trap samples and others were underrepresented in benthic samples. These differences were mainly caused by taxa that emerged by crawling out on the stream bank (e.g., Plecoptera) or whose larvae reside in habitats, such as stream margins, that are underrepresented with traditional benthic sampling (e.g., Dixidae). The flux of insects into traps placed mid-channel did not differ significantly from the flux into traps placed along the stream bank. Taxa collected by mid-channel and streambank traps overlapped considerably, but midchannel traps tended to collect proportionally more Trichoptera, Ephemeroptera, and Diptera, whereas streambank traps collected proportionally more Plecoptera. Our results can be used to improve trapping designs for future assessments of aquatic insect emergence in studies of insect behavior and life histories and as part of foodweb and ecosystem research.

Key words: emergence, emergence traps, benthic insects, adult aquatic insects, trap placement.

Ecologists have been collecting adult insects emerging from aquatic habitats since the early 1900s (Davies 1984). Past collections of emerging insects were made primarily by entomologists to study the biology of aquatic insects, including timing and abundance of emergence (Judd 1962, Corbet 1964, Harper 1978), and for taxonomic purposes (Davies 1984). More recently, adult emergence from freshwater systems, especially streams, has been studied as an important ecosystem process (reviewed by Baxter et al. 2005). Early studies described emerging aquatic insects as a very small portion of the organic matter budgets in watersheds (Vallentyne 1952, Fisher and Likens 1973, Webster and Patten 1979), but recent investigations suggest that the importance of adult aquatic insects as a prey resource for riparian consumers might be disproportional to the size of the flux (Jackson and Fisher 1986, Nakano and Murakami 2001, Sabo and Power 2002). Measurement of emergence as a part of foodweb and ecosystem studies has placed new demands on the techniques used. For example, trap designs have been adjusted (e.g., made more lightweight and inexpensive) to facilitate studies in which large numbers of measurements must be made simultaneously. In addition, a closer evaluation of emergence data is required.

The most typical approach to quantifying aquatic insect assemblages in streams is to sample the benthos (e.g., with Surber or Hess-type samplers), usually via a snapshot sample taken during low-flow conditions. Emergence also is often measured during low-flow periods. However, the components of the insect assemblage sampled and the extent to which emergence samples represent the flux of adult insects are uncertain. The assemblage structure represented by benthic and emerging insect samples have rarely been compared (but see Poepperl 2000), but such a comparison could yield insight into the characteristics of both techniques. Moreover, the placement of

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emergence traps within a stream reach has potential to influence the component of the adult assemblage sampled, just as the distribution of benthic sampling sites among streambed habitats can affect the component of the benthic assemblage sampled. For instance, emergence of some taxa, such as most Diptera and Trichoptera, occurs through the water column, whereas emergence of others, such as Plecoptera and some Ephemeroptera occurs from the stream bank (Merritt et al. 2008). Thus, traps placed mid-channel are likely to sample a different population than those placed along stream banks.

The population sampled by emergence traps must be better understood in a statistical sense to establish the scope of inferences that may be drawn from emergence-trap data. However, differences in taxa sampled with benthic vs emergence sampling and the effects of emergence trap placement on the taxa collected have not been formally evaluated. We used data from 2 different studies of Rocky Mountain streams to compare insect assemblage structure measured via benthic and emergence-trap sampling and to investigate the effect of emergence trap placement (mid-channel vs stream bank) on the assemblage of adult insects sampled.

Methods

Study areas

Salmon River Basin.—The taxonomic composition of insects captured in emergence traps was compared to the taxonomic composition of insects collected from the stream bed in six 2nd- 3rd-order streams in the Frank Church 'River of no Return' Wilderness in the Payette National Forest of central Idaho (USA). Sampling reaches were on tributaries to Big Creek, which flows into the Middle Fork of the Salmon River (elevation 1213–1406 m). The streams are small (wetted width = 2.7 m ± 0.5), shallow (0.19 m ± 0.02), and cold (annual degree days = 2187°C ± 85), and flow through alluviated canyon segments. Sampling sites were in pool/riffle reaches with substrate dominated by cobble or gravel. Upland vegetation is primarily Douglas fir (*Pseudotsuga menziesii*), Ponderosa pine (*Pinus ponderosa*), or extensive bare or sparsely vegetated areas of grass and sagebrush (*Artemisia*) on the drier slopes. Dominant riparian vegetation includes dogwood (*Cornus sericea*), Rocky Mountain maple (*Acer glabrum*), and alder (*Alnus viridis*). The area generally receives ~40 cm of precipitation annually. Most of the precipitation occurs as snow, and peak flows occur from late spring through mid-summer. Further site descriptions can be found in Malison (2008).

Teton River Basin.—The taxonomic composition and biomass of emerging insects captured in mid-channel traps was compared with biomass and composition of emerging insects collected in streambank emergence traps in six 2nd- to 4th-order streams in roadless areas of the Targhee National Forest (southeastern Idaho) or in the Jedediah Smith Wilderness (western Wyoming). The streams are tributaries of the Teton River and are montane (elevation 1994–2175 m), relatively small (wetted width = 4.5 m ± 0.9), shallow (0.16 m ± 0.02), and cold (annual degree days 678°C ± 37). Sampling sites were in pool/riffle reaches with cobble or gravel as the dominant substrate. Upland vegetation is dominated by lodgepole pine (*Pinus contorta*), Douglas fir, Engelmann spruce (*Picea engelmannii*), and blue spruce (*Picea pungens*). Riparian vegetation is dominated by willow (*Salix*) and dogwood. Precipitation is greatest between November and June and falls mainly as snow. High flows, caused by snowmelt, occur between May and July. Further site descriptions can be found in Benjamin and Baxter (2010).

Emergence trap design and deployment

A light-weight and inexpensive 2-piece emergence trap that could be carried by back pack and assembled on site was designed for use in the Salmon River Basin study (for details of trap construction see Malison 2008). Traps were shaped like small tents and covered 0.33 m² of stream surface (Fig. 1A). This size allowed the trap to float with minimal interference with flow while maintaining its efficiency (Morgan et al. 1963, LeSage and Harrison 1979). The frames were constructed of polyvinyl chloride (PVC) pipe. Six pieces (four 28-cm pieces connected with t-joints to form 2 opposite sides, two 58-cm pieces to form 2 opposite sides; all 4 sides joined by elbow-joints) formed the square base and 3 pieces (58-cm pieces connected to each other by elbow joints and to the base by t-joints) formed the upright portion. The frame was covered with a durable (lasting ≥2 field seasons), white, fine-mesh netting (mesh size: ~0.2 mm; no see-um netting 100% polyester knit, Outdoor Wilderness Fabrics, Inc., Caldwell, Idaho). White netting was chosen because it blocks less light, which can influence emergence (Morgan et al. 1963, Kimerle and Anderson 1967), than other colors and provides the best visibility for collection of insects from the trap. Nets were constructed of 3 pieces of material (1 rectangle: 170 × 70 cm, 2 modified pentagons: 80 × 64 cm). The bottom 15 cm of material hung below the tented area (on all sides) and was attached to the PVC frame with 4 styrofoam floats. An aspirator was used to remove emergent insects from the trap through a Velcro opening.
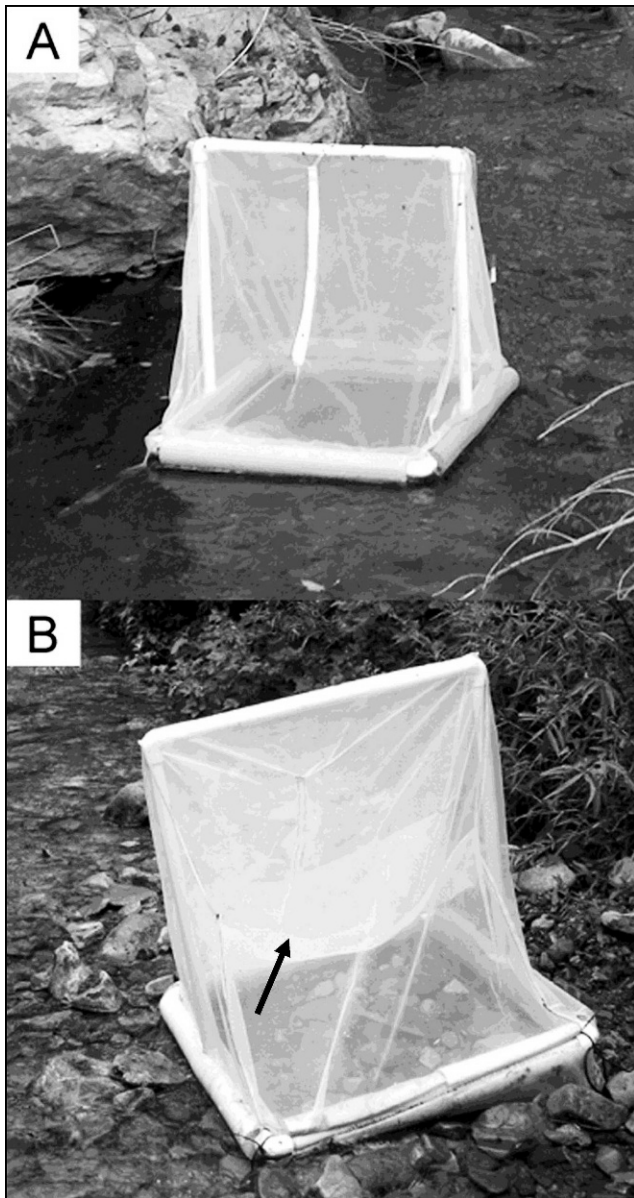
FIG. 1. A.—Light-weight emergence trap designed for use in wilderness or other logistically difficult settings. B.—Modified emergence trap for collection of taxa that emerge from the stream bank. The arrow indicates the location of the catch.

The emergence trap was designed to float on the stream surface and to collect insects emerging at a given location, regardless of their point of origin on the streambed. The upstream corners of the trap were loosely attached to 2 pieces of rebar to facilitate continuous sampling as water level rose or fell. Traps were placed in pools (where we expected the greatest emergence; Iwata 2006) and along stream banks, habitats where large traps could maintain a good seal with the water surface.

The design of the emergence trap was modified slightly for the study in the Teton River Basin (Fig. 1B). Mid-channel traps and streambank traps had a 35 × 50-cm catch sewn to the inside of the net ~30 cm from the top of the trap. The catch was used to capture emerging insects that might otherwise have reentered the water because of rain, wind, or mortality. The streambank traps had a design similar to the channel traps except that the netting panels were 30 cm longer so that the overhanging netting could be buried into the bank substrate to prevent insects from escaping and potential predators from entering the trap (Paetzold and Tockner 2005).

Insect sampling

Emergence was measured from May through October 2005 in the Salmon River Basin and from mid-June through August 2006 in the Teton River Basin. In the Salmon River Basin, 4 traps were placed on pools in each stream, and emergence was collected continuously. Insects were removed from the traps every 4 to 5 d from May through August and every 2 wk from September through October. In July 2005, 5 benthic samples were collected with a Surber sampler at random locations in systematically selected riffles (approximately every 25 m) in each study reach.

In the Teton River Basin, 5 traps were placed on pools and 5 along stream banks. Bank traps were positioned to include the water's edge (Fig. 1B). Before deployment of the bank traps, vegetation was removed and water was poured on the ground to bring any terrestrial arthropods to the surface for subsequent removal from the trap area (Paetzold and Tockner 2005). Vegetation removal was not usually necessary because traps often were deployed on gravel bars. Insects were removed from traps on a 4-d/10-d rotating schedule. Traps were cleared to start the sample run, allowed to collect insects for 4 d, and then sampled. These 4-d sampling runs alternated with 10-d periods, which were not analyzed for this study. This rotation was based on logistical constraints of reaching sites repeatedly. Pulses of emergence might have been missed during the 10-d interim periods, but the comparison of interest was between trap locations within a stream and not the flux of all emerging insects.

Insects from emergence traps and Surber samples were preserved in 90% ethanol. In the laboratory, they were identified, counted, dried (60°C for ≥24 h), and weighed.

Statistical analysis

In the Salmon River Basin study, assemblage composition was compared between sampling meth-

ods on the basis of relative biomass rather than relative abundance because biomass data better reflect insect production than do abundance data. Moreover, biomass data are most often of interest in foodweb and ecosystem studies. Rare taxa (<5% frequency of occurrence) were excluded from the ordination to avoid skewing the results (Gauch 1982). Only the orders Diptera, Ephemeroptera, Trichoptera, and Plecoptera were used for the comparison. Other orders (i.e., Coleoptera) and noninsect taxa were not included in our analysis because the adults in these groups do not emerge from the stream. However, they were present in the benthic samples and represented a clear difference in the components of the assemblage sampled by the 2 methods. Taxa were grouped at the family or order level so that taxonomic resolutions of the benthic and emergence data were similar. For benthos, mean biomass for each taxon was computed for each stream by averaging the biomass from 5 of the replicate benthic samples in each stream. For emergent adults, an overall mean biomass for each taxon from each stream was computed by averaging the mean biomass of emergence (from 4 traps) of all the samples collected between May and October in each stream.

The taxonomic composition of the insect assemblages represented by benthic samples was compared with that of insect assemblages represented by emergence-trap samples. First, benthic and emergence-trap samples were compared coarsely based on taxon presence/absence at the lowest taxonomic level. The goal of this comparison was to determine which method most completely sampled the taxa present in the stream and to determine which taxa were most likely to be missed or underrepresented by each sampling method. Visual inspection of nonmetric multidimensional scaling (NMDS; Kruskal and Wish 1978) ordination plots was used to compare sampling techniques based on sample separation in invertebrate assemblage space. Second, Multiresponse Permutation Procedures (MRPP) were used to test for significant differences in taxonomic composition between benthic and emergence-trap samples (Mielke and Berry 2001).

In the Teton River Basin study, the flux of adults (measured as biomass) into channel and bank traps was compared in 6 streams over similar time periods (19 June–30 Aug 2006). Paired t-tests were used to investigate differences in emergence magnitude between trap locations in each stream. The flux measurements were $\ln(x)$-transformed to meet the assumptions of normality and homogeneity of variances. Potential differences in assemblage composition of samples collected from mid-channel and streambank traps were evaluated with NMDS and MRPP. Taxa were grouped at the family or order level.

Results

Comparison of benthic vs emergence-trap samples

Presence/absence.—Insect assemblage composition measured via benthic and emergence sampling was very similar. The greatest differences were caused by taxa that did not inhabit riffle habitat or that did not emerge directly from the water surface (see Table 1 for examples of the most common taxa). Diptera were well represented in both types of samples, but Blephariceridae were present only in emergence samples and Deuterophlebiidae and Pelecorhynchidae were present only in benthic samples. Ephemeroptera were well represented in both emergence-trap and benthic samples. However, Ephemerellidae (e.g., *Drunella coloradensis*, *Drunella doddsi*, and *Serratella tibialis*) were present mostly in benthic samples, whereas *Ameletus* was collected only in emergence-trap samples from one stream. Trichoptera were found in both benthic and emergence-trap samples, but differences in presence/absence were observed among families (e.g., Apataniidae were rare and only found in benthic samples), and within genera (e.g., *Rhyacophila*; Table 1). In contrast, Plecoptera were poorly represented in emergence-trap samples. Perlodidae, Leuctridae, Peltoperlidae, Pteronarcyidae, and Taeniopterygidae were present only in benthic samples, whereas only Capniidae, Chloroperlidae, Nemouridae, and Perlidae were present in both benthic and emergence-trap samples.

Assemblage comparison between sampling methods.—Taxonomic composition of insects collected differed significantly between sampling methods (MRPP: $A = 0.091$, $p = 0.002$). Benthic and emergence-trap samples were separated in taxon space (Axis 2, 37% of total variation explained), but variation was greater within sample types (along Axis 1, 46%) than between sample types (Fig. 2, see Table 2 for taxon specific correlations for each axis). On average, the relative biomasses of stonefly families (e.g., Perlodidae and Nemouridae) were almost 2× greater in benthic than in emergence-trap samples, whereas the relative biomasses of Blephariceridae and Dixidae were >2× greater in emergence-trap than in benthic samples (Table 1). Relative biomasses of several other families, including Ephemerellidae and Baetidae (higher relative biomass in benthic than in emergence-trap samples) and Rhyacophilidae (higher relative biomass in emergence-trap than in benthic samples) differed strongly between sample types.

TABLE 1. Relative biomass (%) composition of taxa that made up >3% of the biomass of insects in benthic (B) or emergence-trap (Em) samples. Taxa were quantified on the basis of mean relative biomass in 5 replicate benthic samples collected July 2005 and mean relative biomass of emerging adults in 4 replicate emergence traps deployed from June to October 2005. E = Ephemeroptera, P = Plecoptera, T = Trichoptera, D = Diptera.

Site coordinates: Cabin (Lat 45°9′N, Long 114°55′W); Calf (Lat 45°8′N, Long 114°54′W); Cave (Lat 45°7′N, Long 114°57′W); Cliff (Lat 45°6′N, Long 114°50′W); Cow (Lat 45°8′N, Long 114°55′W); Pioneer (Lat 45°5′N, Long 114°50′W).

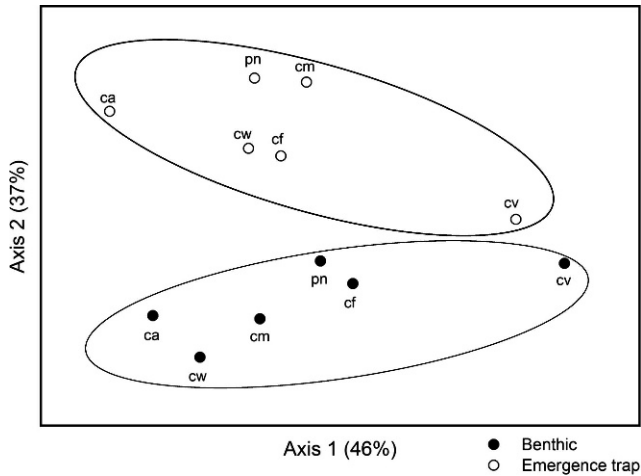| Order	Family	Species	Cabin B	Cabin Em	Calf B	Calf Em	Cave B	Cave Em	Cliff B	Cliff Em	Cow B	Cow Em	Pioneer B	Pioneer Em
E	Baetidae	*Baetis* spp.	4.7	2.9	12.2	5.8	3.1	1.4	9.3	7.3	15.7	7.2	4.9	1.5
	Ephemerellidae	*Drunella coloradensis*	6.8	0.0	18.7	0.0			6.0	0.0	0.5	4.2	3.4	0.0
		Drunella doddsi	5.1	0.0							21.7	0.0	4.9	0.0
		Seratella tibialis			7.0	0.0			0.0	5.3	7.5	0.0	0.0	4.5
	Heptageniidae	*Epeorus longimanus*	12.5	0.0							0.1	9.8		
P	Perlidae	*Doroneuria* spp.					0.1	7.4	0.4	9.0	8.4	0.0	0.3	3.2
		Hesperoperla pacifica					5.4	0.0	4.4	0.0			7.8	0.0
T	Brachycentridae	*Brachycentrus* spp.	0.0	13.8			7.8	0.0	0.0	3.3				
	Glossosomatidae	*Anagapetus debilis*					18.9	0.0					0.0	6.4
		Glossosoma alascense									0.0	3.6	0.0	3.8
	Hydropsychidae	*Arctopsyche* spp.	22.2	0.0			0.4	8.0						
		Arctopsyche grandis					3.1	0.0					0.0	5.1
		Parapsyche elsis	0.2	12.8	0.1	12.0	7.1	0.0	7.7	15.3				
	Rhyacophilidae	*Rhyacophila* spp.			4.0	0.0	0.1	3.9	0.0	4.0	0.7	12.8	2.8	1.9
		Rhyacophila brunnea									4.2	0.0	1.8	28.8
		Rhyacophila coloradensis	3.3	0.0			0.0	3.4	0.0	3.9				
		Rhyacophila vao	0.0	7.7	0.0	4.7	0.0	4.1	3.4	0.0	0.0	7.8	0.0	5.0
	Uenoidae	*Neophylax rickeri*	38.0	9.8	0.0						4.6	0.0	6.8	0.0
		Neophylax splendens			4.5								0.0	4.9
D	Blephariceridae		0.0	3.4	1.5								0.7	4.3
	Chironomidae		2.8	3.0	0.0	5.5	21.3	49.9	8.7	15.3	1.0	7.2	0.0	3.2
	Empididae				0.0	2.9	0.0	6.9	2.8	3.7	0.0	4.4		
	Simuliidae	*Simulium* spp.	4.1	4.2	15.6	5.7	0.0	6.7	0.0	6.4	0.0	3.7		
	Tabanidae					1.8			8.3	0.0	2.7	0.6		
	Tipulidae	*Antocha* spp.			0.0	50.3			0.0	11.6			0.0	9.3
		Hexatoma spp.			4.5	0.0							4.3	0.0
		Tipula spp.	12.9		12.9	0.0			5.6	0.0	1.9	27.5	0.0	3.4

FIG. 2. Nonmetric multidimensional scaling ordination plot of insect assemblages in benthic samples and emergence-trap samples. Taxa were quantified on the basis of mean relative biomass in 5 replicate benthic samples collected July 2005 and mean relative biomass of emerging adults in 4 replicate emergence traps deployed from June to October 2005 in 6 streams (ca = Calf, pn = Pioneer, cm = Cabin Main, cw = Cow, cf = Cliff, cv = Cave) in the Big Creek watershed, Idaho (USA). Numbers in parentheses are % of variation explained by each axis. Ellipses delineate groups of samples that were significantly different based on Multiresponse Permutation Procedure analysis.

Comparison of midchannel vs streambank traps

Total flux analysis.—The total flux of adult aquatic insects that emerged into traps did not differ between midchannel vs streambank traps in any stream (all $p > 0.34$; Table 3). Total flux into streambank traps consisted mostly of Chloroperlidae, Nemouridae, Perlidae, and Perlodidae, whereas total flux into mid-channel traps consisted mostly of Chironomidae, Rhyacophilidae, and Uenoidae. Representation of ephemeropteran families did not differ between trap locations. Flux of plecopterans (Perlidae, Perlodidae) was greater in the 4 larger streams (Darby, Fox, South Leigh, and Teton Creeks; wetted width > 6.0 m) than in the 2 smaller streams (North and South Forks of Mahogany Creek; wetted width < 2.5 m). Perlidae and Perlodidae were more common in streambank than in mid-channel traps.

Total flux varied with trap location and sampling period. Perlidae and Perlodidae emerged in mid- to late July and were found principally in streambank traps. Thus, greater flux occurred during that time period for streambank than mid-channel traps. In contrast, emergence was dominated by Ephemeroptera, primarily Baetidae and Ephemerellidae, during mid-June to July and mid- to late August, respec-

TABLE 2. Taxa correlated with axis 1 and axis 2 in the nonmetric multidimensional scaling ordination plot of insect assemblages for the Big Creek Watershed, USA.

Axis 1	r	Axis 2	r
Tipulidae	−0.58	Rhyacophilidae	0.8
Simulidae	−0.55	Blephariceridae	0.71
Dixidae	−0.52	Dixidae	0.57
Brachycentridae	0.65	Glossosomatidae	0.55
Hydroptilidae	0.67	Perlodidae	−0.53
Chironomidae	0.78	Leuctridae	−0.54
Perlidae	0.79	Taeniopterygidae	−0.54
		Nemouridae	−0.57
		Ceratopogonidae	−0.57
		Thaumaleidae	−0.61
		Baetidae	−0.73
		Ephemerellidae	−0.77

tively, and caused greater flux into mid-channel vs streambank traps. Rhyacophilidae and Uenoidae emerged from late July through August and caused increased flux in mid-channel traps.

Assemblage comparison between trap locations.—Assemblage composition did not differ significantly between trap locations or among streams (MRPP: $A = -0.020$, $p = 0.191$). However, mid-channel and streambank samples were separated along Axis 2, which explained 52% of the variation in the assemblage structure (Fig. 3). Assemblages collected in mid-channel traps had higher relative biomasses of Trichoptera, Ephemeroptera, and Diptera (positive correlation with axis 2 scores), whereas assemblages collected in bank traps had higher relative biomasses of Plecoptera (negative correlation with axis 2, see Table 4 for taxon specific correlations with each axis). Additional variation among streams was shown along Axis 1, which explained 21% of the variation in assemblage structure. Dipteran and plecopteran relative biomasses were positively correlated with Axis 1, whereas Hydropsychidae were negatively correlated with Axis 1. Assemblages also differed with respect to stream size, and assemblages in the 2 smallest streams showed similar patterns with respect to trap location.

Discussion

Benthic vs emergence-trap sampling

Benthic and emergence-trap samples yielded different characterizations of the stream insect assemblages. These differences suggest that, as typically applied, neither method provides a sample that represents the entire assemblage. The differences probably were the result of variation in habitat preferences or life-history strategies of a few taxa.

TABLE 3.   Mean (SE) emergence flux of aquatic insects from streams in the Teton River Basin. Taxa were quantified on the basis of mean relative biomass in 5 mid-channel and 5 streambank emergence traps deployed from June to August 2006. The test statistic was a paired *t*-test comparing samples between mid-June and August.

| Stream | Latitude | Longitude | n | Mean flux ($mg\ m^{-2}\ d^{-1}$) | | t | p |
				Streambank	Mid-channel		
Darby	43°40′N	110°59′W	5	13.51 (6.21)	14.45 (4.14)	0.52	0.63
Fox	43°38′N	111°01′W	5	5.88 (4.44)	6.11 (1.95)	1.38	0.24
North Fork Mahogany	43°55′N	111°11′W	3	1.67 (0.76)	15.68 (6.17)	2.07	0.17
South Leigh	43°48′N	110°56′W	3	30.04 (18.54)	8.02 (1.98)	1.46	0.28
South Fork Mahogany	43°39′N	111°16′W	3	6.12 (2.03)	16.16 (9.54)	1.82	0.21
Teton	43°44′N	110°54′W	3	32.34 (26.94)	12.11 (6.03)	0.34	0.77

For instance, Blephariceridae and Dixidae typically are not collected in benthic samples, probably because their habitats frequently are not sampled. Blephariceridae occur in areas where water velocity can be too great to permit use of a Surber sampler, whereas Dixidae occur in depositional habitats or in the eroded margins of streams, areas that often are not integrated in traditional benthic samples (Merritt et al. 2008). Rhyacophilidae also comprised a greater proportion of the emergence-trap than benthic samples, despite the fact that their larvae do inhabit riffles. In this case, life-history characteristics provide
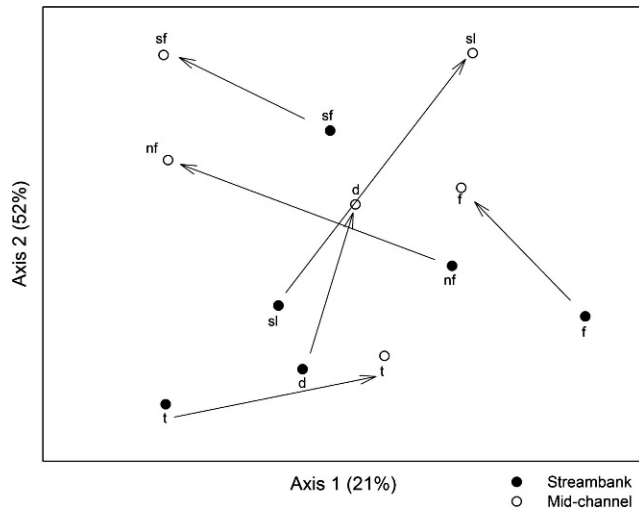

FIG. 3.   Nonmetric multidimensional scaling ordination plot of insect assemblages in samples collected from emergence traps in mid-channel or streambank sites in 6 streams (d = Darby, f = Fox, nf = North Fork Mahogany, sl = South Leigh, sf = South Fork Mahogany, t = Teton) in the Teton River Basin. Taxa were quantified on the basis of mean relative biomass in 5 mid-channel and 5 streambank traps deployed from June to August 2006. Numbers in parentheses are % of variation explained by each axis. Arrows connect streambank and mid-channel samples from the same stream.

a likely explanation for the differences. Rhyacophilidae emerge over the entire summer, thereby depleting the numbers present in the benthos. Differences between benthic and emergence-trap samples probably depend on the timing of the snapshot of the benthic sample compared to the duration and timing of the emergence-trap sample. Overall, the lower biomass of insects in emergence-trap than in benthic samples might reflect periods of emergence that were missed (i.e., traps were not deployed at the time) or because larval life stages are sometimes >1 y. Other differences between sample types were driven in part by taxa, such as Plecoptera, that tend to emerge along stream banks (Stewart and Stark 2002) and were underrepresented in samples from mid-channel emergence traps. Thus, a streambank emergence trap is required to sample this group accurately.

Based on our comparison, samples of the benthos and emergence provide different, but complementary, information. Rigorous, repeated sampling of the benthos can provide a nearly complete collection of taxa present in a stream reach (Hauer and Resh 2006). However, benthic samples often are collected during a single or several sampling events and capture a snapshot of the insects present during a brief sampling time frame. Moreover, they often are

TABLE 4.   Taxa correlated with axis 1 and axis 2 in the nonmetric multidimensional scaling ordination plot of insect assemblages for the Teton River Basin.

Axis 1	r	Axis 2	r
Hydropsychidae	−0.51	Baetidae	0.69
Psychodidae	0.54	Rhyacophilidae	0.68
Chironomidae	0.55	Simuliidae	0.64
Perlodidae	0.72	Chironomidae	0.57
		Glossosomatidae	0.52
		Hydropsychidae	0.52
		Perlodidae	−0.48
		Perlidae	−0.78

constrained to collections from riffle habitats conducive to use of standard tools like Surber and Hess samplers. Species that emerged just before a sampling event might be missed entirely by benthic sampling because individuals are absent from the sample, are at the egg stage, or are too small to be captured by the mesh of the sampler. On the other hand, emergence is often a pulsed event, and adequate sampling of emergent adults often requires collections across multiple time periods (Davies 1984).

We contend that emergence-trap samples are important supplements to benthic samples. For example, if the focus of a study were on cataloguing the insect diversity of a system, benthic samples certainly would be necessary. However, emergence-trap samples would be ideal complements to benthic samples because they include components of the assemblage that might otherwise be missed (e.g., taxa inhabiting faster water, pools, edge, or hyporheic habitats that might not be sampled with benthic techniques; Smock 2006). In contrast, if the focus of a study were on ecosystem fluxes, emergence traps might be an essential tool. Sampling emerging adults provides a measure of flux of aquatic insects over time that could be important to understanding linkages and resource subsidies between aquatic and terrestrial habitats. Emergence trapping also can provide a cumulative index of secondary production that reflects the entire insect life cycle (Statzner and Resh 1993, Benke and Huryn 2006). However, emergence is temporally variable, and benthic samples would provide complementary information that would help investigators determine the component of the assemblage captured in emergence and might offer mechanistic explanations for observed patterns.

Mid-channel vs streambed emergence traps

Mid-channel and streambank trap samples yielded similar measurements of adult insect flux but captured different components of the insect assemblage. Streambank traps collected greater proportions of Plecoptera, especially Perlidae and Perlodidae, whereas mid-channel traps collected more Ephemeroptera, Trichoptera, and Diptera. The strength of this pattern varied among streams, but the differences were consistent across all sites. The importance of including streambank traps in a study design might depend on the question of interest. Accurate estimates of flux might require trapping in both habitats, particularly if most or many taxa in the assemblage emerge from the stream bank. The proportion of larger Plecoptera in the aquatic insect assemblages in the Teton River Basin increased with stream size. Thus, streambank traps would be

important in larger streams, but might not be necessary in smaller streams, especially if only relative comparisons are to be made.

Considerations when designing emergence studies

Accurate sampling of adult insect emergence requires consideration of spatial variability and timing, frequency, and temporal extent of sampling. In our studies, among-stream variability of samples captured in emergence traps was greater than within-stream differences between benthic and emergence-trap samples, despite the fact that these streams were in close proximity and of similar size. We attribute this interstream variability to the relatively high temporal scope (extent and resolution) of the emergence-trap samples. Most studies of emergence are done over shorter sampling periods, despite expected large seasonal variation (Baxter et al. 2005). In studies designed to quantify emergence as an ecosystem flux, insect phenology must be considered so that peak emergence is not missed. Moreover, the number of days between collections of insects from the traps must be considered. In our studies, collections could not be made more often than every 4 to 5 d. The shorter the collection intervals, the less likely it is that undesirable events (i.e., mortality, ovipositing, or inclement weather) will occur that might negatively affect the samples or trap integrity (LeSage and Harrison 1979). In addition to collecting insects from traps often, sampling should be conducted over a long enough period to integrate variability in emergence. For example, if a study were conducted over a period of a few days, results might be obtained that are not representative, and spurious conclusions might be drawn. In such a case, the peak emergence of one taxon could drive a pattern (e.g., differences between sites) that might not be representative of the long-term pattern in total flux. The period encompassed by sampling should depend on the study question, e.g., whether an estimate of total emergence is required.

The number of traps deployed is another important consideration when measuring emergence. The larger the area studied, the more traps will be needed, especially as habitat becomes more heterogeneous. A power analysis should be done to determine the sample size necessary to detect differences in emergence of a particular magnitude in a given system. Studies on a number of small streams have detected patterns in emergence with sample sizes ranging from 2 to 6 emergence traps (Jackson and Fisher 1986, Baxter et al. 2005). Four to 5 traps were deployed in our studies so that if one became compromised

during the sampling period, samples would be available from a minimum of 3 traps. However, we studied small streams (2nd- to 4th order), and more traps might be necessary in larger systems.

All sampling methods, including emergence traps, are biased in some fashion. To our knowledge, the traps we used did not repel or attract emerging adults. Some investigators have suggested that larval Chironomidae might colonize the styrofoam floats of emergence traps (Wrubleski and Rosenberg 1984), and we observed larval Simuliidae on the floats of our traps in a few cases. One of the main differences between our emergence trap and earlier designs is that our traps do not have a collection jar. Collection jars are included in other designs to limit the loss of insects or to concentrate insects in a small area, facilitating removal (LeSage and Harrison 1979). We chose not to use a collection jar to keep the design of the trap simple, to make traps easy to repair in the field, and to avoid the use of chemicals (which is undesirable in wilderness settings). Furthermore, the presence of a collection jar can introduce bias because jars can attract certain taxa more than others (Davies 1984). In our traps, insects typically aggregated in the upper portion of the net and along the seams of the material. If desired, the design we described could be adapted to include a collecting jar or a catch, as was done in our Teton River Basin study, to improve accuracy of collection (in terms of total flux). However, even with these modifications, insects that quickly seek water for oviposition after emergence can be lost from the sample. Prior knowledge of the insect assemblage (e.g., the biology and behavior of the dominant or targeted organisms) would inform adaptation of traps and study designs to yield the most effective sampling of emergence.

Our results helped define the population of insects sampled with typical emergence-trap and benthic techniques and might inform inferences drawn in studies based on such methods. However, additional assessment of emergence measurement techniques is badly needed. For instance, formal analyses have not been made of the effects of varying temporal scope (extent and resolution) of sampling on estimates of emergence flux or composition. In addition, tools and techniques for measuring emergence have not been standardized, and numerous approaches are being used without assessment of their respective biases. We showed dissimilarities in populations sampled with emergence traps at different locations within the stream and dissimilarities in populations sampled via emergence traps and during one-time benthic sampling. The potential biases introduced by our trap design and others used in foodweb studies (e.g., Sabo

and Power 2002, Paetzold et al. 2005) should be evaluated. Additional techniques, such as sticky traps, deployed over and along streams are used frequently to provide indices of emergence (Power et al. 2004). Populations sampled by these techniques also should be compared to populations sampled by emergence traps. Such evaluations are necessary to improve rigor and accuracy in interpreting data obtained during studies of aquatic insect emergence.

Acknowledgements

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