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Effects of riparian arthropod predation on the biomass and abundance of aquatic insect emergence

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Abstract. Adult aquatic insects are important energy subsidies for terrestrial predators, but the effects of terrestrial predators on emerged aquatic insects have been widely neglected. We compared emergence of aquatic insects from predator-free exclosures and open cages to test the hypothesis that riparian arthropod predators can reduce the abundances of emerged aquatic insects. We used emergence traps over the aquatic and terrestrial sides of the shoreline to collect insects that emerged from the water or crawled onto land to emerge. The abundances and taxonomic composition of emerged aquatic insects and riparian arthropod predators changed seasonally. Riparian arthropods consumed 45% of emerged aquatic insect biomass from terrestrial traps in spring and 45% from aquatic traps in summer. The dominant riparian predator at the time of emergence determined the specific predation effect. Stoneflies that emerged into terrestrial traps were significantly reduced when ground beetles were the most abundant predators; caddisflies that emerged into aquatic traps were significantly reduced when spiders were the most abundant predators. Thus, taxon-specific predation by riparian arthropods can affect the taxonomic composition of emerged aquatic insects.

Key words: aquatic–terrestrial linkages, recipient control, subsidies, food web, allochthonous inputs, Plecoptera, Ephemeroptera, Trichoptera.

Movements of resources across habitat boundaries are common in most ecosystems, and allochthonous resources (i.e., resources from outside the focal habitat) can even exceed autochthonous ones (Polis et al. 1997, Webster and Meyer 1997). Empirical and theoretical studies have shown that allochthonous inputs of resources (nutrients, detritus, living organisms) can control populations and foodweb structure in recipient habitats (Polis et al. 1997, Wallace et al. 1997, Huxel and McCann 1998, Pace et al. 2004). Allochthonous inputs to one habitat are losses from another. Therefore, both the source and the recipient habitats can be affected when resources move across boundaries (Loreau et al. 2003). However, the effects of recipient predators on allochthonous prey have been neglected in most foodweb studies.

Emerged aquatic insects provide important subsidies for riparian predators such as spiders, ground beetles, lizards, birds, and bats along rivers (Power and Rainey 2000, Nakano and Murakami 2001, Sabo and Power 2002, Paetzold et al. 2005). Riparian predators can cause high mortality of emerged aquatic insects and, consequently, they have the potential to regulate population size in subsequent generations (Wernecke and Zwick 1992, Enders and Wagner 1996). However, the contribution of riparian predators to the mortality of emerged aquatic insects remains unclear because other factors such as abiotic stress and metabolic exhaustion from swarming (Jackson and Fisher 1986) also cause mortality.

We need to quantify the consumption of emerged and emerging aquatic insects by riparian predators to understand the contribution of riparian predation to mortality in populations of aquatic insects. For instance, Jackson and Fisher (1986) showed that only 3% of emerged aquatic insect biomass returned to the stream, possibly indicating a high loss by riparian predation. Quantitative knowledge of predation on emerged aquatic insects also could provide an estimate of the flux of aquatic secondary production to riparian food webs.

Emerging and emerged aquatic insects are at risk from ground and aerial predators depending on their emergence pathway, predator presence, and habitat complexity (Sweeney and Van-

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note 1982, Iwata et al. 2003). For example, taxon-specific foraging behaviors of riparian forest birds can influence the relative consumption of emerged aquatic insect taxa (Murakami and Nakano 2001). Ground-dwelling riparian arthropods can be subsidized substantially by emerging aquatic insects (Sanzone et al. 2003, Paetzold et al. 2005). As a consequence, populations of carnivorous ground-dwelling arthropods, especially carabid beetles and lycosid spiders, can reach high densities along gravel-bed rivers (Hering and Plachter 1997, Paetzold et al. 2005). We experimentally manipulated arthropod predation on emerging aquatic insects to test the hypothesis that recipient riparian arthropod predators control the abundance of aquatic insect emergence (allochthonous prey). We further tested whether predator-caused adult mortality of individual aquatic insect taxa was controlled by the foraging mode and abundances of riparian predator species at the time of aquatic insect emergence.

Methods

Study site

We conducted field experiments along a gravel bank in a braided section of the 7th-order Tagliamento River in northeastern Italy (lat 46°00′N, long 12°30′E). The wide gravel bank (≤60 m) was bordered by upslope riparian forest. The average width of the adjacent river channel was 20 m. Sediments along the river bank consisted predominantly of gravel and pebble (details in Ward et al. 1999, Tockner et al. 2003). The riparian arthropod fauna was dominated by carnivorous ground-dwelling wolf spiders (Lycosidae), ground beetles (Carabidae), rove beetles (Staphylinidae), and ants (Formicidae). Stable isotope studies showed that the Carabidae, Staphylinidae, and Lycosidae fed substantially on aquatic insects (Paetzold et al. 2005).

Experimental design

We placed pyramidal emergence traps (0.5 × 0.5 m bottom opening, 500-μm white mesh) along the stream edge in open cages and within riparian arthropod exclosures in a replicated block design (Fig. 1A). We positioned 4 experimental blocks, each consisting of an open cage and an exclosure, randomly along a 300-m segment of river bank. In each open cage and exclosure, we positioned a pair of emergence traps so that one trap was over the aquatic (depth = 1–10 cm) and one trap was over the terrestrial side of the shoreline (Fig. 1B). Thus, we sampled insects that emerged directly from the water and insects that crawled on land to emerge. We fixed emergence traps 2 to 3 cm above the ground and water surfaces to allow unimpeded movements of aquatic insects and terrestrial arthropods. We also installed 4 floating emergence traps in mid channel (Fig. 1A) to quantify shoreline emergence relative to overall aquatic insect emergence.

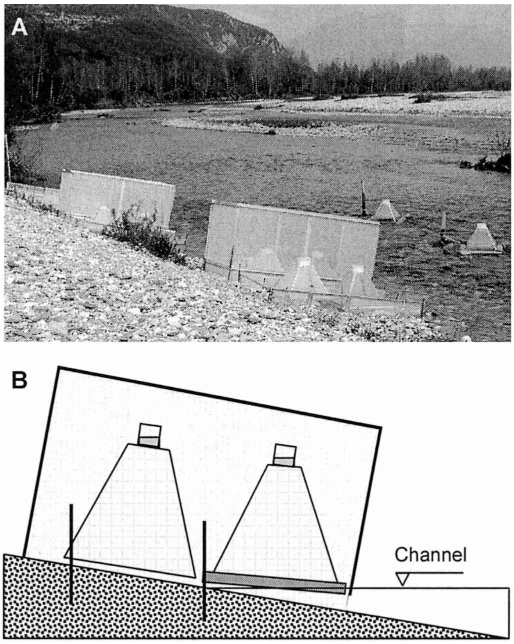

FIG. 1. A.—Emergence traps placed along the shoreline in exclosures and open cages. Two experimental blocks and 2 midchannel emergence traps are shown. B.—Diagram of an exclosure with a pair of emergence traps, one aquatic and one terrestrial, inside the exclosure.

In open cages, we installed mesh shields (2.0 × 0.25 m) perpendicular to the stream on both sides of each pair of emergence traps to control for possible cage effects (e.g., changes in water flow, lateral movements of aquatic insects). Mesh shields extended ∼1 m into the channel. In exclosures, we installed mesh-screen cages (2.0 × 1.0 × 1.2 m, 1-mm white mesh) along the river bank perpendicular to the channel to ex-

TABLE 1. Analysis of variance for abundance and biomass of aquatic insects in emergence traps. Main effects were season (April, June, and August) and habitat (midchannel, aquatic, and terrestrial traps). MS = error mean square.

		Biomass			Abundance		
Factor	df	MS	*F*	*p*	MS	*F*	*p*
Season	2	1.51	12.14	<0.001	2.23	9.48	<0.001
Habitat	2	2.92	23.42	<0.001	0.74	3.13	0.061
Season × habitat	4	0.68	5.43	0.003	0.24	1.02	0.416
Error	26	0.13			0.13		

clude riparian arthropods (Fig. 1B). Cages extended ~1 m into the channel with an opening (1.0 × 0.2 m) underneath the surface of the water to allow movements of aquatic insect larvae. We buried the bottom edges of the cages ~20 cm into the substrate. Inside each cage, we installed a pair of emergence traps. Before installing the emergence traps, we removed all visible riparian arthropods from the exclosures. We also removed all loose stones and poured water on the ground inside each cage to bring hidden terrestrial arthropods to the surface for removal. Additional sampling of riparian arthropods after each sampling interval showed that the cages excluded riparian arthropods efficiently (>90% exclusion).

We sampled emergence continuously over 12-d periods in April, June, and August 2002. We sampled bimonthly because shifts in the taxonomic composition of riparian arthropod taxa were expected in these intervals (see Paetzold et al. 2005). We identified emerged insects to family and counted them. We classified all specimens to morphospecies (sensu Derraik et al. 2002) to estimate total biomass. We dried (60°C) and weighed 10 randomly selected individuals of each morphospecies to determine mean individual dry mass.

Riparian arthropod sampling

Concurrent with emergence experiments, we collected riparian arthropods within 1-m^2 quadrats, randomly placed along the shoreline of our study section ($n = 9$/season). We sampled arthropods from sediments using aspirators and forceps. We removed all loose stones, gravel, and debris from each sampling plot to a depth of 10 to 20 cm during each collection. We identified arthropods to genus or species. We classified the dominant lycosid spiders (*Pardosa wagleri* and *Arctosa cinerea*) as juveniles or adults on the basis of body size and the development of copulatory organs. Juvenile *P. wagleri* were <4 mm, and juvenile *A. cinerea* were <10 mm body length. We dried and weighed at least 10 individuals of each taxon and size class to determine mean individual dry mass.

Data analysis

We tested seasonal (April, June, and August) differences in the biomass and abundance of emerged aquatic insects in the different habitats (midchannel, terrestrial shore, and aquatic shore) with factorial analysis of variance (ANOVA). We tested seasonal differences in the abundance and biomass of riparian arthropods with 1-way ANOVA. We adjusted significance levels of post hoc Student's *t*-tests for differences among means with Bonferroni corrections. We tested predation effects of riparian arthropods on aquatic insect emergence for each season separately (1-sided paired Student's *t*-tests, paired by experimental blocks) because aquatic insect emergence and the taxonomic composition of riparian arthropods showed seasonal differences. We used SYSTAT 10.0 (SPSS, Chicago, Illinois) for all analyses, and we ln(x+1)-transformed data to standardize variances and improve normality.

Results

The biomass of emerged aquatic insects differed significantly by season and habitat, and the interaction term was significant (Table 1, Fig. 2A). The biomass of insects that emerged into aquatic traps was highest in August and higher in April than in June ($p < 0.01$). The biomass of insects that emerged into terrestrial traps was higher in April than in June and August ($p <$

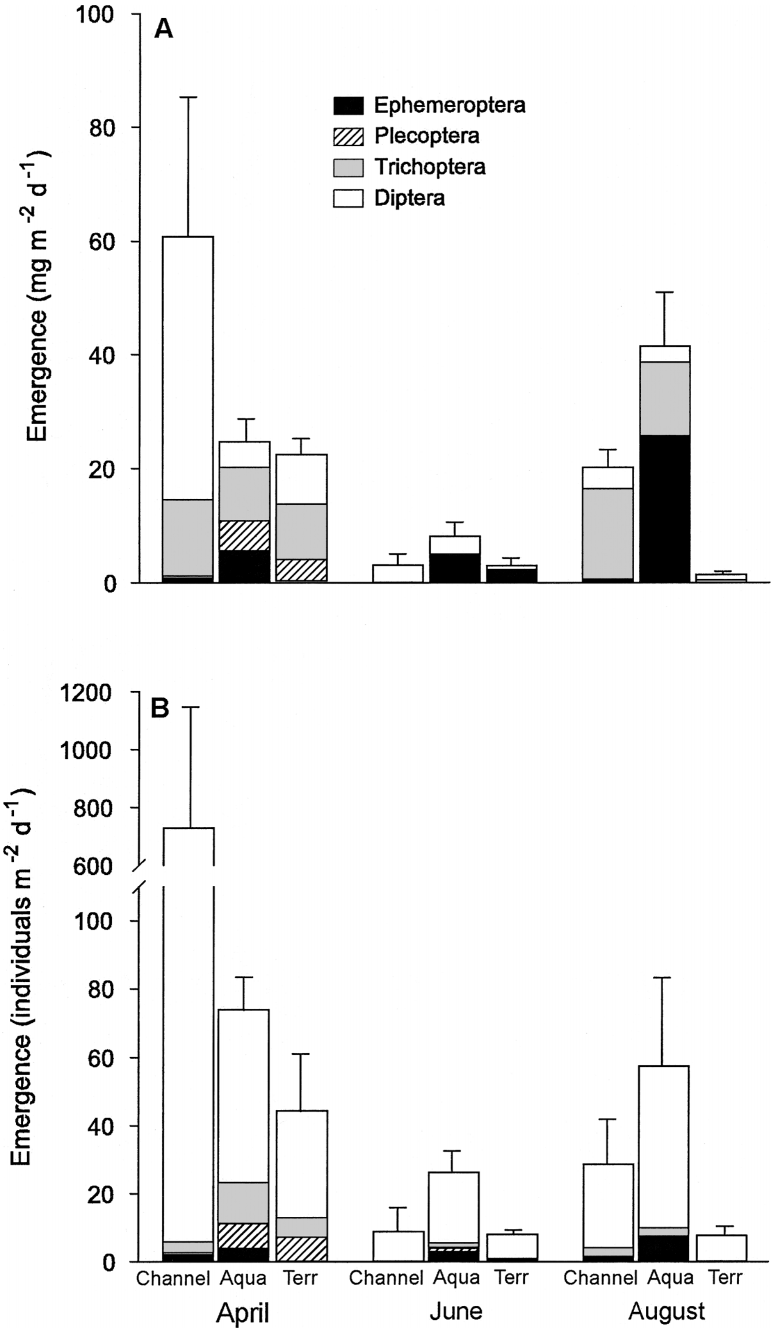

FIG. 2. Mean (+1 SE) biomass (A) and abundance (B) of aquatic insects that emerged into the midchannel emergence traps (Channel), aquatic traps in exclosures (Aqua), and terrestrial traps in exclosures (Terr). $n = 4$ for each bar.

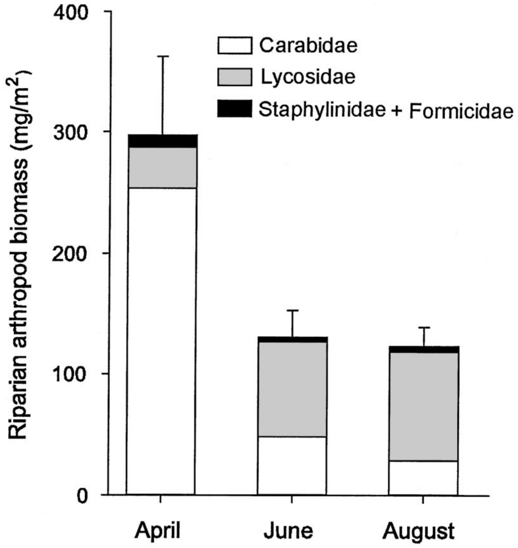

FIG. 3. Mean (+1 SE) biomass of riparian arthropods collected from quadrats along the shoreline. n = 9 for each bar.

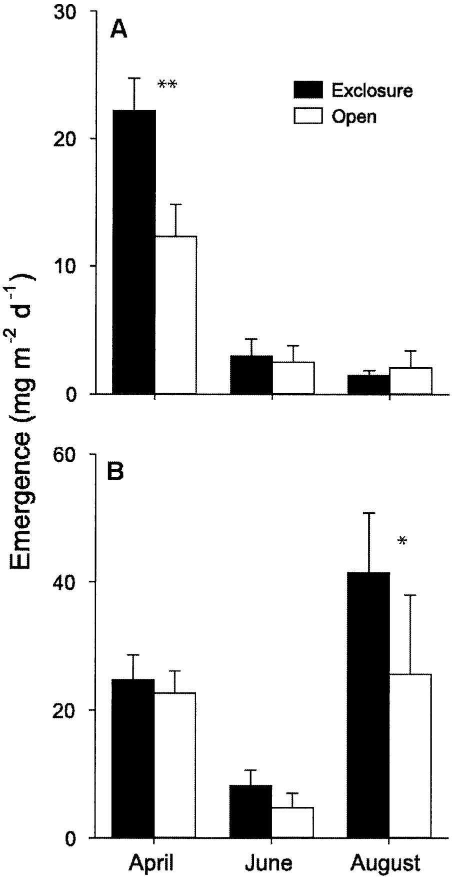

FIG. 4. Mean (+1 SE) biomass of aquatic insects that emerged into terrestrial (A) and aquatic (B) emergence traps with (Open) and without (Exclosure) predation by riparian arthropods. n = 4 for each bar. Asterisks indicate significant differences between bars within months: * = $p < 0.05$, ** = $p < 0.01$.

0.01). The abundance of emerged insects differed significantly by season but not by habitat, and the interaction term was not significant (Table 1, Fig. 2B). Emerged insects consisted mostly of Diptera (predominantly Chironomidae and Empididae) at all sites during all seasons, but the taxonomic composition changed seasonally (Fig. 2A, B). In April, Plecoptera (Chloroperlidae) emerged only from aquatic (58%) and terrestrial (42%) traps near the shoreline.

The riparian arthropod assemblage changed seasonally. The biomass of Carabidae was significantly higher in April than in June and August ($F_{2,24}$ = 8.68, $p < 0.001$; Fig. 3). The abundance of Carabidae was higher in April (17.3 individuals/m^2) than June and August (2.3 and 4.6 individuals/m^2, respectively; $F_{2,24}$ = 11.99, $p < 0.010$). Carabidae made up 85% of the riparian arthropod biomass in April, and one species, *Nebria picicornis*, accounted for 69% of the total biomass. Carabidae made up 68% of the riparian arthropod abundance in April, and one genus, *Bembidion* spp., accounted for 50% of the total abundance. The biomass of Lycosidae was significantly higher in June and August than in April ($F_{2,24}$ = 7.46, $p < 0.020$; Fig. 3). The abundance of Lycosidae was significantly higher in June and August (12.8 and 12.3 individuals/m^2, respectively) than in April (3.8 individuals/m^2; $F_{2,24}$ = 14.31, $p < 0.001$). Lycosidae made up 60% and 74% of the biomass and 76% and 55% of the abundance of the riparian arthropod assemblage in June and August, respectively. The biomass and abundance of Lycosidae were made up mostly of *Pardosa wagleri*, except in June when *Arctosa cinerea* made up 58% of the biomass. The proportion of juveniles contributing to the abundance of Lycosidae changed from 78% in June to 22% in August.

In terrestrial traps in April, the total biomass of emerged aquatic insects was 45% lower (t = 4.86, df = 3, p = 0.009; Fig. 4A) and the biomass and abundance of Plecoptera were 75% lower (biomass: t = 4.97, df = 3, p = 0.008; abundance:

$t = 5.82$, df = 3, $p = 0.005$) in open cages than in exclosures. In June, no significant differences between open cages and exclosures were observed for either terrestrial or aquatic traps (Fig. 4A, B). In aquatic traps in August, the total biomass of emerged aquatic insects was 45% lower ($t = 3.05$, df = 3, $p = 0.022$; Fig. 4B) and the biomass and abundance of Trichoptera were 81% and 75%, respectively, lower (biomass: $t = 2.88$, df = 3, $p = 0.032$; abundance: $t = 2.56$, df = 3, $p = 0.042$) in open cages than in exclosures.

Discussion

Riparian predators and aquatic insect population dynamics

Predation by ground-dwelling arthropods can significantly affect aquatic insect emergence. Emerging aquatic insects are an important food source for ground-dwelling spiders and beetles (Hering and Plachter 1997, Collier et al. 2002, Sanzone et al. 2003). Ground-dwelling predators appear to be particularly important along braided rivers where they reach high densities and feed mostly on aquatic insects (Paetzold et al. 2005). Shoreline length is extensive in braided rivers (up to 17 km/river km in our system; van der Nat et al. 2002), suggesting that the overall predation effect by riparian arthropods may be substantial in such habitats.

Predation by ground-dwelling arthropods affects emerging aquatic insects before they reach the aerial reproductive stage. Moreover, terrestrial oviposition along the stream bank is known for some Trichoptera (Enders and Wagner 1996), so additional predation on aerial reproductive individuals returning to the ground for resting or oviposition can be expected. Thus, these predators may have a major impact on the reproductive success of aquatic insects, and they have the potential to affect population dynamics of aquatic insects because mortality during the terrestrial stage can be important for population regulation (Zwick 1990, Wernecke and Zwick 1992).

However, the importance of adult mortality to aquatic insect population dynamics is controversial. A few females may be sufficient to repopulate a stream because most aquatic insects have high fecundity and larvae show density dependent effects (Wilzbach and Cummins 1989, Anholt 1995, Schmidt et al. 1995). *Baetis* mayfly populations appear to be controlled by processes operating at the larval stage rather than by the supply of recruits (Peckarsky et al. 2000). On the other hand, the quantitative importance of emerged aquatic insects in streams is implied by the colonization cycle in which oviposition by emerged adults compensates for downstream drift of larval stages (Müller 1982). Quantitative compensation of larval losses by emerged adults has been found for *Baetis* mayflies in an artic river (Hershey et al. 1993), but further research is needed to understand whether the mortality of emerged insects affects subsequent generations.

Top-down control of in situ prey by subsidized predators has been demonstrated in empirical studies, but control of allochthonous prey generally is assumed to occur in the donor habitat (Polis and Hurd 1996, Polis et al. 1997, Murakami and Nakano 2002). For instance, emerged aquatic insects (allochthonous prey) can support high riparian bird densities (subsidized predators), and high riparian bird densities, in turn, can depress terrestrial insect populations (in situ prey) (Murakami and Nakano 2002). Our results suggest that riparian arthropods (subsidized predators) also may affect aquatic insect populations (allochthonous prey) by feeding on emerged aquatic insects before they can reproduce.

Taxon-specific predator effects

Distinct seasonal changes in the relative abundances of different riparian arthropod taxa allowed us to evaluate taxon-specific predator effects on aquatic insect emergence. In April, Carabidae, particularly *N. picicornis*, which emerged from spring to early summer (Manderbach and Plachter 1997), were the dominant predators. Significant reductions of emerged aquatic insects occurred only in terrestrial traps in open cages where predation by riparian arthropods, predominantly *N. picicornis*, reduced Plecoptera emergence by 75%, on average (abundance and biomass). Plecoptera represented the greatest proportion of recognizable prey items in the guts of *N. picicornis* along the gravel banks of the Isar River, Germany (Hering and Plachter 1997). Carabidae apparently feed predominantly on emerging insects along the terrestrial shoreline habitat, and Plecoptera are particularly prone to predation by Carabidae because many Plecoptera emerge on land (Collier and Scarsbrook 2000).

In August, the significant reduction of aquatic insects emerging into aquatic traps near the shoreline was probably a result of predation by adult lycosid spiders. Lycosidae are almost as mobile on water as on land (Foelix 1996). Predator effects were significant only for Trichoptera even though most of the biomass of emerged insects in aquatic traps was made up of Ephemeroptera. Ephemeroptera are less prone than Trichoptera to predation by ground-dwelling arthropods because Ephemeroptera make the transition from nymph to flying subimago rapidly, often within seconds, and they emerge mostly in daytime (Bauernfeind and Humpesch 2001). Riparian Carabidae and most Lycosidae are nocturnal and crepuscular (Foelix 1996, Sabo and Power 2002). The high proportion of Ephemeroptera among insects emerging along the shoreline in June may also explain the absence of predator effects during this month. Moreover, in June, a high proportion of Lycosidae were juveniles that probably could not kill large emerging insects.

Seasonal changes in abiotic conditions, such as temperature, also can control predator–prey interactions (Pennuto 2003), but no significant changes in temperature or discharge occurred between June and August in our study (AP, unpublished data). Our results indicated that the effects of predation on different insect taxa were controlled by the foraging mode of the dominant riparian predator at the time of emergence. Thus, taxon-specific predation by riparian arthropods can affect the taxonomic composition of emerged aquatic insects. Riparian birds also have taxon-specific foraging behaviors when feeding on emerged aquatic insects (Murakami and Nakano 2001). Therefore, additional bird-specific predation effects on emerged aquatic insects can be expected in riparian habitats.

In conclusion, terrestrial predators can significantly affect the adult mortality of aquatic insects. The predator community at the time of emergence determines which aquatic insect taxa are affected. Therefore, riparian predators can affect the taxonomic composition of emerged aquatic insects and should be integrated into our understanding of aquatic insect population dynamics.

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