

Running head: Arthropod predation on aquatic insects

**Riparian arthropod predation affects biomass and abundance of aquatic  
insect emergence**

Achim Paetzold and Klement Tockner

Department of Limnology, EAWAG/ETH, Switzerland

Correspondence:

Achim Paetzold

Department of Limnology, EAWAG/ETH

Überlandstrasse 133, P.O. Box 611

CH-8600 Dübendorf

e-mail: [achim.paetzold@eawag.ch](mailto:achim.paetzold@eawag.ch)

Klement Tockner

e-mail: [klement.tockner@eawag.ch](mailto:klement.tockner@eawag.ch)

## **Abstract**

Although the importance of emerged aquatic insects as energetic subsidies for terrestrial predators has been demonstrated, effects of terrestrial predators on emerging aquatic insects have been widely neglected. We tested the hypothesis that riparian arthropod predators can reduce populations of emerging aquatic insects by comparing emergence from predator-free exclosures and open cages. We placed emergence traps over the aquatic and terrestrial side of the shoreline to collect aquatic emergers as well as aquatic insects that crawl on land to emerge. Emergence of different insect orders and the riparian arthropod assemblage changed seasonally. Riparian arthropods consumed 45% of emerging aquatic insect biomass from terrestrial plots in spring and 45% from aquatic plots in summer. The dominant riparian predator at the time of emergence determined the predation effect. Stoneflies emerging from terrestrial plots were significantly reduced when ground beetles dominated; caddisflies emerging from aquatic plots were reduced when spiders dominated. Thus, taxon-specific predation by riparian arthropods can affect the community composition of emerging aquatic insects.

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

## Introduction

Movements of resources across habitat boundaries are common in most ecosystems, and allochthonous sources (i.e. sources 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 food web structure in recipient habitats (Polis et al. 1997, Wallace et al. 1997, Huxel and McCann 1998, Pace et al. 2004). Allochthonous inputs in one habitat are losses in another and, therefore, the source and the recipient habitat can be affected (Loreau et al. 2003). However, effects of recipient predators (i.e. predators feeding on allochthonous prey) on allochthonous prey have been neglected in most food web studies.

Along rivers, emerged aquatic insects provide important subsidies for riparian predators such as spiders, ground beetles, lizards, birds, and bats (Power and Rainey 2000, Nakano and Murakami 2001, Sabo and Power 2002, Paetzold et al. in press). Riparian predators together with environmental stress can cause high mortality of emerged aquatic insects and, consequently, have the potential to regulate population size in subsequent generations (Wernecke and Zwick 1992, Enders and Wagner 1996). The relation of aquatic insect emergence to deposition of emerged insects on the water surface provides a good estimate of adult biomass that returns to the aquatic environment (Stagliano et al. 1998). 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. However, the contribution of riparian predators to the mortality of aquatic insects remains unclear because other factors, such as abiotic stress and metabolic exhaustion from swarming (Jackson and Fisher 1986), also cause mortality of emerged aquatic insects. To understand the contribution of riparian predation to the mortality of emerging aquatic insects, we need to quantify the consumption of emerging aquatic insects by riparian predators. Quantitative knowledge of predation on emerged aquatic insects also provides an estimate of the flux of aquatic secondary production to riparian food webs.

Emerging aquatic insects are prone to ground and aerial predation depending on their emergence pathway, predator presence, and habitat complexity (Sweeney and Vannote 1982, Iwata et al. 2003). Taxon-specific foraging behaviors of riparian forest birds can influence the relative

consumption of aquatic insect emergence (Murakami and Nakano 2001). Ground-dwelling riparian arthropods also can be substantially subsidized by emerging aquatic insects (Sanzone et al. 2003, Paetzold et al. in press). As a consequence, populations of carnivorous ground-dwelling arthropods, carabid beetles and lycosid spiders in particular, can achieve high densities along gravel-bed rivers (Hering and Plachter 1997, Paetzold et al. in press). To test the hypothesis that recipient riparian arthropod predators control the amount of aquatic insect emergence (allochthonous prey), we experimentally manipulated arthropod predation on emerging aquatic insects. We further tested whether the predator-caused adult mortality of individual aquatic insect taxa is controlled by the foraging mode of the riparian predator species and its abundance at the time of emergence.

## **Methods**

### Study site

Field experiments were conducted along a gravel bank in a braided section of the 7<sup>th</sup>-order Tagliamento River, NE-Italy (46° N, 12°30' E). The wide gravel bank ( $\leq 60$  m) was bordered by upslope riparian forest. The adjacent river channel had an average width of 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. in press).

### Experimental design

Pyramidal emergence traps for aquatic insects ( $0.5 \times 0.5$  m, white mesh: 500  $\mu\text{m}$ ) were placed along the stream edge in open plots and within riparian arthropod exclosures in a replicated block design (Fig. 1a). Four experimental blocks, each consisting of an open plot treatment and an exclosure, were positioned randomly along a 300-m riverbank segment. Emergence was sampled continuously over 12-day periods in April, June and August 2002. Sampling was conducted bi-monthly because shifts in the dominance of riparian arthropod taxa were expected in these intervals (see Paetzold et al. in press).

Mesh-screen cages ( $2.0 \times 1.0 \times 1.2$  m, white mesh: 1 mm,  $N = 4$  per season) were installed along the riverbank perpendicular to the channel to exclude riparian arthropods (Fig. 1b). Cages extended about 1 m into the channel with an opening ( $1.0 \times 0.2$  m) underneath the water surface to allow movements of aquatic insect larvae. Cages were buried about 20 cm deep into the substrate. Inside each cage we installed a pair of emergence traps: one trap over the aquatic (depths: 1-10 cm) and one trap over the terrestrial side of the shoreline to include aquatic insects that crawl on land to emerge (Fig. 1b). Emergence traps were fixed 2-3 cm above the ground and water surface, respectively, to allow unimpeded movements of aquatic insects and terrestrial arthropods. Prior to the installation of emergence traps, we removed all riparian arthropods from the enclosures. We removed all loose stones and poured water on the ground inside each cage to bring hidden terrestrial arthropods to the surface. Additional sampling of riparian arthropods after each sampling interval showed that the cages efficiently excluded riparian arthropods ( $> 90\%$  exclusion).

In open plots ( $N = 4$  per season), mesh shields ( $2.0 \times 0.25$  m) perpendicular to the stream were installed on both sides of each emergence trap pair. Mesh shields extended about 1 m into the channel to control for possible cage effects (e.g., changes in water flow, lateral movements of aquatic insects). In all seasons, we installed 4 floating emergence traps in the mid-channel to quantify the amount of emergence near the shoreline relative to the overall aquatic insect emergence (Fig. 1a).

Emerging insects were identified to family and counted. All specimens were classified as “morphospecies” (*sensu* Derraik et al. 2002) to estimate total biomass. Ten individuals of each “morphospecies”, randomly selected, were dried ( $60^{\circ}\text{C}$ ) and weighed to determine average individual dry mass.

### Riparian arthropod sampling

Concurrently with emergence experiments, we collected riparian arthropods within  $1 \text{ m}^2$  quadrats, randomly placed along the shoreline of our study section ( $N = 9$  per season). Arthropods were sampled from sediments using aspirators and forceps. During collection, all loose stones, gravel and debris were removed from each sampling plot up to a depth of 10-20 cm. Collected arthropods were identified to genus or species. The dominant lycosid spiders (*Pardosa wagleri* and *Arctosa cinerea*)

were classified as juveniles (*P. wagleri* < 4 mm, *A. cinerea* < 10 mm body length) or adults by size and development of copulatory organs. At least 10 individuals of each taxon and size class were dried and weighed to determine average individual dry mass.

### Data analysis

Seasonal differences in the biomass and abundance of emerging aquatic insects in the different habitats (mid-channel, terrestrial shore, and aquatic shore) were tested with factorial ANOVA.

Seasonal differences in the abundance and biomass of riparian arthropods were tested with one-way ANOVA. Significance levels of post hoc tests were adjusted to Bonferroni corrections. We tested predation effects of riparian arthropods on aquatic insect emergence for each season separately (one-sided paired Student's t-tests, paired by experimental blocks) since aquatic insect emergence and the taxonomic composition of riparian arthropods exhibited seasonal differences. Tests were performed in SYSTAT 10.0 (SPSS 2000) with  $(\ln+1)$  transformed data to standardize variances and improve normality.

## **Results**

The biomass of emerging aquatic insects from the different habitats differed with season (Fig. 2, Table 1). Biomass of insect emergence from the aquatic plots was highest in August followed by April. Biomass of emerging insects from terrestrial plots was significantly higher in April than in June and August ( $P < 0.01$ ). Abundance of emerging insects significantly differed by season (Fig. 2, Table 1). Abundance was dominated by Diptera, predominantly Chironomidae and Empididae, at all sites during all seasons. The composition of aquatic insect emergence also changed seasonally (Fig. 2). Plecoptera (Chloroperlidae) emerged only from aquatic (58%) and terrestrial plots near the shoreline (42%) in April.

The riparian arthropod assemblage changed seasonally (Fig. 3). Biomass and abundance of Carabidae were significantly higher in April, 17.3 individuals / m<sup>2</sup>, than June and August, 2.3 and 4.6 individuals / m<sup>2</sup>, respectively (biomass:  $F_{(2, 24)} = 8.68$ ,  $P < 0.001$ , abundance:  $F_{(2, 24)} = 11.99$ ,  $P < 0.010$ ). Carabidae comprised 85% (*Nebria picicornis* = 69%) of biomass and 68% (*Bembidion* spp. = 50%) of

abundance of the riparian arthropod assemblage in April. Biomass and abundance of Lycosidae were significantly higher in June and August, 12.8 and 12.3 individuals / m<sup>2</sup>, respectively, than in April, 3.8 individuals / m<sup>2</sup> (biomass:  $F_{(2, 24)} = 7.46$ ,  $P < 0.020$ , abundance:  $F_{(2, 24)} = 14.31$ ,  $P < 0.001$ ). Lycosidae made up 60% and 74% of biomass and 76% and 55% of abundance of the riparian arthropod assemblage in June and August, respectively. The biomass and abundance of Lycosidae was dominated by Pardosa wagleri except in June when Arctosa cinerea comprised 58% of biomass. The relative proportion of juveniles in the abundance of Lycosidae changed from 78% in June to 22% in August.

Riparian arthropod predation significantly reduced the biomass of aquatic insect emergence in terrestrial plots by 45% in April ( $t = 4.86$ ,  $df = 3$ ,  $P = 0.009$ , Fig. 4) and in aquatic plots by 45% in August ( $t = 3.05$ ,  $df = 3$ ,  $P = 0.022$ ). Biomass and abundance of emerging Plecoptera was significantly reduced by 75% on terrestrial plots in April (biomass:  $t = 4.97$ ,  $df = 3$ ,  $P = 0.008$ , abundance:  $t = 5.82$ ,  $df = 3$ ,  $P = 0.005$ ). Biomass and abundance of emerging Trichoptera was significantly reduced by 81% and 75%, respectively, on aquatic plots in August (biomass:  $t = 2.88$ ,  $df = 3$ ,  $P = 0.032$ , abundance:  $t = 2.56$ ,  $df = 3$ ,  $P = 0.042$ ).

## Discussion

Predation by ground-dwelling arthropods can significantly affect aquatic insect emergence. The importance of aquatic insect emergence as a food source for ground-dwelling arthropods has been demonstrated for spiders and ground beetles (Hering and Plachter 1997, Collier et al. 2002, Sanzone et al. 2003). Ground predators appear to be particularly important along braided rivers, where ground-dwelling arthropods reach high densities and feed substantially on aquatic insects (Paetzold et al. in press). The extensive shoreline length in braided rivers, up to 17 km per river km in our system (van der Nat et al. 2002), suggests that the overall predation effect by riparian arthropods can be substantial. Ground-dwelling arthropod predation affects emerging aquatic insects before they reach the aerial reproductive stage, thus potentially having a major impact on reproductive success. Additional predation by ground-dwelling arthropods can be expected during aerial stages on individuals returning to the ground for resting or oviposition. Terrestrial oviposition along the stream bank is known for

some Trichoptera (Enders and Wagner 1996). Thus, riparian predators have the potential to affect population dynamics of aquatic insects, since mortality during the terrestrial stage can be decisive for population regulation (Zwick 1990, Wernecke and Zwick 1992). For instance, estimated mortality rates for the trichopteran Apatania fimbriata were 8% during egg development, 11% during the larval stage and 80% during the adult stage in a first order stream, Breitenbach, Germany (Enders and Wagner 1996).

Studies on the role of adult mortality on aquatic insect population dynamics are controversial. A few females might be sufficient to repopulate a stream because of high fecundity in most aquatic insects and 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). The colonization cycle implies the quantitative importance of emerged aquatic insects to compensate population losses via downstream drift of larval stages (Müller 1982). Quantitative population compensation of larval losses by emerged aquatic insects have been found for *Baetis* mayflies in an arctic river (Hershey et al. 1993). Further research on the role of the terrestrial adult stage in aquatic insect population dynamics is needed to understand whether the mortality of emerged insects affects subsequent generations.

Empirical studies have demonstrated top down control of subsidized predators on *in situ* prey (Polis and Hurd 1996, Polis et al. 1997, Murakami and Nakano 2002). For instance, aquatic insect emergence can support high riparian bird densities which in turn can depress terrestrial insect populations (Murakami and Nakano 2002). Our results suggest that recipient riparian predators can potentially affect aquatic insect populations (allochthonous prey) by feeding on emerging aquatic insects.

Distinct seasonal changes in the relative dominance of different riparian arthropod taxa allowed us to compare taxon-specific predator effects on aquatic insect emergence. In April when Carabidae, particularly N. picicornis, were the dominant predators, significant reductions of emerging aquatic insects only occurred in terrestrial plots. Carabidae apparently feed predominantly on emerging insects along the terrestrial shoreline habitat. The dominance of N. picicornis in spring relates to its life cycle; it emerges from spring to early summer (Manderbach and Plachter 1997).

Predation by riparian arthropods, predominantly N. picicornis, reduced on average 32% (abundance and biomass) of the Plecoptera emergence in April. Plecoptera are particularly prone to predation by Carabidae because many Plecoptera emerge on land (Collier and Scarsbrook 2000). Plecoptera represented the greatest proportion of recognizable prey items in the guts of Nebria picicornis along the gravel banks of the Isar River, Germany (Hering and Plachter 1997).

The significant reduction of aquatic insects emerging from aquatic plots near the shoreline in August was probably a result of lycosid spider predation because Lycosidae are almost as mobile on water as on land (Foelix 1996). Predator effects were significant only for Trichoptera even though Ephemeroptera dominated the biomass of emergence from aquatic plots in August. Ephemeroptera are less prone to predation by ground-dwelling arthropods because of their rapid development, often within seconds, from the nymph to the flying subimago and their predominant emergence in daytime (Bauernfeind and Humpesch 2001). Riparian Carabidae and most Lycosidae are nocturnal and crepuscular (Foelix 1996, Sabo and Power 2002). The dominance of emerging Ephemeroptera along the shoreline in June also explains the overall low predation rate during this month. Further, a high proportion of Lycosidae in June were juveniles, which probably could not kill large-sized emerging insects. Seasonal changes in abiotic conditions, such as temperature, can also control predator-prey interactions (Pennuto 2003), but no significant changes in temperature or discharge occurred between June and August in our study (A. Paetzold, unpublished data). Our results show that predation effects on individual aquatic 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 community composition of emerging aquatic insects. Different foraging behaviors also occur by riparian birds that feed on aquatic insects (Murakami and Nakano 2001). Therefore, additional 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 predominantly affected. Therefore, riparian predators can affect the community composition of emerging aquatic insects and need to be integrated in the understanding of aquatic insect population dynamics.

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Table 1 ANOVA results for abundance and biomass of aquatic insect emergence with season (date) and habitat (mid-channel, aquatic plots, and terrestrial plots) as main effects.

Factor	df	MS	F	P	MS	F	P
		abundance			biomass		
Season	2	2.23	9.48	<0.001	1.51	12.14	<0.001
Habitat	2	0.74	3.13	0.061	2.92	23.42	<0.001
Season × Habitat	4	0.24	1.02	0.416	0.68	5.43	0.003
Error	26	0.13			0.13		

## Figure legends

Figure 1 A) Experimental design: emergence traps were placed along the shoreline in exclosures and open traps to quantify the predation by riparian arthropods using pair-wise comparisons (2 experimental blocks are shown). B) Diagram of exclosure with a mesh-screen cage used to exclude riparian arthropods from aquatic insect emergence traps.

Figure 2 Seasonal changes in average biomass (upper panel) and abundance (lower panel) of emerged aquatic insect orders (without predation) from the mid-channel (Channel, N = 4 per season), aquatic exclosures (Aqua., N = 4 per season) and terrestrial exclosures (Terr., N = 4 per season). Error bars show standard errors of total biomass and abundance.

Figure 3 Seasonal changes in the average biomass ( $\pm$  SE) of riparian arthropod families along the shoreline (N = 9 per season).

Figure 4 Biomass of emerged aquatic insects (mean  $\pm$  SE) in terrestrial (a) and aquatic shoreline plots (b) with (Open) and without (Exclosure) predation by riparian arthropods in April, June, and August 2002 (N = 4 per season, habitat, and treatment). Stars indicate significant differences between emergence in open traps and exclosures (one-sided Student's t-tests paired by experimental block).

\*\* = P < 0.01, \* = P < 0.05.

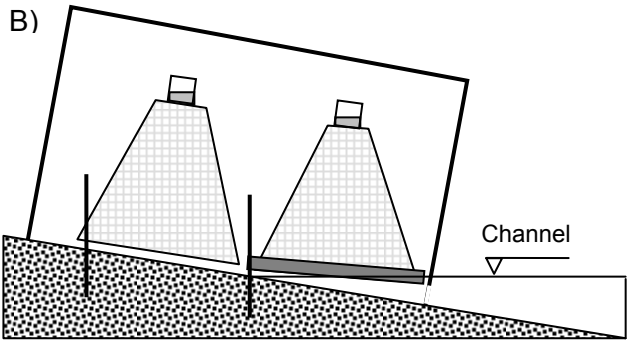


Fig. 1

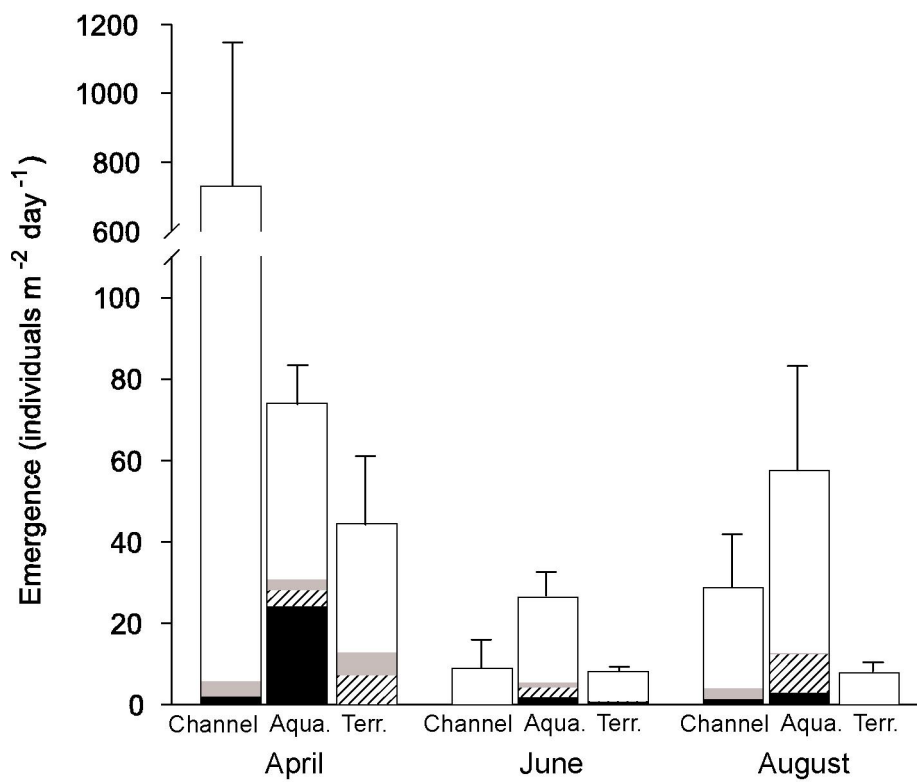
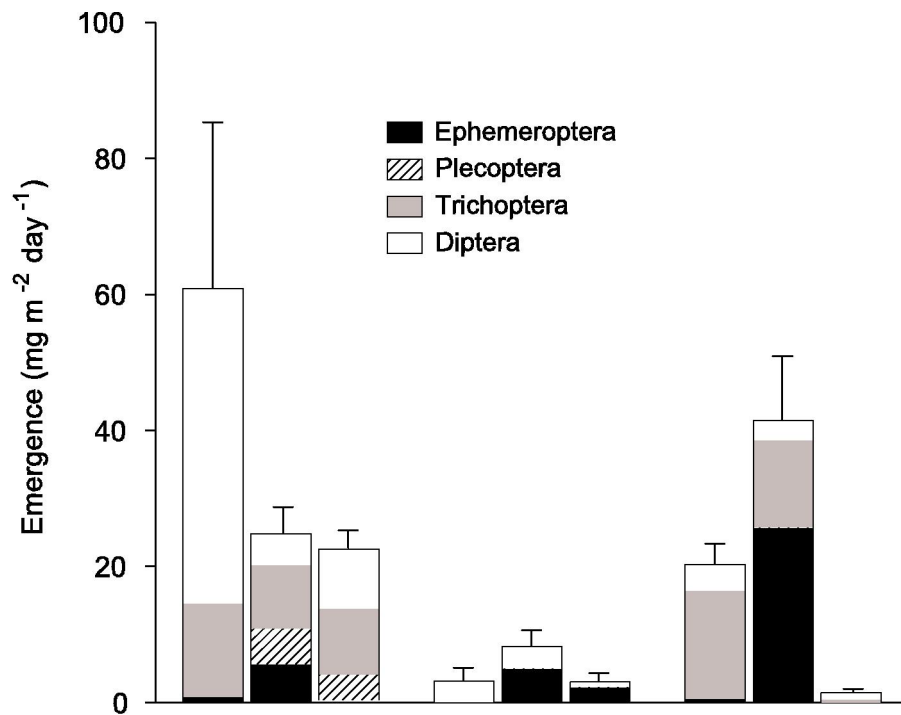


Fig. 2

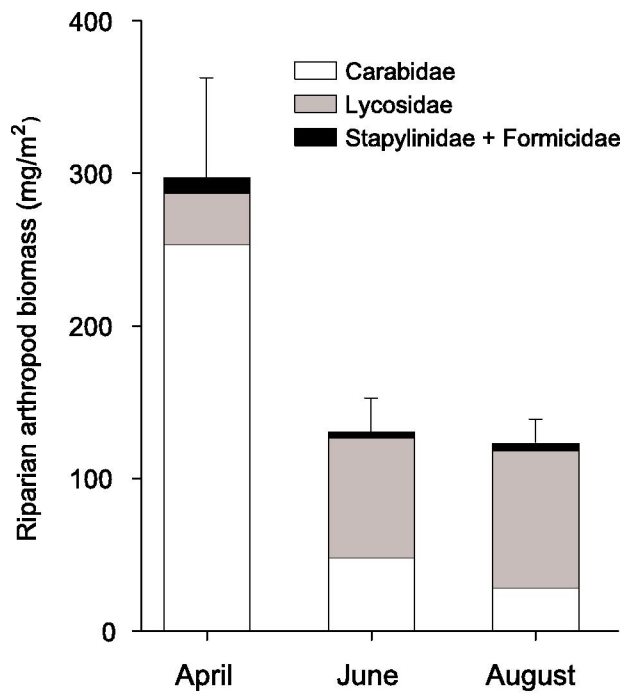


Fig. 3

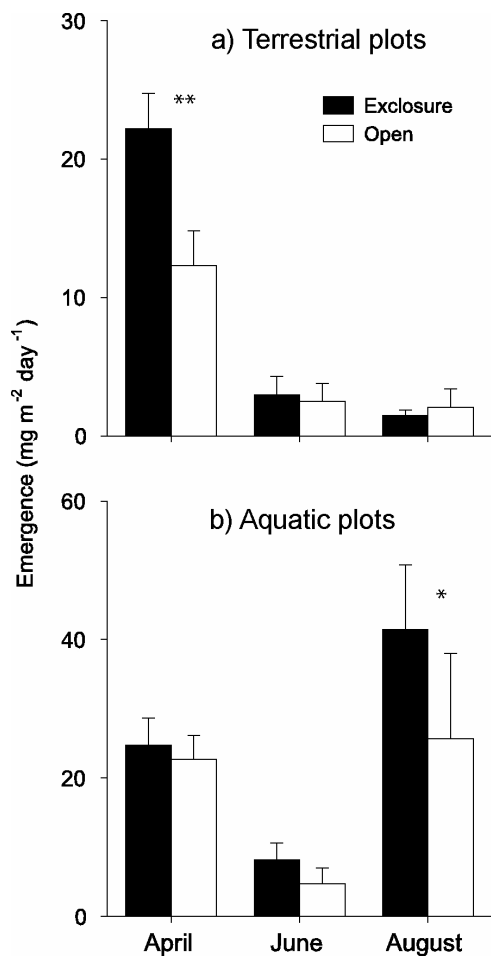


Fig.4