Limnologica 54 (2015) 44–57

Contents lists available at ScienceDirect

Limnologica

journal homepage: www.elsevier.com/locate/limno

Environmental drivers of biotic traits and phenology patterns of Diptera assemblages in karst springs: The role of canopy uncovered

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ARTICLE INFO

Article history:
Received 24 June 2015
Received in revised form 2 September 2015
Accepted 2 September 2015
Available online 9 September 2015

Keywords:
Chironomidae
Illuminance
Particulate organic matter
Similarity
Water velocity

ABSTRACT

Springs are stable environments with constant abiotic factors and therefore of use in variety of ecological experiments. We investigated the influence of canopy coverage on abundance, diversity, phenology and feeding guilds among Diptera assemblages at two rheocrene karst springs located near each other. The springs differed by canopy coverage while physicochemical characteristics of the water were similar. We set six emergence traps for one year at each spring covering all available microhabitats proportionally. We hypothesized that canopy coverage will have a strong effect on assemblage composition of Diptera as well as on diversity, abundance, phenology and feeding guilds composition between sites and that it will have a stronger effect than microhabitat characteristics. Similarity of species composition among springs was only 37.5%, with 23 common species/taxa out of 74 species/taxa. Abundance of Diptera was 8.5× higher at the open canopy spring, while diversity and number of species/taxa was higher at closed canopy spring. Emergence started earlier at open canopy site and was prolonged even in winter months. The majority of species were detritus feeders followed by collectors and there was no substantial difference among sites. We conclude that at springs with similar water characteristics, canopy coverage is the main driver of Diptera assemblage structure, with water velocity as a complementary factor. Substrate and other physicochemical factors seem less important.

1. Introduction

Groundwater-dominated springs are generally thermally stable lotic habitats compared to the majority of streams (Barquin and Death, 2004). Springs, especially coldwater rheocrenes, are natural laboratories well suited for examining environmental gradients because of the constancy of abiotic conditions which reduce the number of variables to be considered in field investigations (Glazier, 1991, 2009; Carroll and Thorp, 2014). Springs represent ideal locations to examine the relationships between faunal communities and the environmental parameters that influence their distribution as they usually contain a limited number of macroinvertebrate species of diverse origin, including a number of spring specialists (Danks and Williams, 1991; Smith et al., 2003). The level of scientific interest in springs has increased due to their sensitivity to environmental change (Cantonati et al., 2006). Their contribution to epigean systems represents as much as one third of the benthic species richness of freshwater biodiversity but their ecological importance has rarely been recognized (Danks and Williams, 1991). Springs have been designated as "hot spots" for aquatic biodiversity (Barquin and Death, 2006; Cantonati et al., 2006) and are home to great number of rare, relict and endemic species (Hynes, 1983; Smith et al., 2003). Springs and headwater streams are a source of biotic and abiotic inputs to downstream ecosystems (Haigh et al., 1998) and they export large amounts of biomass into terrestrial ecosystem via emergence of aquatic insects (Henschel et al., 2001; Nakano and Murakami, 2001; Progar and Moldenke, 2009).

Assemblage composition in the springs has been attributed to historical and geographical factors (Williams and Williams, 1998), water chemistry (Glazier, 1991), spring flow permanence (Erman and Erman, 1995; Smith and Wood, 2002; Smith et al., 2003), species life history traits (Williams, 1991) and general hydrogeology (Hoffsten and Malmqvist, 2000). Additional characteristics of karst springs that have effect on assemblage composition are highly fluctuating discharge rates and hard water (Mori and Brancelj, 2006). On some occasions the physical habitat, most notably substrate composition and the presence of aquatic vegetation, have been found to be the dominant controls of assemblage composition (Williams and Williams, 1998; Dumnicka et al., 2007). In others, it

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http://dx.doi.org/10.1016/j.limno.2015.09.001

has not been possible to relate any instream habitat characteristic to the faunal community structure (Lindegaard et al., 1998).

Surprisingly, until now few studies have considered light availability or canopy coverage as important factors in spring habitats, although they were already established as important factors for streams and rivers (Davies et al., 2005; Banks et al., 2007; Progar and Moldenke, 2009). Riparian vegetation surrounding streams controls light and temperature regimes, so it influences primary production and overall stream metabolism. It also provides allochthonous food supply for consumers and generally regulates aquatic ecosystem processes (Danks and Williams, 1991; Pollock, 1998; Kiffney et al., 2003; Death and Collier, 2010).

Algal and macrophyte abundance is positively related to the increased availability of light to the stream surface. Reduced canopy shading in streams increases algal biomass and macrophyte abundance (Danks and Williams, 1991; Davies et al., 2005). This ultimately leads to higher densities of benthic macroinvertebrates that feed on algae (grazers) e.g. especially of Dipteran family Chironomidae (Murphy et al., 1981; Fuller et al., 2008; Progar and Moldenke, 2009). In addition, even though macroinvertebrates rarely feed on the macrophytes they are important as a mechanism for detritus accumulation and biofilm growth so it can be expected that more detritus feeders and grazers occur at macrophyte rich habitat (Miliša et al., 2006a). Finally, macrophytes provide a myriad of microhabitats for macroinvertebrates causing higher diversity and abundance of macroinvertebrates (Špoljar et al., 2012).

There are obvious shifts in feeding guild composition in open canopy streams compared to closed canopy streams (Stone and Wallace, 1998; Banks et al., 2007) as well changes in taxon diversity (Banks et al., 2007). These changes are evident in higher emergence rates of adults, thus the greater number of adult aquatic insect emerge from open than from forested streams (Davies et al., 2005; Banks et al., 2007).

Studying insect diversity and particularly Diptera diversity in aquatic ecosystems is only reliable using emergence methods that provide adult specimens precisely from the studied habitat (Smith et al., 2003; Gerecke et al., 2011). Gerecke et al. (2011) established in their extensive research of springs that for rheocrene springs in particular, having emergence traps distributed around an entire spring is the best way to study changes in diversity of aquatic insects and Diptera especially. Also, using emergence traps enables obtaining exact phenology data (Wagner et al., 2011).

Spring communities may demonstrate most of the structural and functional properties seen in other aquatic communities, yet are naturally less complex than those found in other lotic habitats (Williams and Williams, 1998). When studying insect assemblages in the springs, one deals with a comparatively small number of the “larger” aquatic insects (Ephemeroptera, Plecoptera, Trichoptera), but with a great number of Diptera (Danks and Williams, 1991; Wagner et al., 1998) and in karst springs, especially with chironomids (Mori and Brancelj, 2006; Gerecke et al., 2011). Diptera are usually only 1/3 or less of total biomass, but they comprise more than 2/3 of total abundance (Anderson, 1992; Progar and Moldenke, 2009) and Diptera are usually the most species-rich (Gerecke et al., 2011). Dipteran fauna is commonly neglected in ecological research due to extremely complex and demanding method for identification and is mostly referred to and analyzed at the family level. Since this is the most abundant order both by number of species and by abundance, to neglect them may disguise many of the ecological processes and relationships. We therefore chose to uncover those hidden relationships analysing Diptera thoroughly at the species level. Focusing the study on the Diptera assemblages of the springs is a good method for researching taxonomical richness, diversity and feeding guild categories in the spring habitats.

The goal of our study was to compare Diptera assemblages in biotic traits (taxonomic richness, abundance, diversity and feeding guilds composition) and phenology patterns between two rheocrene karst springs that differ in riparian canopy coverage. We hypothesized that: (1) differences between Diptera assemblages will be high, with low proportion of shared species between springs, (2) the open canopy spring will have more specimens and higher diversity of Diptera then the closed canopy spring, (3) emergence will start earlier at open canopy spring and it will last longer, and (4) feeding guilds will differ between springs primarily in proportion of detritus feeders, which we expect to be a dominant guild at the open canopy spring.

2. Materials and methods

2.1. Study sites

The study sites were two rheocrene karst springs which supply water to the tufa barrier lake system of the Plitvice Lakes National Park (NP) in Croatia: Springs of Crna rijeka and Bijela rijeka (Fig. 1).

The vegetation around Crna rijeka spring (closed canopy spring, CS) forms a closed canopy. The water emerges through large cobbles and boulders covered with moss, but at the part of the spring, where the water flow is slower, the substrate consists of small cobbles and sand (Marušić and Ćuruvija, 1990/1991).

The vegetation around Bijela rijeka spring (open canopy spring, OS) forms an open canopy and the spring partially dries out during extremely dry years. Water comes out through substrate mainly composed of cobbles, pebbles and sand with a few bigger boulders that are covered by moss (Marušić and Ćuruvija, 1990/1991). The spring is rich in aquatic and semiaquatic macrophytes and allochthonous organic particles, especially during autumn and winter. Table 1 lists the main differences between sites.

2.2. Experimental protocol

We installed six pyramid-type emergence traps at each study site and they were operational from February 2007 to February 2008. Traps were sited to ensure representative sampling of emergence from all identifiable microhabitats present at each spring (Table 1). Each trap was a 50 cm tall, four-sided pyramid with a base of 45 × 45 cm, fastened to the streambed in a way that allows the free movement of larvae in and out of the sampling area. The side frames of the traps were covered with 1 mm mesh netting. At the tip of each trap was a collecting container filled with preservative (2% formaldehyde with detergent). The containers were emptied monthly and samples preserved in 80% ethanol.

We identified the specimens to species level using Szadziewski et al. (1997) for Ceratopogonidae; Serra-Tosio (1970a, 1970b), Sæther (1976), Willassen (1982), Cranston et al. (1989), Makarchenko and Makarchenko (2006), Langton and Pinder (2007), Giłka et al. (2013) and Ashe and O'Connor (2009, 2012) for Chironomidae; Disney (1999) for Dixidae; Collin (1961), Engel (1938–1946) and Wagner (1984) for Empididae; Zatwarnicki (1997) for Ephydridae; Freeman (1951), Savchenko (1961, 1964), Stary (1971, 1994, 2009, 2014), Dienske (1987), Hofsvang (1997) and Ujvarosi and Balint (2012) for Tipuloidea groups; Vaillant (1971), Wagner (1997), Krek (1999) and Kvifte et al. (2013) for Psychodidae; Rozkošný and Gregor (2004) and Pont and Ivković (2013) for Muscidae; and Rozkošný (2002) for Sciomyzidae.

For feeding guilds composition we used Moog (2002). For species that were not listed in Moog (2002), we supplemented with data from Armitage et al. (1994), Lindegaard (1995), Sæther and Wang (1995), Nilsson (1997), Delettre (2000) and de Beauvesère-Storm and Tempelman (2009).

Once a month, we measured oxygen content, pH and conductivity using WTW probes (WTW Oxi 330/SET, WTW pH 330 and WTW