

SIZE-STRUCTURE OF AQUATIC INSECT LARVAE DURING COLONIZATION

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Matoničkin Kepčija, R., Sertić Perić, M., Miliša, M., Špoljar, M., Mihaljević, Z., Radanović, I., Habdija, I. & Primc-Habdija, B.: Size-structure of aquatic insect larvae during colonization. *Nat. Croat.*, Vol. 19, No. 1, 121–131, 2010, Zagreb.

Colonization of aquatic insect larvae was investigated in a second order woodland stream using trays filled with natural substrate. Patterns of colonization differed significantly between seasons in terms of number of taxa, density and biomass of aquatic insect assemblages. Larvae in the first (out of five) size class made up 35.5% of all colonizers during the spring, highest share of 54.1 % during the summer, 40.8% and 17.5% during the autumn and winter, respectively. Many peak values in density during spring and summer matched with single-species mass colonization of first or second size classes, explained by »distributional drift« of newly-hatched insects, or direct oviposition on substrate. Size structure of the community did not change with time of exposition, although it reflected life histories of the aquatic insects, which led to seasonal changes in colonization patterns.

Key words: woodland stream, seasons, life cycles, dispersal

Matoničkin Kepčija, R., Sertić Perić, M., Miliša, M., Špoljar, M., Mihaljević, Z., Radanović, I., Habdija, I. & Primc-Habdija, B.: Veličinska struktura ličinki vodenih kukaca tijekom naseljavanja. *Nat. Croat.*, Vol. 19, No. 1, 121–131, 2010, Zagreb.

Naseljavanje ličinki vodenih kukaca praćeno je u šumskom potoku drugog reda upotrebom podloga s prirodnim supstratom. Kolonizacija se značajno razlikovala između godišnjih doba s obzirom na broj svojiti, brojnost i biomasu zajednica vodenih kukaca. Ličinke prvog (od pet) veličinskog razreda imale su udio od 35,5% među svim kolonizatorima tijekom proljeća, najveći udio od 54,1% tijekom ljeta, 40,8% i 17,5% tijekom jeseni i zime. Mnoge vršne vrijednosti brojnosti tijekom proljeća i ljeta odgovarale su masovnom naseljavanju jedne svojite prvog ili drugog veličinskog razreda, što je objašnjeno »distribucijskim driftom« mladih ličinki, ili direktnim polaganjem jajašaca na podlogu. Veličinska struktura cijele zajednice nije se mijenjala s vremenom ekspozicije, već je odražavala svojstva životnih ciklusa vodenih kukaca što je dovelo do sezonskih promjena u obrascima naseljavanja.

Ključne riječi: šumski potok, godišnja doba, životni ciklusi, rasprostiranje

INTRODUCTION

Colonization is a process whereby organisms disperse to and become established in new areas or habitats, or in disturbed habitats they inhabited previously (SMOCK, 2006). Giving the heterogeneity in time and space of aquatic habitats, colonization is thought to be an integral part of the life histories of most aquatic insects (SHELDON, 1984). Invertebrate movements involved in colonization are downstream drift, aerial sources, upstream and vertically directed and lateral movements (WILLIAMS & HYNES, 1977; GILLER & CAMBELL, 1989). Seasonal differences in the process of colonization reflect differences in general life history characteristics and benthic densities of macroinvertebrate communities (ROBINSON *et al.*, 1993). Difference in timing of dispersal and/or colonization phases among aquatic insect species is an outcome of differences between the life histories of species (WILLIAMS & FELTMATE, 1992). MACKAY (1992) reviewed possible effects of season on colonization emphasizing synergistic effect of temperatures and life history stages.

To address the questions concerning seasonal differences in colonization of macroinvertebrates, we conducted a series of *in situ* experiments in a second order woodland stream. The results of the experiments for changes in substrate composition, detritus accumulation and colonization of macrofauna are reported in MATONIĆKIN *et al.* (2001). The authors modeled season-specific curves for certain taxa, assuming that they reflect different colonization potential due to life history. In this study, we wanted to test this hypothesis and find out how much does the size structure of colonizers change during colonization and throughout a year, and weather colonization potential is age-dependent.

MATERIALS AND METHODS

Colonization was investigated in a second order woodland stream Veliki Potok on Medvednica Mountain near Zagreb, Croatia. The experiment took place between April 1998 and April 1999. Colonization trays (23 x 18 x 10 cm) were filled with natural substrata, which consisted of dried and burned cobbles (41%), pebbles (35%), gravel (15%), sand (7%) and silt (2%). Thirty trays were placed in the stream at the beginning of each season. Three replicate trays were collected each week. The last nine trays in the summer were lost due to flooding (highest measured Q was 0.83 m³/s), so the summer experiment lasted 7 weeks, while the other seasonal series comprised 10 weeks. Aquatic insects were separated by eye and by washing and sieving through a 500 µm screen, followed by preservation in 4% formalin. Individuals were identified at least to the genus level (except Chironomidae), counted, measured (body lengths from the front of the head to the posterior edge of the abdomen to the nearest 1 mm) and weighed (AFDW). Body lengths were classified into five size-classes for each taxon. Physical and chemical parameters of the investigated stream are given in Tab. 1.

Statistical analysis of data was mainly done with one-way ANOVA, with *post-hoc* Unequal N HSD test (as we had 7 samples in summer and 10 in other seasons). ANCOVA was used to test differences in community parameters of aquatic insects between seasons with time as a co-variate.

Tab. 1 Physical and chemical parameters of Veliki Potok during the period of investigation, and p-values of one-way ANOVA for the effect of season on measured parameters. The same letters for seasonal values indicate no significant difference ($p > 0.05$) according to *post-hoc* Unequal HSD tests

	Spring	Summer	Autumn	Winter	p
Discharge ($\text{m}^3 \text{s}^{-1}$)	0.049 \pm 0.022 a	0.048 \pm 0.031 a	0.078 \pm 0.039 a, b	0.098 \pm 0.074 b	< 0.001
t ($^{\circ}\text{C}$)	12.0 \pm 2.5 b	16.8 \pm 2.1 c	5.8 \pm 3.1 a	6.8 \pm 3.0 a	< 0.001
O ₂ (mg l^{-1})	10.8 \pm 0.7 a	8.4 \pm 0.4 c	11.6 \pm 0.8 b	11.3 \pm 0.7 a, b	< 0.001
KPK/KMnO ₄ ($\text{mg O}_2 \text{l}^{-1}$)	3.1 \pm 0.9 a	6.0 \pm 3.2 b	2.8 \pm 0.6 a	2.6 \pm 0.5 a	< 0.001
o-phosphate (mg l^{-1})	0.044 \pm 0.024	0.046 \pm 0.009	0.031 \pm 0.007	0.033 \pm 0.018	> 0.05
Nitrite (mg N l^{-1})	0.017 \pm 0.010 a, b	0.010 \pm 0.005 a	0.015 \pm 0.002 a, b	0.021 \pm 0.002 b	< 0.01
Nitrate (mg N l^{-1})	0.033 \pm 0.014	0.015 \pm 0.019	0.032 \pm 0.011	0.025 \pm 0.017	> 0.05

RESULTS

Highest number of aquatic insect taxa was recorded during the winter (64), and the lowest during the summer colonization experiment (38), with spring and autumn being intermediate (54 and 56 taxa). Patterns of colonization differed significantly between seasons (Fig. 1), with time being statistically significant co-variate for all tested community parameters (Tab. 2). According to the *post-hoc* test (unequal HSD), the number of taxa differed between winter and the other three seasons ($p < 0.01$ for all combinations), while there was no significant difference in taxa number between spring, summer and autumn. Density of aquatic insects differed significantly between spring and autumn (unequal HSD, $p < 0.05$) and spring and winter (unequal HSD, $p < 0.001$). Seasonal differences were most pronounced for biomass (Tab. 2, Fig. 1), with *post-hoc* results showing differences between all seasons (unequal HSD $p < 0.001$ for winter \neq spring, winter \neq summer and winter \neq autumn, $p < 0.01$ for spring \neq summer, and $p < 0.05$ for summer \neq autumn) except autumn and spring (unequal HSD, $p > 0.05$). During the summer experiment, biomass was on average 11 times lower compared to the winter experiment.

The most numerous taxa included Ephemeroptera (*Baetis* spp., *Rhithrogena* gr. *semicolorata*, *Habroleptoides modesta*), Plecoptera (*Protonemura* spp., *Leuctra fusca*), Trichoptera (*Hydropsyche* spp., *Synagapetus dubitans*) and Chironomidae (Orthocladiniinae sp. 3, Chironomini sp. 1). Some species were virtually absent from experimental trays during the summer, while being abundant during the rest of the year. Such a

Tab. 2. p-values of ANCOVA for community parameters of aquatic insects during colonization experiment; time was a co-variate (continuous predictor) and season was a categorical predictor. Bold values are statistically significant (> 0.05)

	Number of taxa	Density	Biomass
Time	0.00005	0.00490	0.00851
Season	0.00008	0.00029	0.00000

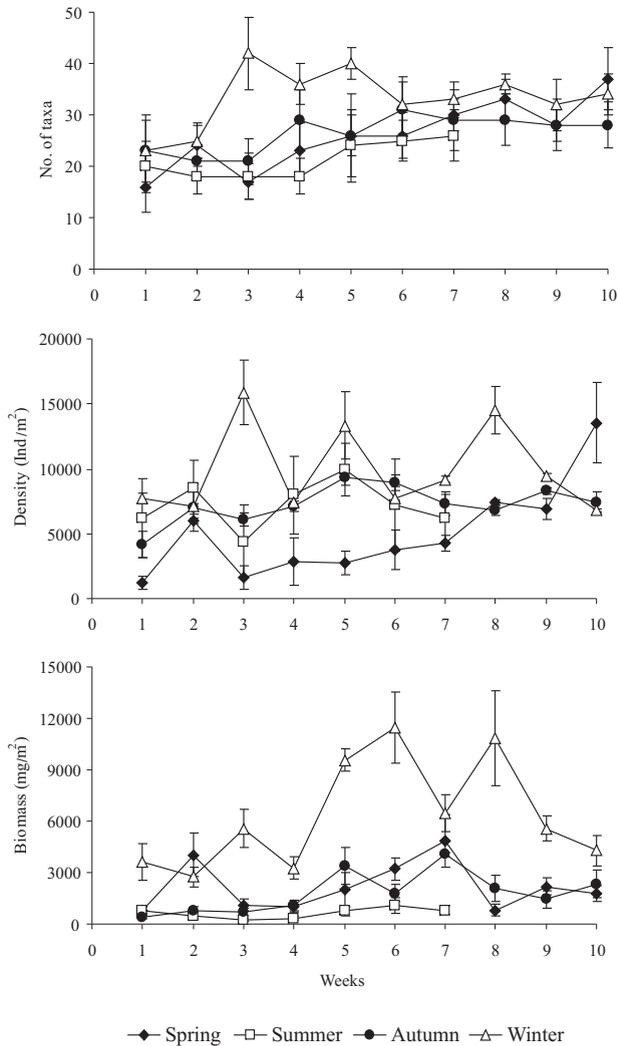


Fig. 1. Aquatic insect community parameters (mean \pm SE of number of taxa, density and biomass) in four seasonal colonization experiments.

pattern was observed for *Synagapetus dubitans*, *Ephemerella* sp. and Orthocladiinae sp. 2.

Density fluctuated strongly during each seasonal experiment, with a synchronized first peak after 2 weeks of colonization in spring, summer and autumn (Fig. 1). Size structure changed mostly during spring, with larger individuals prevailing at the beginning and smaller ones at the end of the spring experiment (Fig. 2). During the summer and autumn, the first two size classes dominated the community. The first size class had an average share of 54.1 % during summer and 40.8 % dur-

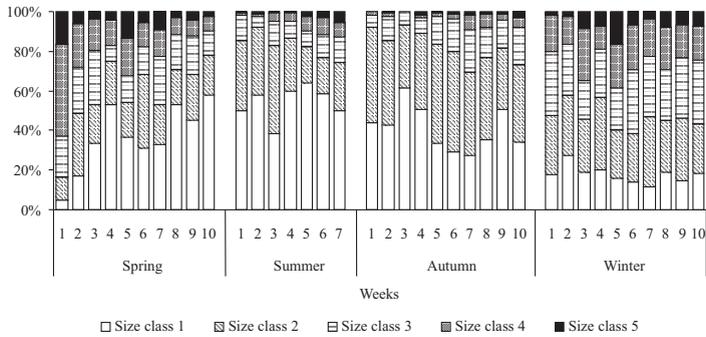


Fig. 2. Size-class distribution of aquatic insects in four seasonal colonization experiments.

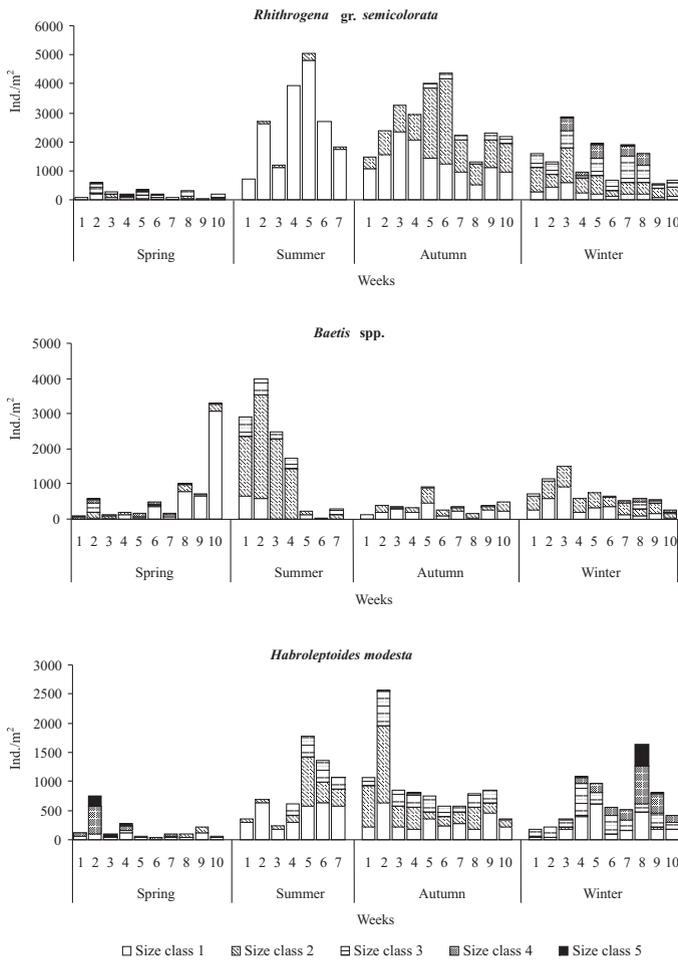


Fig. 3. Density and size-class distribution of the three most abundant taxa of Ephemeroptera

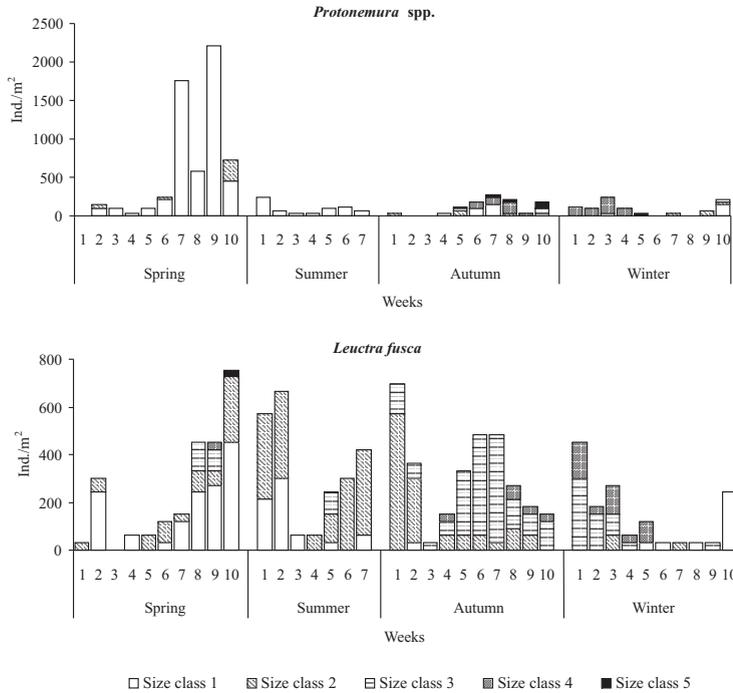


Fig. 4. Density and size-class distribution of the two most abundant taxa of Plecoptera

ing autumn, while the second size class accounted for 28.8 % during summer and 41.7 % during autumn. The size structure in winter was most unified among all seasons (Fig. 2). In general, density and biomass patterns during the colonization experiments corresponded to the observed size structure (Figs 1 and 2).

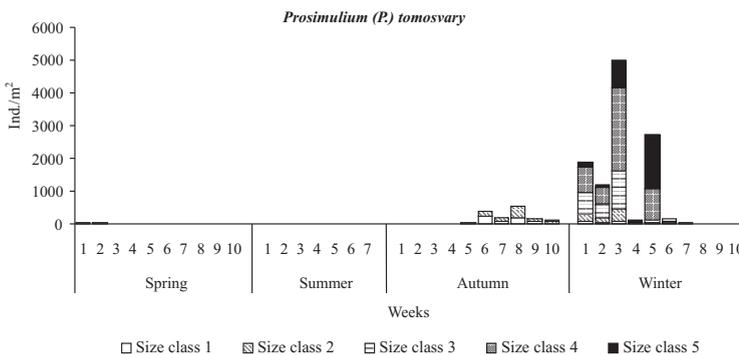


Fig. 5. Density and size-class distribution of the blackfly larvae *Prosimulium (P.) tomosvary*

Analysis of the distribution of size classes for the most numerous taxa mainly showed higher colonization potential of smaller individuals (Figs 3 and 4). Colonization of the first size class was obviously the cause of the observed increase in density during the last three weeks in the spring colonization experiment. Specifically, two taxa (*Baetis* spp. and *Protonemura* spp.) accounted for 37 %, 18 % and 40 % in total density on the 8th, 9th and 10th week, respectively. *Protonemura* spp. had a low share in the other three seasons (Fig. 4) while *Baetis* spp. (its 2nd size class, Fig. 3) continued to be among the most numerous colonizers in summer, where it accounted for 26-27 % of total density in the first three weeks. *Rhithrogena* gr. *semicolorata* (first size class, Fig. 3) dominated the last four weeks with a share as much as 49 % of total density. The same taxon dominated colonization assemblage in autumn with highest share in density after the 4th week (53 %), with *Habroleptoides modesta* following with the highest share of 36.1 % in the 2nd week. Dynamics of *R. gr. semicolorata* showed an evident negative correlation between mean size of larvae and its density on trays (confirmed by Spearman $R = -0.69$, $p < 0.001$). Stonefly larvae *Leuctra fusca*, however, did not show significantly higher colonization potential of smaller individuals (Spearman R between mean size of larvae and its density was -0.08 , $p > 0.05$), although certain peaks correspond to a prevalence of the first two size classes (Fig. 4). Blackfly larva *Prosimulium* (*P.*) *tomosvaryi* had a share of 24.3 %, 31.4 % and 20.2 % in density of aquatic insect larvae after 1, 3 and 5 weeks in winter, respectively, while otherwise having low density or being absent from colonizing trays. Most blackfly larvae were of size class 4 and 5 (Fig. 5), and many were observed with pupal gills (last instar according to JENSEN, 1997).

DISCUSSION

Patterns of colonization in this study differed significantly between seasons. Taking into consideration the number of taxa, colonization was shown to be fastest in autumn (22 days to reach 99% of equilibrium number) and summer (24 days), slower in winter (34 days) and the slowest in spring (63 days) (MATONIČKIN *et al.*, 2001). Differences were the most distinct for biomass (in accordance with ROBINSON *et al.*, 1993) and the least pronounced for density, suggesting a strong influence of life history of aquatic insects on colonization. Generally, colonization was relatively fast in all seasons, supporting data on rapid colonization of hard substrata in streams (MACKAY, 1992; QUINN *et al.*, 1998).

Size class distributions showed highest turnover during the spring experiment, suggesting mass emergence at the beginning of the experiment, followed by the appearance of dense populations of first size classes at the end of exposition (Fig. 2). Mass immigration and emigration may be occurring in the stream as a result of egg hatching and emergence, having an effect on colonization (MACKAY, 1992). Under these conditions, it probably took longer for the community to stabilize; i.e. immigration and emigration rates certainly changed considerably from the beginning to the end of the spring experiment. Changes in size class distribution probably also changed the strength of interspecific competition. Thus, increased density to the end of the spring experiment could be explained by new niches being created as a result of adult emergence. Summer had the lowest number of recorded taxa, how-

ever the number of taxa in successional sequence was comparable; i.e. was not significantly different between the spring and autumn experiments. This pattern also indicated less competition in summer due to virtual absence of some species, probably those with highly synchronized life cycles. Seasonal variation in the importance of biotic factors, such as competition and predation was discussed by ROBINSON *et al.* (1993). Summer and autumn had highest share of size classes 1 and 2 and similar densities (both value and pattern) during colonization, while winter showed the most uniform spectrum of size classes. The high number of taxa between the 3rd and 5th week followed by decline in the winter experiment might correspond to conceptual model of succession (JACKSON, 2003); i.e. represent peaks in species richness that subsequently declines as some of the colonizing populations are less competitive and do not survive. The highest number of taxa recorded during the winter experiment supports the idea of competition being most pronounced in this season.

Many peak values in density during spring and summer match with single-species mass colonization of first and second size classes. WILLIAMS (1980) also recorded mass movements by first-instar larvae. This »distributional drift« is common in newly-hatched insects, explaining a possible source of those colonizers (WILLIAMS & FELTMATE, 1992). MACKAY (1992) suggested that larvae could have developed from eggs laid directly on the substrates, hence considering oviposition a means of rapid colonization. All three analysed taxa of Ephemeroptera (*Baetis* spp., *Rhithrogena* gr. *semicolorata*, *Habroleptoides modesta*) showed higher colonization ability of smaller larvae, hence variation of seasonal mobility, associated with life cycle stage (WILLIAMS, 1980). *Baetis* is an active drifter, often dominating the drift (GILLER & CAMBELL, 1989), suggesting drift as a primary mechanism of its dispersal. On the other hand, *R. gr. semicolorata* is a rare passive drifter, but when the distances between empty and populated substrates are small, crawling can equally contribute to colonization as drift (GILLER & CAMBELL, 1989), thus explaining its high density on substrate trays. Correlation between mean size of larvae of *R. gr. semicolorata* and its density might be explained by smaller individuals being more affected by passive dislodgment, leading to a shift towards larger individuals in the size-composition of benthic populations (CÉRÉGHINO *et al.*, 2004). Dynamics of size-classes for this taxon indicate synchronized unimodal life-cycle, corresponding to the so-called »winter species« (LANDA, 1968). Age-dependent colonization properties were also evident in the case of the Plecopteran genus *Protonemura*, while *Leuctra fusca* seemed to be equally successful at colonizing substrate trays, regardless of size class distribution. In the case of *L. fusca*, it was possible to follow the growth of a synchronized population. The egg incubation period for *L. fusca* is greatly influenced by ambient water temperature (LILLEHAMMER 1985), suggesting synchronicity. The results of our study are in compliance with PETERSEN *et al.* (1999) who found this species emergence to be well-defined and unimodal.

Some taxa were transitionally present on substrate trays, obviously just exploring the potentials and moving on, thus not presenting »true colonization« according to MACKAY (1992). Among abundant taxa in this investigation, such dynamics was observed for *Prosimulium* (*P.*) *tomosvaryi*. Rapid colonization and subsequent decline in abundance of Simuliidae was discussed to reflect this group's behaviour as refugial opportunists (QUINN *et al.*, 1998). These authors suggest that blackfly larvae

search clean, fauna-depleted substrata. However, it is also possible that winter mass colonization of blackfly larvae were the result of downstream pre-emergent migration (WILLIAMS, 1980).

Taking all four seasonal experiments into consideration, it emerges that the size structure of the whole community did not change with time of exposition, although it reflected life history features of the aquatic insects. Life history stages of aquatic insects influenced their abilities to colonize new substrate, leading to seasonal changes in colonization patterns.

Received March 29, 2010

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SUMMARY

Size-structure of aquatic insect larvae during colonization

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Colonization of aquatic insect larvae was investigated in a second order woodland stream Veliki Potok on Medvednica Mountain near Zagreb, Croatia during 1998 and 1999. Colonization trays were filled with natural substrata (cobble (41%), pebbles (35%), gravel (15%), sand (7%) and silt (2%)). Design of the experiment included simultaneous placement of substrate trays at the beginning of each season with sampling once a week for 10 consecutive weeks. Aquatic insect larvae were identified, counted, measured (body lengths) and weighed (AFDW). Body lengths were classified into five size-classes for each taxon. Patterns of colonization differed significantly between seasons in terms of number of taxa, density and biomass of aquatic insect assemblages. Highest number of taxa was recorded during the winter (64), and lowest during the summer colonization experiment (38). Density fluctuated strongly during each seasonal experiment, with a synchronized first peak after 2 weeks of colonization in spring, summer and autumn. Other observed peaks were most probably consequences of mass colonization of first-instar larvae, especially in late spring and during summer. The distribution of size classes for the most numerous taxa indicated higher colonization potential of smaller individuals. During the winter there were two mass colonizations by simuliid prepupal larvae, probably due to pre-emergent downstream drift. Biomass fluctuated mostly during the winter.

The most numerous taxa included Ephemeroptera (*Baetis* spp., *Rhithrogena* gr. *semicolorata*, *Habroleptoides modesta*), Plecoptera (*Protonemura* spp., *Leuctra fusca*), Trichoptera (*Hydropsyche* spp., *Synagapetus dubitans*) and Chironomidae (Orthoclaadiinae sp. 3, Chironomini sp. 1). Some species were virtually absent from experimental trays during the summer, while being abundant during the rest of the year.

Size structure of the whole community did not change with time of exposition, although it reflected life history features of aquatic insects. Life history stages of aquatic insects influenced their abilities to colonize new substrate, leading to seasonal changes in colonization patterns.

S A Ž E T A K

Veličinska struktura ličinki vodenih kukaca tijekom naseljavanja

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Naseljavanje ličinki vodenih kukaca praćeno je u Velikom Potoku, šumskom potoku drugog reda na Medvednici u blizini Zagreba, tijekom 1998. i 1999. godine. Podloge za naseljavanje sadržavale su prirodni supstrat (valutice (41%), krupni šljunak (35%), šljunak (15%), pijesak (7%) i mulj (2%)). Dizajn eksperimenta sastojao se od simultanog postavljanja podloga na početku svakog godišnjeg doba uz uzorkovanje jednom tjedno idućih deset tjedana. Ličinke vodenih kukaca su identificirane, brojane, izmjerene (dužina tijela) i izvagane (AFDW). Dužine tijela su klasificirane u pet veličinskih razreda za svaku vrstu.

Naseljavanje se značajno razlikovalo između godišnjih doba s obzirom na broj svojiti, brojnost i biomasu zajednica vodenih kukaca. Najveći broj svojita zabilježen je tijekom zime (64), a najmanji tijekom ljetnog eksperimenta (38). Brojnost je veoma fluktuirala tijekom svih godišnjih doba, uz sinhroniziranu prvu vršnu vrijednost nakon 2 tjedna naseljavanja tijekom proljeća, ljeta i jeseni. Ostale zapažene vršne vrijednosti bile su posljedica masovnog naseljavanja ličinki prve veličinske kategorije, posebno tijekom kasnog proljeća i ljeta. Raspodjela veličinskih razreda za najbrojnije svojite ukazuje na veći kolonizacijski potencijal manjih jedinki. Tijekom zime zabilježena su dva masovna naseljavanja ličinki braničevki u njihovu zadnjem razvojnom stadiju, vjerojatno zbog nizvodnog drifta. Biomasa je najviše fluktuirala tijekom zime.

Nabrojnije svojite bile su svojite Ephemeroptera (*Baetis* spp., *Rhithrogena* gr. *semicolorata*, *Habroleptoides modesta*), Plecoptera (*Protonemura* spp., *Leuctra fusca*), Trichoptera (*Hydropsyche* spp., *Synagapetus dubitans*) i Chironomidae (Orthocladiinae sp. 3, Chironomini sp. 1). Neke svojite naizgled su nestale tijekom ljeta, dok su tijekom ostatka godine bile brojne.

Veličinska struktura čitave zajednice nije se mijenjala s vremenom ekspozicije, već je odražavala svojstva životnih ciklusa vodenih kukaca. Razvojni stadiji vodenih kukaca utjecali su na njihovu sposobnost da nasele novu podlogu, što je dovelo do sezonskih razlika u obrascima naseljavanja.