Colonization of natural substrata of different roughness and colour by Ephemeroptera nymphs using retrieval and direct observation techniques

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Abstract

We investigated the colonization of stream substrata by Ephemeroptera nymphs in a Canadian Rocky Mountain stream. Stream substrata used in our study were different textures (smooth and rough) and colours (dark and light); the taxonomic groups studied were *Drunella coloradensis* Dodds (Ephemerellidae), Heptageniidae (*Cinygmula* and *Epeorus*) and a *Baetis-Ameletus* group (Baetidae and Siphlonuridae). We tested the hypothesis that as *D. coloradensis* nymphs and other abundant Ephemeroptera nymphs increase in size they choose a dark substratum to remain cryptic and a substratum of greater texture to reduce the risk of being swept from the substratum by the water flow. Two approaches were used to test this hypothesis, a substratum basket experiment and direct observations.

For the substratum basket experiment, there were no statistical differences in abundance of nymphs on the substratum types. But there was a general tendency that the *D. coloradensis* nymphs were least abundant on the rough dark-coloured substratum and developmental stage three nymphs were most abundant on the smooth white-coloured substratum.

Colonization was investigated for other Ephemeroptera nymphs by making direct observations on the substratum baskets using a glass-bottomed box. For the taxonomic groups and two colonization periods, nymphs were statistically at greatest density on the smooth white-coloured substratum and lowest on the smooth black-coloured substratum. The *Baetis-Ameletus* groups were also found at greatest densities on the rough dark-coloured substratum.

Introduction

There have been many studies on the colonization of freshwater benthic macroinvertebrates on substrata in lotic environments. In most studies, artificial substrata have been used simply as a method of sampling the zoobenthos. More recent work has concentrated on colonization dynamics and specific physical attributes of the substrata that might affect the 'choice' of a substratum by benthic macroinvertebrates (see reviews by Rosenberg & Resh, 1982; Minshall, 1984; Sheldon, 1984). We have used 'choice' where it does not necessarily imply active selection by an organism but the over-abundance of organisms on a substratum suggests a strong association. Minshall (1984) extensively reviewed recent work on substratum characteristics thought to be important to organism-substratum relationships. Some specific studies for colonization of substratum types have included substratum size (e.g., Cummins & Lauff, 1969; Rabeni & Minshall,

1977; Shelly, 1979; Khalaf & Tachet, 1980; Reice, 1980), particle size mixtures (e.g., Wise & Molles, 1979; Williams, 1980; Erman & Erman, 1984), surface area (e.g., Minshall & Minshall, 1977; Khalaf & Tachet, 1980), and substratum shape and microspatial complexity (Hart, 1978). Other abiotic factors of substrata which have been suggested to be important to benthic macroinvertebrate colonization but have received little attention are surface roughness (or texture) (Erman & Erman, 1984) and colour of inorganic substrata (Clifford et al., in press).

Surface roughness is a measure of surface irregularities of substratum particles. Roughness may include macroscale or microscale irregularities. In our study, we examine the importance of micro-texture, which is considered to be important to immature aquatic insects. On a rough substratum the immature aquatic insects may attain a more secure foothold than on smooth substratum and hence reduce the chance of being swept downstream. Tarsal structure and dorsoventral flattening in mayfly nymphs may be related to substratum choice (Percival & Whitehead, 1929; Madsen, 1968). Elliott (1967) suggested that the absence of certain insect species in the drift may be related to differences in the nymph's ability to hold onto a substratum.

Colour is defined here as a relative measure of dark- and light-contrasting substrata and how these contrasting substrata may be important to colonization by zoobenthos. Many immature aquatic insects exhibit different colour patterns, and this may be a response to predation pressure from visually-foraging predators (Hutchinson, 1981; Peckarsky, 1982). An organism may reduce predation by choosing a suitable background colour on which to forage in the daylight, thereby potentially reducing predation in the field and laboratory (Hynes, 1970: 207; Popham, 1941; Otto, 1984). For example, in the laboratory, Popham (1941) observed a fish predator attacked mainly the corixids that contrasted with background colour.

The stream bed materials of the eastern foothills of the Canadian Rocky Mountains, Alberta, provided an opportunity to determine whether aquatic insects were more abundant on a particular substratum type. These stream bed particles are diverse in their geological types; they include sandstone, shale, limestone, and conglomerates, of various textures and colours.

For the principal organism, we chose *Drunella coloradensis* Dodds (Ephemeroptera: Ephemerellidae) nymphs. These nymphs are generally light-coloured with variable dark mottled markings, especially on older nymphs. Gilpin & Brusven (1970) stated that their dark colour makes *D. coloradensis* nymphs difficult for a visually-foraging predator to see on dark rocks. Behaviourally, *D. coloradensis* nymphs have been classified as clingers and sprawlers (Cummins et al., 1984). This suggests that the nymphs are thigmotactic and texture may be important.

Our hypothesis was that as *D. coloradensis* and other mayfly nymphs increase in size they choose a dark substratum to remain cryptic and a substratum of greater micro-texture to reduce the risk of being detached from the substratum. We used two approaches, both involving substratum baskets at a field site. The first method was to count four developmental stages of *D. coloradensis* nymphs in substratum baskets of different texture and colour after a colonization period. The second approach was to make direct observations of colonization by two size classes of Ephemeroptera nymphs on the substratum baskets. The latter method would cause the least disturbance to the zoobenthos on the substratum (see Material and methods). We attempted to standardise the physical characteristics of the substrata by taking measurements of size and texture, and the environment by placing substrata in a uniform habitat.

Description of the study area

The study area was conducted in Dyson Creek (50° 37' N, 114° 39' W), a second order Alberta stream (map scale = 1 : 50000) in the eastern foothills of the Canadian Rocky Mountains. The study site was a slow-flowing riffle (elevation = 1 555 m) located about 100 m downstream from a waterfall-pool-riffle-pool series,

and upstream from a log-dammed pool. The substratum here was relatively uniform pebble size (mean size = 4.7 cm, range = 2.1–8.2 cm). The mean width and discharge of the study riffle were 4.9 m and 0.21 m^3s^{-1}, respectively. Maximum diel range in water temperature was from 0.5 °C to 18 °C. Throughout our study, there was no major disturbance to the stream's substratum and turbidity was low, except during spring runoff.

Material and methods

Substratum basket experiment

The experimental design included three types of naturally occurring substratum (henceforth known as the experimental substrata), a smooth-light (SL), a smooth-dark (SD), and a rough-dark (RD) substratum. We chose the rocks based on their mineral composition, shape, size, and colour. Mineral composition of substrata was used because this would determine textural differences between the substrata (also, see below). The SL substratum was a white limestone, the SD substratum was a black limestone, and the RD substratum was a dark olive green sandstone. We also placed the rocks from the study site, Dyson Creek, in the substratum baskets to determine if similar densities were present on the natural stream bed rocks. The Dyson Creek substratum was predominantly dark-coloured sandstones and conglomerates. For all substrata, we usually chose oval shaped rocks. The size of the substrata was determined by measuring the maximum and minimum lengths, through the central point of each rock, and the diagonal length (i.e., midway between the maximum and minimum lengths) for each rock. A mean length (or diameter) was calculated from these measurements. Colour was determined by visually matching all substrata of one colour and shade together.

Although the differences in substratum texture were based on their mineral components, limestone versus sandstone, a quantitative measure of texture was obtained using a stylus-type roughness meter (Clifford et al., in press). A detailed description of this instrument is in preparation.

The four substrata were placed in 1.3 cm screen wire baskets, 25 × 25 × 10 cm, with larger rocks overlain by smaller rocks level to the top of each basket. Six replicates of each substratum type were used. The 24 substratum baskets were placed in the study riffle, with the top of the basket flush with the stream bed surface. The baskets were positioned in a systematic grid in eight rows of three baskets each; each substratum type was duplicated in each longitudinal column of baskets. The mean lateral distance and upstream-downstream distance between the substratum baskets was 1.0 m and 2.9 m, respectively.

The baskets were allowed to be colonized by zoobenthos for 14 days. There were two exceptions: the third colonization period was 15 days and the ninth colonization period was 13 days. There were nine trials, five during 1983 (June to September) and four in 1984 (May to July), to assure that the D. coloradensis developmental stages would be included. Drunella coloradensis is a univoltine species in Dyson Creek. The eggs hatch during the winter, the nymphs grow rapidly after ice breakup (ca. May) and the adults emerge in August and September. The nymphs were categorised into developmental stages one to four (DSI to DSIV) (after Clifford, 1970).

At the end of a colonization period, the baskets were taken out beginning at the downstream baskets. A stainless steel three-sided shovel (28 x 28 x 10 cm) was scooped under the substratum basket, while holding a net (frame = 30 x 30 cm, length = 1 m, mesh = 0.037 mm) immediately downstream. The organisms from the substrata were sieved (mesh = 0.037 mm) and preserved in 90% ethanol. In the laboratory, D. coloradensis nymphs were sorted (magnification 60 ×) and separated (240 × magnification) into developmental stages. The Kruskal-Wallis test was performed for each developmental stage and trial date to test the null hypothesis that there was no difference in abundance of nymphs on the three experimental substrata. Water velocity (at 0.6 × depth using an Ott C-1 current meter) and depth were recorded weekly over each basket. Temperature was recorded using a thermograph (Peabody Ryan, model H).

Direct observations

Sixteen baskets from the previous substratum basket experiment were placed in the study riffle in four groups of the substratum types (SL, SD, RD and Dyson Creek substrata); each group formed a matrix. The substratum types in the matrices occupied all possible positions in the arrangement relative to the current direction and stream banks. Mean distance between the up-stream and downstream edge of each group of baskets and to the stream bank was 1.1 m and 0.8 m, respectively. Water velocity and depth were recorded at irregular intervals.

We made direct observations of organisms on the substrata using a Plexiglass box (50 × 25 × 30 cm) with a glass bottom. Observations were made at a 30 min interval; the organisms were counted in 10 × 10 cm quadrats, four quadrats per substratum basket. This method has been described in detail and used in another study with little observer bias, for example, due to substratum colour or behaviour of nymphs (Casey, 1987).

Observations were made for two colonization periods, after 2–5 days (short colonization), and 13–14 days (long colonization), on seven dates in 1984. For each observation date, the organisms on a substratum were counted in a downstream to upstream direction on each of the 16 baskets. All observations were recorded at approximately the same period of the day (0700–1300 h) to reduce any diel change in the density of organisms. The organisms were identified to the lowest taxonomic group and the body length (excluding cerci) of each organism was recorded with the aid of a scale in the bottom of the observation box.

We observed three families of Ephemeroptera nymphs and the results were analysed by groups: total fauna (this group included all of the Ephemeroptera taxa), Heptageniidae (mostly *Cinygmula* and small numbers of *Epeorus*), and a *Baetis-Ameletus* group (mostly *Baetis*) (Baetidae and Siphlonuridae). Data for *Cinygmula* and *Epeorus* nymphs and for *Baetis* and *Ameletus* nymphs were lumped because of the large number of small nymphs present making identification of genera difficult. For each taxonomic group, the

nymphs were grouped in to small (1–4 mm), and large (5–12 mm) size classes and the two size classes together (1–12 mm). For each colonization period and size class, the Kruskal-Wallis test was used to test the null hypothesis of no difference in density of nymphs among the three experimental substratum types.

Results

The mean diameters of the four substrata were significantly different (Kruskal-Wallis test, p < 0.01). The mean diameter of the Dyson Creek substratum (mean = 6.0 cm) was less than the three experimental substrata (mean range = 7.6–8.3 cm) (Dunn multiple comparison test, p = 0.05). Texture of the substrata were significantly different (ANOVA, p < 0.01). The textures were categorised into two groups (Newman-Keuls test, p = 0.05), the Dyson Creek substratum with the RD substratum, and the SL substratum with the SD substratum; the former group was about two and one-half times rougher than the latter group.

Substratum basket experiment

Water velocity was significantly different among the substratum types (ANOVA, p < 0.01); the RD substratum was exposed to significantly slower velocities (mean = 15.8 cm s^{-1}) than the other substrata (mean range = 20.7–24.3 cm s^{-1}) (Newman-Keuls test, p = 0.05). Water depth over the baskets was not significantly different between substratum types (mean range = 11.1–13.1 cm) (Newman-Keuls test, p = 0.05).

Mean abundance and standard deviation (of six replicates) of the developmental stages of *D. coloradensis* nymphs for each substratum type and trial date are presented in Table 1. Colonization of the substratum types was the same for all developmental stages and trial date on the three experimental substrata (Kruskal-Wallis, p > 0.05). Although the numbers of the four developmental stages of nymphs were not significantly different between the three experimental

Table 1. Mean abundance and standard deviation (in parentheses) of the four developmental stages of *Drunella coloradensis* for trial dates one to nine (T1 to T9) in the substratum baskets. The substratum types were the experimental substrata: the smooth-light (SL), the smooth-dark (SD), and the rough-dark (RD) substratum, and the Dyson Creek substratum.

Developmental stage	Trial date	Substratum type			
		SL	SD	RD	Dyson Creek
DSI	T1	39.7(13.9)	36.0(19.8)	33.7(33.5)	36.3(14.5)
	T2	10.0 (5.1)	12.8 (8.1)	10.0 (5.6)	20.0(10.5)
	T3	2.2 (1.2)	2.3 (1.4)	2.7 (2.3)	1.8 (1.5)
	T4	1.3 (2.8)	1.7 (1.6)	1.0 (0.9)	1.0 (1.3)
DSII	T1	12.2 (7.4)	9.7 (6.6)	7.5 (7.3)	9.3 (7.0)
	T2	35.2 (9.4)	36.3(21.5)	28.5(18.3)	60.5(26.0)
	T3	16.0 (5.0)	15.5(11.0)	12.5 (8.6)	17.5 (4.6)
	T4	26.8(16.6)	28.0(13.0)	12.7(10.9)	24.3(14.3)
	T5	9.7 (4.5)	10.2 (6.3)	6.7 (8.5)	14.5 (6.1)
	T6	0.3 (0.5)	0.2 (0.4)	0.3 (0.5)	0.7 (0.5)
DSIII	T5	0.2 (0.4)	0.2 (0.4)	0.0	0.9 (0.6)
	T6	12.7 (6.5)	8.3 (3.5)	8.0 (8.0)	9.7 (4.8)
	T7	12.8 (7.8)	8.5 (3.9)	7.5 (5.4)	14.2 (7.8)
	T8	5.3 (2.9)	2.0 (2.5)	3.7 (3.0)	6.3 (3.1)
	T9	0.3 (0.5)	0.0	0.0	0.3 (0.8)
DSIV	T7	0.8 (1.2)	0.8 (1.2)	0.5 (0.8)	1.0 (0.6)
	T8	2.3 (2.0)	1.7 (2.4)	1.5 (0.6)	2.7 (2.1)
	T9	0.8 (0.4)	1.2 (1.2)	0.8 (0.8)	0.8 (0.4)

Table 2. Mean density and standard deviation (in parentheses) for each taxonomic group of the 1-12 mm size class observed after the short and long colonization periods on each substratum type. See Table 1 for details of the substratum types.

Taxonomic group	Colonization period	Substratum type			
		SL	SD	RD	Dyson Creek
Total fauna	Short	12.4 (7.2)	5.6 (6.2)	7.8 (4.4)	8.1 (4.9)
	Long	25.9(11.0)	12.1 (4.3)	21.5 (6.7)	20.6 (5.9)
Heptageniidae	Short	7.7 (5.1)	2.7 (3.2)	2.8 (2.1)	3.8 (3.2)
	Long	12.6 (8.2)	8.5 (2.1)	8.8 (6.1)	11.6 (5.5)
Baetis-Ameletus	Short	4.9 (5.3)	2.8 (3.8)	5.0 (4.3)	4.3 (4.0)
	Long	13.3 (6.8)	3.6 (2.8)	12.8 (2.8)	9.0 (3.5)

substrata, there was a tendency for the lowest mean number of nymphs to be on the RD substratum, and for developmental stage three nymphs, the greatest number of nymphs was on the SL substratum.

Direct observations

During the direct observations, water depth and velocity at each substratum basket were similar among dates. Results for each taxonomic group and colonization period on the substrata are presented in Table 2. For the experimental substrata and for the short and long colonization periods, the nymphs were at greatest densities on the SL substratum, especially relative to the SD substratum where there was a two-fold or greater decrease in density (Table 2). For the seven observation dates, making up the short and long

colonization periods, total fauna were significantly different for two dates, Heptageniidae for one date, and *Baetis-Ameletus* nymphs for four dates. For these dates, the densities were greatest on the SL substratum except for two dates where *Baetis-Ameletus* nymphs were greatest on the RD substratum. Trends in density for the small and large size classes were the same as those when the two sizes classes were considered together.

Discussion

The substrata of our study were made up of different minerals and, therefore, the chemical constituents of the rocks may have influenced the choice of substratum. But in an extensive study of the benthic fauna of 52 streams in Scotland, Egglishaw & Morgan (1965) found a remarkable similarity in species composition between seven limestone and five sandstone streams. Their study suggests that the mineral composition of limestone and sandstone, the experimental substrata in our study, may not be important to colonization by benthic organisms. We also found similar numbers of Ephemeroptera nymphs on the Dyson Creek substratum as on the three experimental substrata.

Comparing the smooth substrata, the SL and SD substrata were the most similar of the experimental substrata in terms of their substratum characteristics (with the exception of colour) recorded in our study and exposure to the physical environment in the study riffle. In the substratum basket experiment, it is difficult to determine why there was a tendency for *D. coloradensis* nymphs in the developmental stage three group to be at greater abundances on the SL (white-coloured) substratum, especially relative to the SD (black-coloured) substratum.

Few studies have experimentally investigated the importance of substratum colour to colonization by aquatic insects. Hughes (1966) examined the role of light in choice of microhabitat by *Baetis* and *Tricorythus* (Tricorythidae: Ephemeroptera) nymphs; he used white and black backgrounds in an experimental stream.

But Hughes' data show only a slight tendency (between 54 and 62% calculated from Hughes 1966: 20, Fig. 4) for nymphs positioned on a black surface relative to a white surface. In another study using sand-cast tiles, Clifford *et al.* (in press) found little evidence of differences between the abundance of stream invertebrates on dark-brown and white tiles for several taxa, only *Ameletus* nymphs were statistically at greatest numbers on the dark-brown tiles.

For our direct observations, we expected the other taxonomic groups studied to show similar substratum choices to those predicted for *D. coloradensis*, assuming that all insect nymphs evolved similar mechanisms to reduce predation and ability to remain on substratum surfaces. The taxa observed were cryptically coloured, and behaviourally they have been classified as clingers (similar to *D. coloradensis*) by Cummins *et al.* (1984).

However, we cannot explain why direct observations showed a strong tendency for nymphs of all taxonomic groups to be at greatest densities on the SL substratum and at lowest densities on the SD substratum. In our study, the older dark-coloured nymphs when on the light-coloured substrata would be most conspicous to a visually-foraging predator. The white- and black-coloured substrata were physically and chemically similar and subjected to the same physical conditions in the study riffle. We postulate that algal production and or quality of algae (relative to the zoobenthos) is greater on white substrata, and this is due at least in part to more light being reflected from the white surface relative to that of the black rocks.

According to our hypothesis, we expected greater numbers of nymphs to occur on the rough and dark-coloured substrata. Erman & Erman (1984) examined the colonization of three rock types of increasing surface texture from quartzite, to granite, to sandstone. They found that the total numbers of mayfly and stonefly nymphs increased significantly from the smoothest to roughest substrata. Clifford *et al.* (in press) found more individuals, including *D. coloradensis*, *Baetis*, and *Ameletus* nymphs and more taxa on rough tiles than on smooth tiles.

For the substratum basket experiment, there was no statistical difference in abundance of nymphs between the rough and smooth substrata, but for the direct observations, *Baetis-Ameletus* were at greater densities on the RD substratum. However, the water velocity was low at the RD substratum and the results are inconclusive. The RD substratum was also modified because deposition of fine particulate material occurred in minute crevices making up the rough surface. Siltation may or may not affect zoobenthos abundances (see Minshall, 1984). For example, Ephemeroptera nymphs may be attracted to such deposits as a food source or the deposit may physically repulse the animals. Deposition and it's potential effect on colonization by nymphs on rough substrata, such as used in our study, would be difficult to prevent in a natural situation.

Conclusions

For the substratum basket experiment and especially the direct observation study an interesting trend was evident. The results from our two methods suggest that Ephemeroptera nymphs, contrary to what we expected, were most abundant on smooth white-coloured substratum relative to the smooth black-coloured substratum. Our results for the rough substratum are not conclusive because of the possible bias in results for the RD substratum due to water velocity and siltation.

Acknowledgements

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