

## Burrowing behavior and biogenic structures of mud-dwelling insects

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**Abstract.** Little is known about the burrows of sediment-dwelling insects because these structures are concealed by the sediment in which the animals live. We used X-ray images to reveal and compare the burrowing behavior in the laboratory of aquatic insects from several orders (Diptera, Ephemeroptera, Megaloptera, Trichoptera). Most of the taxa studied constructed U-shaped burrows. Exceptionally, individual caddisfly larvae (*Polycentropus* sp.) varied greatly in the type of burrow they constructed, i.e., I-, J- and U-shaped burrows were observed. Most taxa begin new burrows from preexisting ones under the sediment surface, obviating the need for the animals to leave the sediment and thereby minimizing their exposure to potential predators. Nymphs of the mayfly *Hexagenia limbata* exceeded all of the other taxa studied in terms of the depth and length of their burrows and their burrowing rate. Our data suggest that nymphs of *H. limbata* could be responsible for 98% of the volume of sediment disturbed by littoral insects in our study lake. Observations on 3 species of *Chironomus* suggest that the rate of burrow construction can differ among congeners. Individuals of *H. limbata* and *Sialis velata* burrowed to greater depth in the autumn than in the spring. Our study illustrates the potential of radiographs to study the behavior of burrowing animals, and the range of variability in burrowing behaviors among genera and species of insects.

**Key words:** sediment, burrow, behavior, bioturbation, Chironomidae, *Hexagenia*, *Polycentropus*, *Sialis*.

Our knowledge of the structures produced by burrowing insects and the behavior of these animals in sediment is limited because their activities are hidden by the matrix in which they live. Information on the depth and form of animal burrows, and the rate at which they are constructed, is important in defining the niches of taxa coexisting in the apparent uniformity of sediment (Downing 1984, Berg 1995, Pinder 1995). Behavioral information is also important in the design of realistic models of the effects of benthic animals on surficial sediments. Because the feeding, burrowing, and irrigation activities of macroinvertebrates redistribute particles and fluids near the sediment-water interface, animals can strongly influence the physical, chemical, and microbiological properties of the sedimentary deposits in which they live (Rhoads 1974, Aller and Aller 1986, Matisoff 1995). The burrowing behavior of animals is also reported to influence their exposure to sedimentary contaminants (Warren et al. 1998).

The form and extent of animal burrows in the field has been determined by sectioning samples of substrate (e.g., Cole 1953, Ford 1962). Resins

and plastics that harden in water have also been used to preserve burrow structure in firm marine sediment (Dworschak and Pervesler 1988, Cadée et al. 1994). Such approaches are generally of little use for observing animal activities in soft muds that cannot be readily manipulated without altering the structure and position of burrows. Observations of burrows through the walls of transparent containers (e.g., Pesch et al. 1995) are generally fragmentary.

X-rays have been used to a very limited extent for observing the burrows of large animals in high-density substrates. In low-density muds there is insufficient contrast between sediment and water-filled animal burrows for biogenic structures to be visible on radiographs. Recently, Charbonneau et al. (1997) developed a means of recording the burrowing behavior of small animals in soft lacustrine muds. They amended sediment with inert, X-ray-dense particles to increase the contrast between burrows and sediment. We used this technique to obtain information on the development in space and over time of animal burrows in the laboratory. We report on the burrowing behavior of a broad range of lacustrine insect taxa in 4 orders (Diptera, Ephemeroptera, Megaloptera, Trichoptera), including both predators and detritivores.

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TABLE 1. Wet weight (mean  $\pm$  1 SE), length (mean  $\pm$  1 SE), number of individuals, and functional feeding group (FFG, Merritt and Cummins 1996) of the insects used in our study. All taxa were collected in the autumn, and additional individuals of *Hexagenia limbata* and *Sialis velata* were collected in the spring ( $n = 8$  for both species in the autumn, or 15 and 8, respectively, for the 2 species in the spring). *Chironomus tigris* (M. G. Butler, North Dakota State University, personal communication) is described as *Chironomus* sp. r in Butler et al. (1995).

Order	Taxon	<i>n</i>	Length (mm)	Wet weight (mg)	FFG
Ephemeroptera	<i>Hexagenia limbata</i>	23	25.0 $\pm$ 0.8	138.0 $\pm$ 10.4	detritivore
Megaloptera	<i>Sialis velata</i>	16	11.0 $\pm$ 0.8	15.0 $\pm$ 3.6	predator
Trichoptera	<i>Polycentropus</i> sp.	4	9.0 $\pm$ 1.2	12.0 $\pm$ 1.7	predator
Diptera	<i>Chironomus</i> ( <i>decorus</i> gp.) sp.	11	12.8 $\pm$ 0.6	5.7 $\pm$ 1.2	detritivore
Diptera	<i>Chironomus staegeri</i>	13	16.4 $\pm$ 2.5	5.5 $\pm$ 3.6	detritivore
Diptera	<i>Chironomus tigris</i>	11	14.7 $\pm$ 1.9	9.0 $\pm$ 3.7	detritivore
Diptera	<i>Glyptotendipes</i> sp.	7	11.0 $\pm$ 0.2	4.0 $\pm$ 0.7	detritivore
Diptera	<i>Procladius</i> sp.	7	7.5 $\pm$ 0.3	3.0 $\pm$ 0.3	detritivore

### Methods

Sediment and insects for our experiments were collected from depths of either 9 m (*Chironomus* spp.) or 3 m (other taxa) in Lake St. Joseph (46°55'N, 71°40'W), a 5 km<sup>2</sup> lake located on the Canadian Shield near Québec City, Québec. Insects were collected by divers using an underwater benthic sampling net (0.5-mm mesh), placed in plastic bags, and returned to the laboratory in coolers. Sediment for later use in observing animal burrows was collected at the same sites with an Ekman grab; care was taken to decant overlying water so as not to alter sediment density (70% water, as measured by drying sediment samples to constant weight). Animals were acclimated to laboratory conditions (10°C in darkness) in holding aquaria containing sediment and lake water for a minimum of 2 wk prior to recording their behavior.

In the laboratory, sediment was sieved through a 1-mm-mesh net to remove animals and large debris. A dense, inert compound, molybdenum carbide (8 g Mo<sub>2</sub>C/L), was mixed into the sediment to increase the density differential between the sediment and animal burrows to make the biogenic structures visible on radiographs (Charbonneau et al. 1997). Two L of sediment amended with the contrasting agent were placed into 1 of a series of 2.5-L-capacity Plexiglas<sup>®</sup> aquaria (40 × 2.5 × 24 cm). Lake water (0.5 L) was added slowly onto a piece of Styrofoam<sup>®</sup> placed on the sediment surface to avoid resuspending sediment. After 24 h, 1 individual was added to each aquarium without bubbling air (to avoid disturbing the in-

sects). Repeated measurements showed that the pH and dissolved oxygen concentration of aquarium water did not change over time. One radiograph was taken prior to the introduction of insects to record the presence of artifacts, and a series of images was taken at various times after animal introduction. X-ray film was loaded into a cassette designed to increase film sensitivity and placed behind a microcosm. Film was exposed with a portable X-ray unit (Kramex<sup>®</sup> model PX-20N) at settings determined by trial and error to produce good quality images (exposure 0.2 s at a distance of 40 cm) and radiographs were developed in our laboratory.

Littoral taxa (3 m water depth) studied included the mayfly *Hexagenia limbata*, the alderfly *Sialis velata*, the caddisfly *Polycentropus* sp., and the chironomids *Glyptotendipes* sp. and *Procladius* sp. The body size, functional feeding group, and number of individuals on which observations were made are given in Table 1. All littoral taxa were collected in the autumn (October). An additional collection of *H. limbata* and *S. velata* was made in the spring (May) to measure seasonal differences in their burrowing behaviors. Observations on littoral taxa were made at 1-d intervals and were limited to a total duration of 3 d because after this time it became difficult to distinguish among the large number of burrows dug by individual *H. limbata* nymphs.

To assess the extent of variation within a genus, observations were made on 3 species of *Chironomus* (Table 1) collected in the autumn from the 9-m depth. The burrows of 4th-instar larvae were recorded at 3-d intervals up to 9 d.

Observations on various taxa were made sequentially. Burrow form and dimensions of all taxa were measured directly on each radiograph (1:1 scale) using a manual curvimeter. Data on *Chironomus* species were tested for normality and equal variance prior to conducting ANOVA, and the Bonferroni correction was applied to multiple comparisons to take into account chance significance values.

## Results and Discussion

### *Burrow forms and dimensions*

Representative radiographs of burrows constructed by each taxon are shown in Fig. 1. The burrows of most of the taxa we studied are U-shaped, as has been reported for most burrowing aquatic insects, e.g., alderflies (Pritchard and Leischner 1973), mayflies (Hunt 1953, Ladle and Radke 1990, Edmunds and McCafferty 1996), and chironomids (Hilsenhoff 1966, McLachlan and Cantrell 1976, Rasmussen 1984, Ferrington 1992). Reports of J-shaped burrows have been ascribed to either unfinished U-shaped burrows (*Sialis* sp., Pritchard and Leischner 1973) or to insufficient sediment depth in newly constructed reservoirs (*Chironomus* sp., McLachlan and Cantrell 1976). In contrast, the J-shaped burrows of *Chironomus anthracinus* are reported to be the characteristic form for this species (Jónasson 1972, 1996).

Our observations suggest that larvae of the caddisfly *Polycentropus* sp. may be particularly variable in their burrowing behavior; of the 4 individuals that we studied, 3 constructed I- or J-shaped burrows, whereas 1 constructed a U-shaped burrow. Furthermore, *Polycentropus* sp. larvae collected from another nearby Canadian Shield lake (Lake Laflamme, 47°19'N, 71°07'W) did not burrow at all in the laboratory, but lived in their silken nets on the sediment surface. This difference in behavior between *Polycentropus* sp. larvae collected from the 2 lakes could be a result of either a taxonomic difference between larvae (larvae were not identified to species) or, more likely, the more liquid character of the sediment in Lake Laflamme (95% water, versus 70% water by weight for L. St. Joseph sediment), which made it unsuitable for larval burrows. These results suggest that sediment character can affect the form of burrows constructed by a

given taxon (Wallace and Merritt 1980, Berg 1995).

Burrow depth varied greatly among taxa (Fig. 2). In the autumn, the greatest mean burrow depth was recorded for *H. limbata* (Fig. 2), and individual burrows of this species extended up to 10 cm below the sediment-water interface. These results are consistent with those of Hunt (1953) who reported a maximum burrow depth of 12.7 cm for *H. limbata*. Eriksen (1968) observed a mean burrowing depth of 4.2 cm for this species, which compares closely to the 4.7 cm that we measured for *H. limbata* in the spring (Fig. 2). The mean depth to which both *H. limbata* and *S. velata* burrowed (Fig. 2) was significantly greater in the autumn than in the spring ( $p = 0.03$  and  $0.01$ , respectively, Mann-Whitney rank sum test). These seasonal differences in burrowing depth cannot be explained by differences in individual size (as has been reported by Hunt 1953) because there were no significant differences in the mean length of individuals collected between the 2 seasons ( $p = 0.5$  and  $0.3$  for *H. limbata* and *S. velata*, respectively, Mann-Whitney rank sum test). We observed *Chironomus* spp. burrows to a depth of 7.5 cm, which is similar to the maximum depth reported for members of the genus by Wang et al. (1994). Hilsenhoff (1966) also reported that *Chironomus plumosus* larvae feeding in the laboratory at 10°C (as in our study) remained in the top 8 cm of the sediment. However, there may be a strong seasonal variability in burrowing behavior; Hilsenhoff (1966) observed that at 5°C larvae did not feed and burrowed to a depth of up to 50 cm. The burrows of *Glyptotendipes* sp. larvae (Fig. 2) reached a mean depth ( $\pm 1$  SE) of 1.5 cm ( $\pm 0.02$  cm,  $n = 7$ ) and a maximum depth of 2 cm, which is similar to the 2–3 cm depth reported by Rasmussen (1984) for this taxon.

The mean length of an individual burrow was directly related to the body size of the taxon that produced it, with the longest burrows being made by *H. limbata* (Fig. 3). Burrow lengths of between 3 and 5 cm have been reported for *Glyptotendipes paripes* (Rasmussen 1984), which agrees with the mean value of 3.5 cm measured in our study for this genus. There are few other published data with which we can compare our observations. Burrows constructed by *H. limbata* and *S. velata* were significantly shorter in the spring than in the autumn ( $p = 0.03$ ,  $0.01$ , respectively, Mann-Whitney rank sum test).

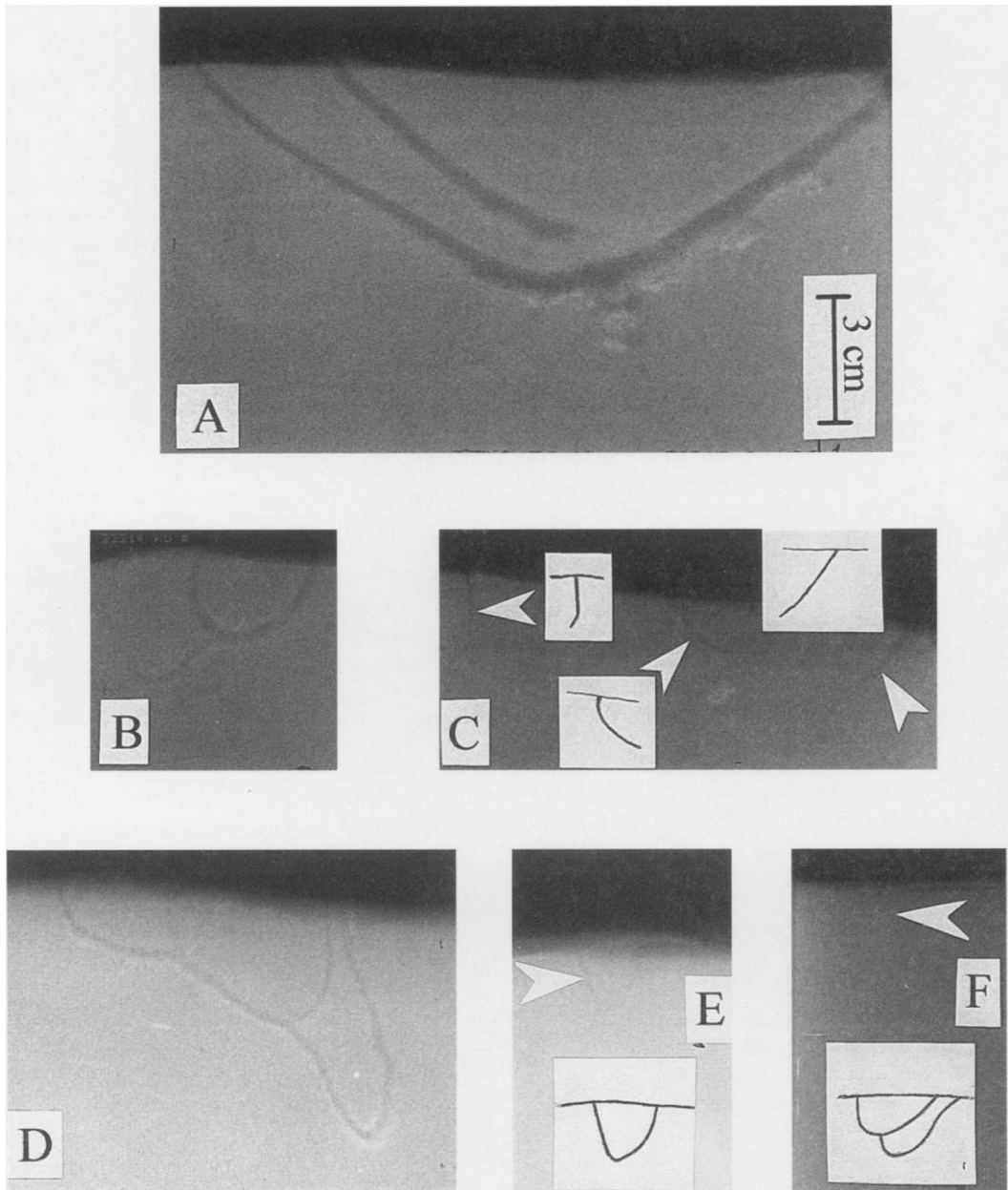


FIG. 1. Radiographs of burrows made by immatures of (A) the mayfly *Hexagenia limbata*, (B) the alderfly *Sialis velata*, (C) the trichopteran *Polycentropus* sp., and the chironomids (D) *Chironomus* sp., (E) *Glyptotendipes* sp., and (F) *Procladius* sp. Insets in C, E, and F are tracings from original radiographs and arrows indicate burrows. All radiographs are to the same scale.

The burrows constructed by most taxa had either approximately the same width as their bodies (*Glyptotendipes* sp. and *Procladius* sp.) or were somewhat wider, i.e., from 13% for *H. lim-*

*bata* to 36% for *Chironomus* spp. If we assume that larval burrows are approximately round in cross-section (measurements were made only in the vertical plane), then these data suggest that

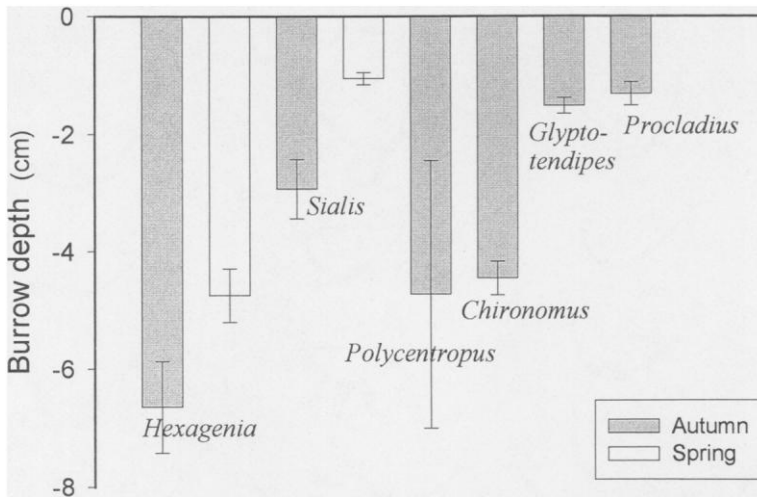


FIG. 2. Mean ( $\pm 1$  SE) depths to which the study taxa burrowed based on the maximum value for each individual recorded during a 3-d observation period. Both autumn and spring values are shown for *Hexagenia limbata* and *Sialis velata*, whereas autumn values only are shown for the other taxa.

larvae are not able to turn around without leaving their burrows. However, because the sediment in which larvae live is very liquid (70–95% water by weight), it probably provides little resistance to a turning larval body.

Individual *H. limbata* varied in the forms of their burrows and the rate at which they were

constructed (Fig. 4). Individual *H. limbata* nymphs remained in a given burrow for several hours at a time, and new burrow construction started below the sediment surface from a previous burrow (Fig. 4). A strategy of remaining in the sediment while constructing a series of burrows should minimize an insect's exposure

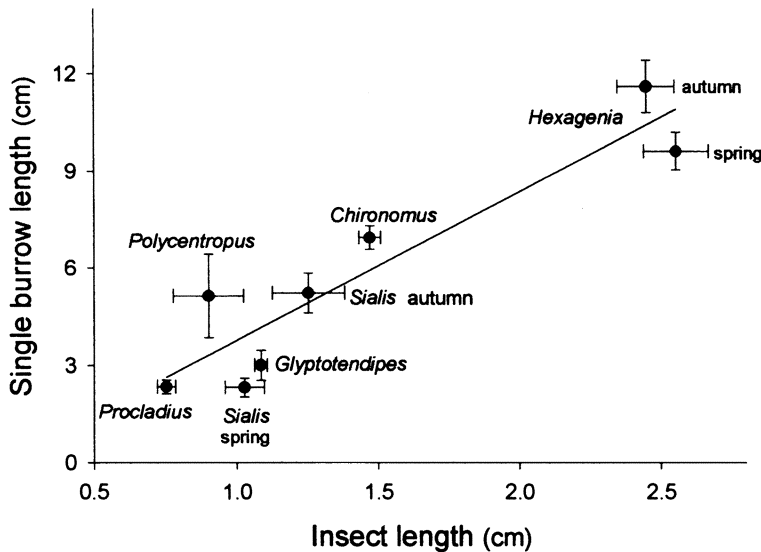


FIG. 3. Relationship between the mean length ( $\pm 1$  SE) of an individual insect and the mean length ( $\pm 1$  SE) of its burrow ( $r^2 = 0.86$ ). Both autumn and spring values are shown for *Hexagenia limbata* and *Sialis velata*, whereas autumn values only are shown for the other taxa.

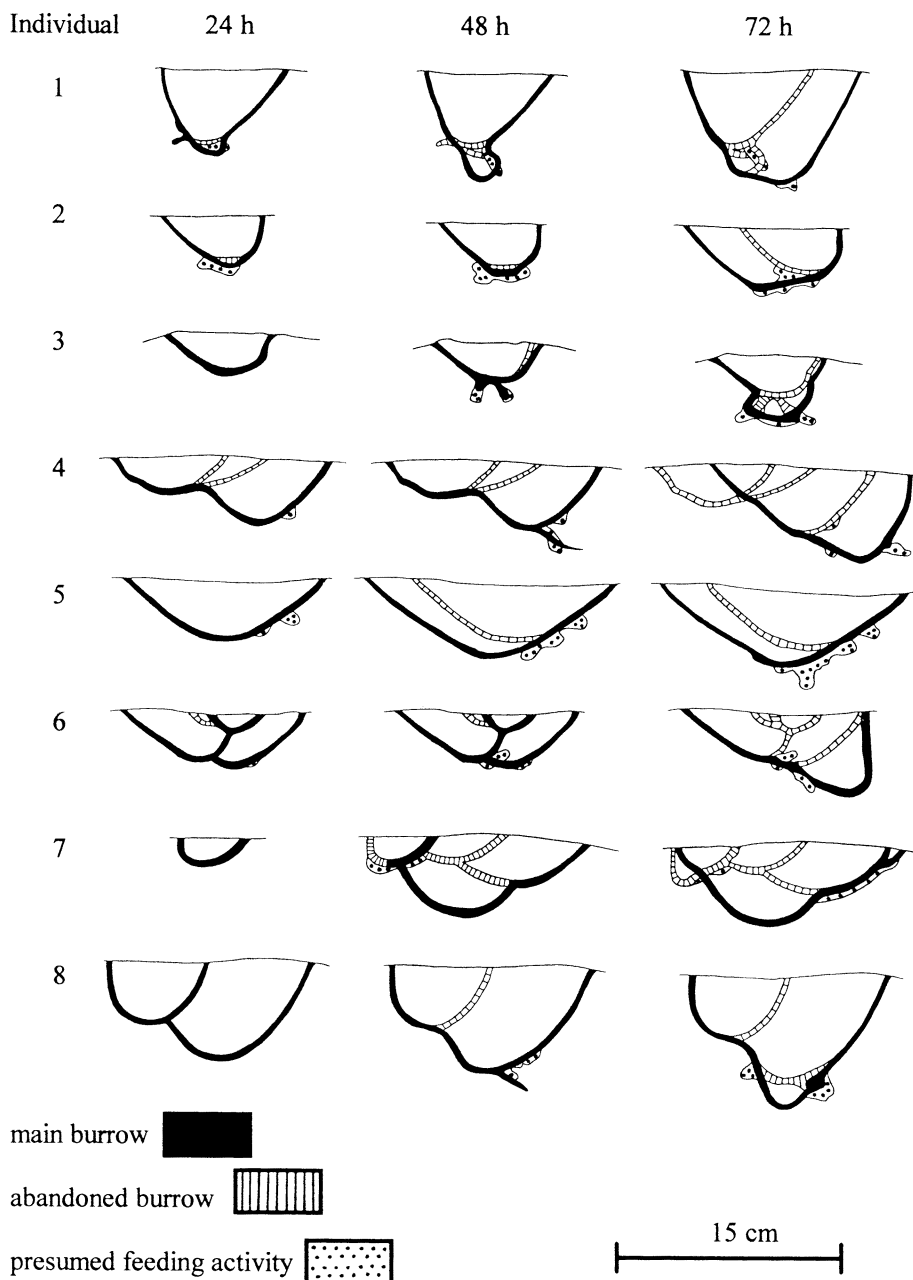


FIG. 4. Temporal progression in the burrow systems of 8 *Hexagenia limbata* nymphs illustrating individual variability in burrowing activity. Drawings are direct tracings from radiographs.

to predators. Old burrows appear to be blocked off and abandoned by *H. limbata* nymphs (Figs. 1 and 4). This behavior contrasted with that of *S. velata* and the chironomids we studied, all of which appeared to use their complete burrow

system, i.e., old burrows are not blocked off as new burrows are constructed (Fig. 1). Sediment-filled excavations along the burrows of *H. limbata* (Figs. 1 and 4) appeared to be the result of feeding activity. This observation is consistent

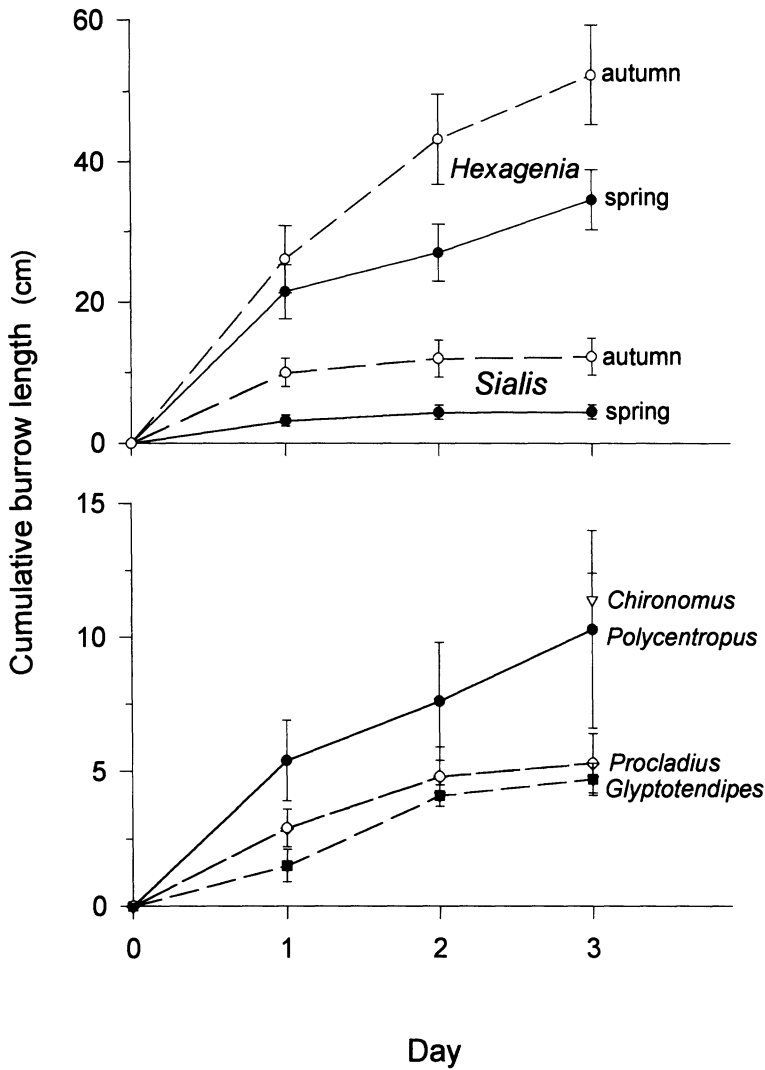


FIG. 5. Cumulative mean lengths ( $\pm 1$  SE) of burrows constructed over 3 d by 6 insect taxa. Both autumn and spring values are shown for *Hexagenia limbata* and *Sialis velata* (upper panel), whereas autumn values only are shown for the other taxa (lower panel). Datum for *Chironomus* spp. is the mean of the 3 species for day 3.

with the suggestion that *H. limbata* nymphs feed on sediment within their burrows (Zimmerman and Wissing 1980).

#### Burrowing rate

The mean number of burrows dug by nymphs of *H. limbata* increased over time and was greater than the number constructed by other taxa during a 3-d observation period, i.e., individual *H. limbata* nymphs had dug an average of 6 burrows, whereas other taxa had con-

structed only 2. Consistent with the increase in burrow number, the cumulative length of burrows constructed by the mayfly exceeded that of all other taxa at any given time (Fig. 5). Zimmerman and Wissing (1978) also reported that *H. limbata* nymphs are very active, feeding both day and night. However, individuals varied greatly in their activity level. At 1 extreme, an individual nymph was observed to construct a new extension to its gallery system every 2 h over a 30-h observation period. At the other extreme, 1 nymph did not add to its burrow over

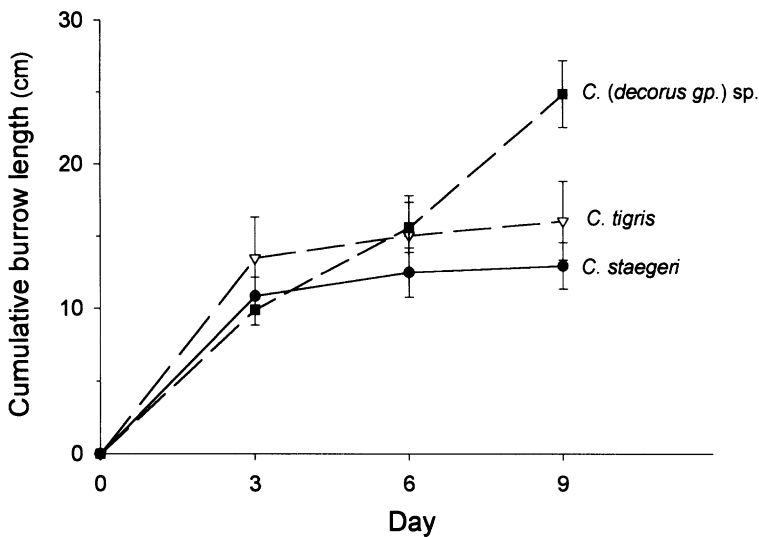


FIG. 6. Cumulative length of burrows (mean  $\pm$  SE) constructed over a 9-d period by larvae of 3 species of *Chironomus*.

a 3-d period despite remaining active during this time (judged by the turbidity of the water above its openings; cf. Fremling 1967). The variation in activity among nymphs did not appear to be related to their body size. For example, 2 *H. limbata* nymphs 28 mm in length built burrows 17 and 104 cm long over a 3-d period.

*Sialis velata* constructed single burrows during the 1st day of observation, but made no more over the following 2-d period (Fig. 5). These results are consistent with observations made on *S. cornuta* (Pritchard and Leischner 1973), and support the idea that larvae of *Sialis* are sit-and-wait predators rather than being active searchers for prey. However, the inactivity of the predator could also be explained by an absence of prey in the predator's laboratory surroundings.

#### Variation among congeners

We compared the burrowing behavior of 3 species of *Chironomus* to assess the extent of behavioral differences among sympatric congeners. There were no significant differences among the species (ANOVA,  $p > 0.3$ ) in the mean depth to which they burrowed (Fig. 2 for the genus) or the mean length of single burrows (Fig. 3 for the genus). However, over a 6-d period, larvae of *C. (decorus gr.) sp.* dug an average of 6 burrows, whereas the other *Chironomus* species constructed only 2. As a consequence, there

was a significant difference among the species in the cumulative lengths of their burrows (ANOVA,  $p = 0.005$ ), with those of *C. (decorus gr.) sp.* larvae being significantly longer ( $p < 0.05$ , SNK test) than those of either *C. staegei* or *C. tigris* (Fig. 6). There was no significant difference between the cumulative burrow lengths of the latter 2 species ( $p > 0.05$ , SNK test). Our results suggest that sympatric congeners can differ in their burrowing behavior, which could partly explain their ability to coexist.

#### Application of X-ray images to the study of bioturbation

The burrowing, feeding, and irrigation behaviors of benthic insects can influence solute transport and the physical and chemical properties of sedimentary deposits (Granéli 1979, Lawrence et al. 1982, Wang et al. 1994, Levinton 1995). The greater activity of *H. limbata* compared to the other taxa we studied (Fig. 5) suggests that this taxon will have the greatest impact on the sedimentary environment of Lake St. Joseph. We estimated that the seasonal mean daily burrow volume created by an individual *H. limbata* was 4 cm<sup>3</sup>. Given a density of 13 nymphs/m<sup>2</sup> in Lake St. Joseph (L. Hare, unpublished data), we estimated that *H. limbata* nymphs excavated 52 cm<sup>3</sup> m<sup>-2</sup> d<sup>-1</sup>. Given our estimates of the population densities and bur-



rowing volumes of the other insect taxa present, the total volume of sediment likely to be burrowed by these taxa ( $1 \text{ cm}^3 \text{ m}^{-2} \text{ d}^{-1}$ ) would represent only a small proportion ( $\sim 2\%$ ) of the estimated total burrow volume created by *H. limbata*. *Hexagenia* nymphs are absent at 9 m, where the volume of sediment excavated by larvae of the dominant genus *Chironomus* spp. was  $< 1 \text{ cm}^3 \text{ m}^{-2} \text{ d}^{-1}$  (given a larval density of  $18/\text{m}^2$  and a burrow volume of  $0.1 \text{ cm}^3$ ).

We can also estimate the volume of sediment that would be excavated by a hypothetical *H. limbata* population with a density corresponding to the mean calculated from 13 studies in 20 lakes located in Kansas (Horst and Marzolf 1975), Manitoba (Heise et al. 1988), Michigan (Hunt 1953), Ohio (Rutter and Wissing 1975, Zimmerman 1977), Oklahoma (Craven and Brown 1969, Sublette 1953), Ontario (Britt 1955), Québec (Rasmussen 1988, Hare 1995, L. Hare, unpublished data), South Dakota (Swanson 1967), and Texas (Welch and Vodopich 1989). Given a mean population density ( $\pm 1$  SE) of  $160 \pm 33$  individuals/ $\text{m}^2$  and our individual bioturbation estimates, an average-sized population would excavate  $591 \pm 125 \text{ cm}^3 \text{ m}^{-2} \text{ d}^{-1}$  (mean  $\pm 1$  SE). Nymphal burrowing activity would likely be greater at temperatures above that at which our laboratory observations were made ( $10^\circ\text{C}$ , Zimmerman and Wissing 1978). If we suppose that the average-sized population ejects excavated material above the sediment surface, then its deposition would represent a daily sedimentation rate of  $0.06 \text{ mm}$ . Animal burrowing also increases the effective surface area of the sediment-water interface, which is likely to influence the flux of nutrients and possibly contaminants between sediment and the overlying water.

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