

Sediment Suspension by Burrowing Mayflies (*Hexagenia* spp., Ephemeroptera: Ephemeridae)

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ABSTRACT. Burrowing and ventilation activities of benthic invertebrates can influence water column turbidity, nutrient concentrations, and possibly oxygen balance of lakewide ecosystems. In laboratory experiments, we determined rates of bioturbation-induced suspension of fine Lake Erie sediments caused by the burrowing mayfly *Hexagenia* of various sizes (lengths 13–28 mm) and multiple densities (70–1,111 larvae/m²) and water temperatures (10–25°C). Larvae were inoculated into 2-L jars containing Lake Erie sediment and water. Bioturbation and sediment settling rates were independently estimated from sediment concentrations in water, measured twice daily for 14–18 d. Nonlinear regression was used to estimate sediment suspension rate for each jar (flux, mg/L/h). Logarithmic transformations of size, density, and temperature best described sediment flux. Separate experiments demonstrated that flux was unaffected by sediment depth, but did vary by sediment type, which was related to location from which Lake Erie sediment had been collected. Sediment suspension rates increased as food became depleted. Sediment suspension by pre-emergent (25 mm long) larvae at densities and water temperature typical for late spring in western Lake Erie (400 larvae/m² at 22°C) averaged 12 g/m²/h. Although this level of bioturbation by *Hexagenia* larvae in western Lake Erie likely contributes only a small fraction of the basinwide annual sediment load, sediment suspension is possibly an important epibenthic source of nutrients and sediment-associated contaminants during spring. Such concentrations would exceed the clearance capacity of dreissenid mussels and may partially explain why dreissenids have not become abundant in soft sediments of the western basin.

INDEX WORDS: *Hexagenia*, bioturbation, sediment suspension, Lake Erie.

INTRODUCTION

Aquatic invertebrate activity, especially burrowing and ventilation activities, can influence aquatic ecosystem processes, such as sediment flux (McCall and Tevesz 1992, Bartsch *et al.* 1999), contaminant mobilization (McCall and Tevesz 1992), and nutrient cycling (Matisoff and Wang 1998). The magnitude and importance of aquatic invertebrate activity is influenced by both biotic and abiotic factors, including organism size (Rhoads 1967), health

(Henry *et al.* 1986), population density (Zimmerman and Wissing 1978), food availability (Sweeney 1984), contaminant stress (Oseid and Smith 1974, Henry *et al.* 1986, Briggs *et al.* 2003), and water temperature and oxygen content (Sweeney 1984, Eriksen 1963a). Changes in any of these features can affect bioturbation.

The burrowing mayfly *Hexagenia* has major potential to influence sediment flux by its burrowing activities. The larvae of this insect construct burrows (Hunt 1953, Charbonneau and Hare 1998) through which they circulate water using metachronal movements of their abdominal gills (Wingfield 1939, Lyman 1943, Eriksen 1963a). The circulation of water through burrows also brings

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food particles toward the mouthparts (Zimmerman and Wissing 1980) and helps maintain burrow integrity (Keltner and McCafferty 1986). Larvae also ingest benthic sediment at the mouth of their burrows (Zimmerman and Wissing 1980). *Hexagenia* burrowing activity, burrow irrigation, and benthic feeding behavior all contribute to sediment suspension (Bartsch *et al.* 1999) and solute flux (Matisoff and Wang 1998). Since both turbidity and nutrients regulate phytoplankton and epibenthic photosynthetic production, this organism may play an important role in the food web of shallow, soft-bottomed lakes.

After a prolonged absence (Britt 1955), *Hexagenia* have recently recolonized much of the western basin of Lake Erie (Krieger *et al.* 1996, Edsall *et al.* 1999, Schloesser *et al.* 2000). This return has been attributed to pollution abatement programs of the 1970s (Rockwell *et al.* 2005) and the arrival of dreissenid mussels, leading to oligotrophication of western Lake Erie (Haffner 1994) and the creation of conditions suitable for mayfly colonization (Corkum *et al.* 1997a). By 1997, larval populations had reached basin-wide average densities close to historical levels (Schloesser *et al.* 2000) of approximately 350 larvae/m² (Reynoldson *et al.* 1989). However, larvae have still not reappeared throughout the basin (Schloesser *et al.* 2000). The timing of *Hexagenia* reappearance broadly parallels other trends in water quality parameters observed in the western and central basins. Concentrations of total phosphorus in late spring, which had been gradually declining until the mid-1990s, began to rise over the period 1996–2002 (Rockwell *et al.* 2005). Turbidity increased through the 1990s in the central basin (Barbiero and Tuchman 2004, Burns *et al.* 2005), although it had been expected to decline as a consequence of dreissenid filtering activity (Nicholls and Hopkins 1993). One objective of our study was to assess whether *Hexagenia* bioturbation could be theoretically sufficient to influence basin-wide suspended sediment or nutrient concentrations.

Larvae are approximately 1 mm long when they hatch during late summer and early fall. Mature larvae achieve pre-emergent lengths of 23 mm (males) to 30 mm (females) in late spring, prior to the mass emergence of subimagos (Hunt 1953). *Hexagenia* exhibit a 1 to 2-year life cycle in Lake Erie (Manny 1991, Corkum *et al.* 1997a), largely regulated by water temperature (Corkum and Hanes 1992, Winter *et al.* 1996), dissolved oxygen (Winter *et al.* 1996), and food availability (Hanes and Ciborowski

1992). In western Lake Erie, epibenthic water temperatures vary from 1°C in winter to about 25°C in summer (unpubl. data). Sediment suspension due to *Hexagenia* larval activity is likely to be greatest in early June just prior to emergence, when water temperatures are rising and larvae are largest.

We conducted laboratory experiments to quantify the potential for sediment flux by *Hexagenia* larvae in western Lake Erie by examining the effects of larval size, larval density, and water temperature on sediment suspension rates. Variation in responses to sediments collected from different locations within western Lake Erie, and to different sediment depths were also investigated.

MATERIALS AND METHODS

Study Organism and Experimental Set-up

Experimental animals were reared in the laboratory from eggs collected from female *Hexagenia* spp. imagos at the head of the Detroit River, Windsor, Ontario and at Colchester Harbour on the north shore of western Lake Erie, following protocols of Friesen (1981) and Hanes and Ciborowski (1992). At both collection locations the *Hexagenia* population consists of a mixture of *H. limbata* (Serville) and *H. rigida* McDunnough (Corkum *et al.* 1997b), which are functionally and ecologically similar (Hunt 1953, Edmunds *et al.* 1976). Larvae were reared and maintained in bulk cultures (aerated aquaria containing Lake Erie sediment and dechlorinated tapwater) until required.

Sediment was collected annually with a Ponar grab as needed from a location near the center of western Lake Erie (N 41°48'51" W 82°59'17", Fig. 1) that has historically supported high densities of *Hexagenia* (Reynoldson and Hamilton 1993). Sediment was stored in plastic 20–25 L buckets at 4°C. Prior to use, it was passed through a 1-mm mesh sieve to remove any large resident organisms and returned to cold storage for at least 1 week.

Experiments were conducted in 12 × 12 × ca. 15 cm deep 2-L cuboidal, glass jars. Each jar contained 3.5 cm depth of sediment (500 mL) and 8.5 cm depth (1,220 mL) of dechlorinated, aerated water. Jars were covered with plastic lids, and allowed to clear for 4 d prior to larval addition and the start of the experiment. Forty-eight h prior to the start of the experiment, jars were placed into the appropriate temperature treatments to acclimate, and aerated with capillary tubing inserted through small holes in the lids and attached to the main air supply using hypodermic needles (Corkum and Hanes 1989).

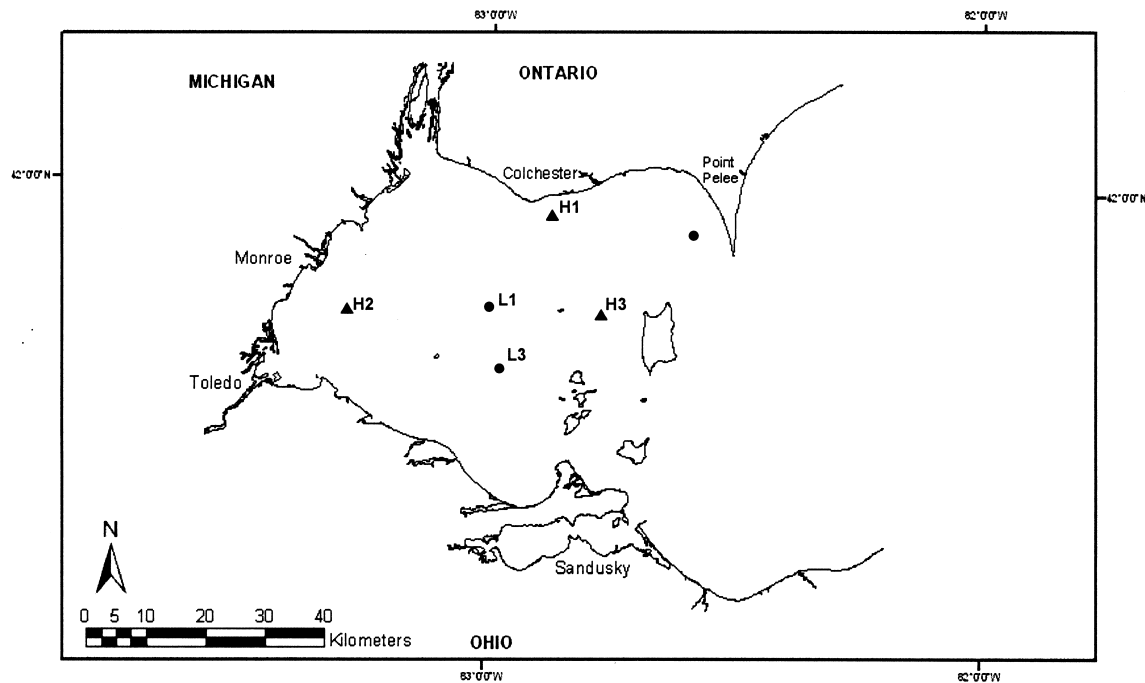


FIG. 1. Sediment collection locations in western Lake Erie.

Jars were housed in either black Plexiglas water baths ($128 \times 44 \times 40$ cm) whose temperature was regulated by circulating refrigerated water (treatments below room temperature), or into cardboard boxes, painted black inside to simulate the light reflectance of the Plexiglas chambers situated in controlled-environment chambers (treatments at or above room temperature).

Hexagenia size and density combinations were randomly assigned to each jar in a given temperature treatment and checked for appropriate interspersions. Food (10 mg/larva suspension of yeast/alfalfa/Tetrafin fish food mixture (Hanes and Ciborowski 1992) was added to jars 48 h prior to adding larvae to the jars at the beginning of the experiment.

Prior to adding larvae to the experimental jars, an initial water sample was collected (time = 0 h). Larvae were then added to the jar. Water samples were subsequently taken every 3 h for the first 12 h and then every 12 h thereafter for a total of 14 d. Water samples were collected using a rigid plastic tube (11 cm long \times 9 mm inside diameter) placed as close to the sediment-water interface as possible without disturbing the sediment. Two aliquots were collected from each jar during a given sampling period and emptied into a test tube. Food was again

added to each jar after 200 h. Each experiment ran for a total of 332 h (14 d).

Larvae were retrieved by sieving them from culture sediment, anaesthetized in carbonated water (Winter 1994), transferred into a Petri dish, separated into one of five size classes according to their total length (tip of head to the end of the abdomen), and allowed to recover in aerated dechlorinated water for 1 h prior to transfer to experimental jars.

Spectrophotometry

Suspended sediment concentrations were estimated by spectrophotometry within 2 h of sample collection. Each test tube was agitated to resuspend any particles that may have settled. The sample was then poured into a cuvette and read at 750 nm in a Bausch and Lomb Spectronic 20[®] spectrophotometer equipped with an infrared phototube and a red filter (12-mm path length). Distilled water was used as the reference liquid. The water samples were returned to the jars from which they were collected to ensure as little water loss as possible. The water level in each jar was checked daily. Any loss due to evaporation was replaced with distilled water.

Absorbance readings obtained for each jar at each sampling period were converted to Total Suspended Solids (TSS [mg/L]) using a standard curve created from sequential 1:1 dilutions of culture tank

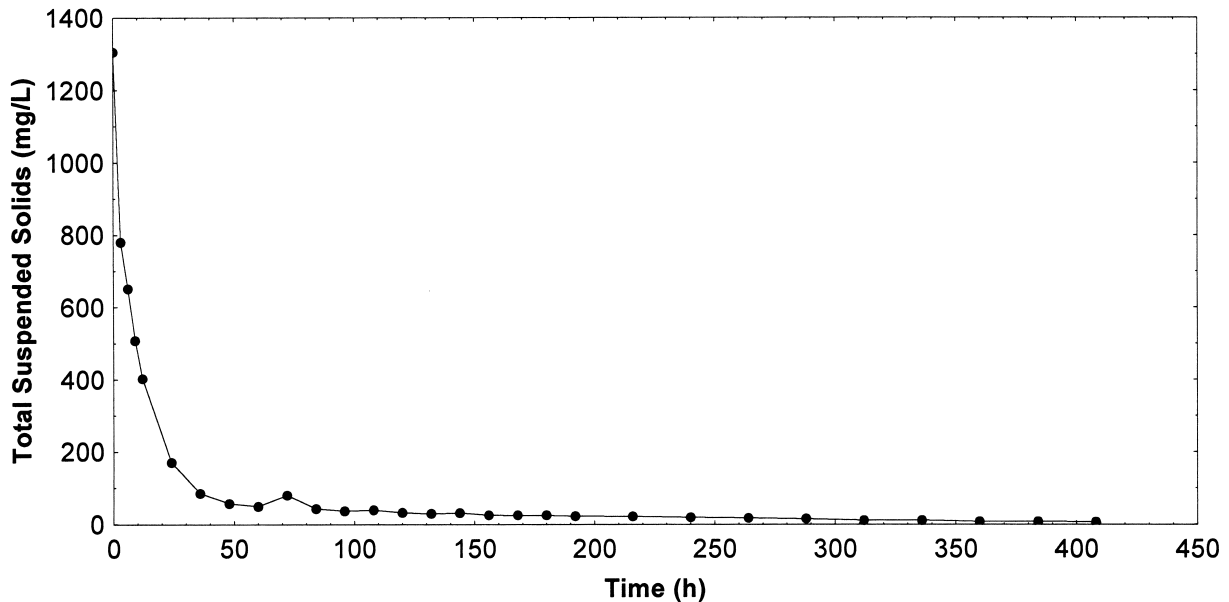


FIG. 2. Sediment settling rate for 22°C temperature treatment. Water used contained sediment suspended by *Hexagenia* larvae in a mass culture tank containing Lake Erie sediment from site L1.

water containing suspended Lake Erie sediment. Culture tank water was diluted with distilled water. A standard curve was created for an absorbance of 750 nm for each of the spectrophotometers. A known volume of water from each dilution was vacuum filtered through a pre-ashed, preweighed Whatman GF/C glass microfiber filter. The total volume filtered depended on the amount of suspended solids in each dilution. Filters were dried overnight at 100°C, cooled in a desiccator, and reweighed to the nearest 0.01 mg (Rosa 1985; J. Milne, Environment Canada, pers. comm. 2001). Linear regression was used to determine the relationship between TSS and absorbance at 750 nm.

Sediment Settling Rate

The settling rate of particles in water depends on the water viscosity (which is affected by temperature), particle diameter, and possibly on turbulence due to aeration of the jars. Consequently, a sediment settling rate was determined for each of the temperature treatments at the conclusion of a 14-d trial. The overlying water was drawn off from the jar with the highest larval density for each temperature and poured into a clean, empty jar. These jars were maintained, aerated in the initial housing. Water samples were collected every 3 h for the first

12 h and every 12 h thereafter for 18 d. Total suspended sediment concentration was estimated for each time point from spectrophotometric readings (Fig. 2). Settling rates were determined by calculating the instantaneous settling rate for each time point and then taking an average of the first 6 data points after the instantaneous settling rate became constant. A line was fitted to the average settling rate for each temperature and was used to calculate the settling rate for a given temperature treatment.

Determination of Sediment Flux

Nonlinear regression (STATISTICA version 6.0 (StatSoft Inc. 2001)) of TSS as a function of time was used to determine the sediment flux according to the formula :

$$\text{TSS}_t = (\text{B}_{\text{Bioturb}}/\text{B}_{\text{Settle}}) * (1 - \exp(-\text{B}_{\text{Settle}} * t)) \quad (1)$$

where

TSS_t is the concentration of suspended sediment at time t (mg/L)

$\text{B}_{\text{Bioturb}}$ is the rate of sediment suspension (mg/L/h),

B_{Settle} is the settling rate (mg/L/h), and t is time (h).

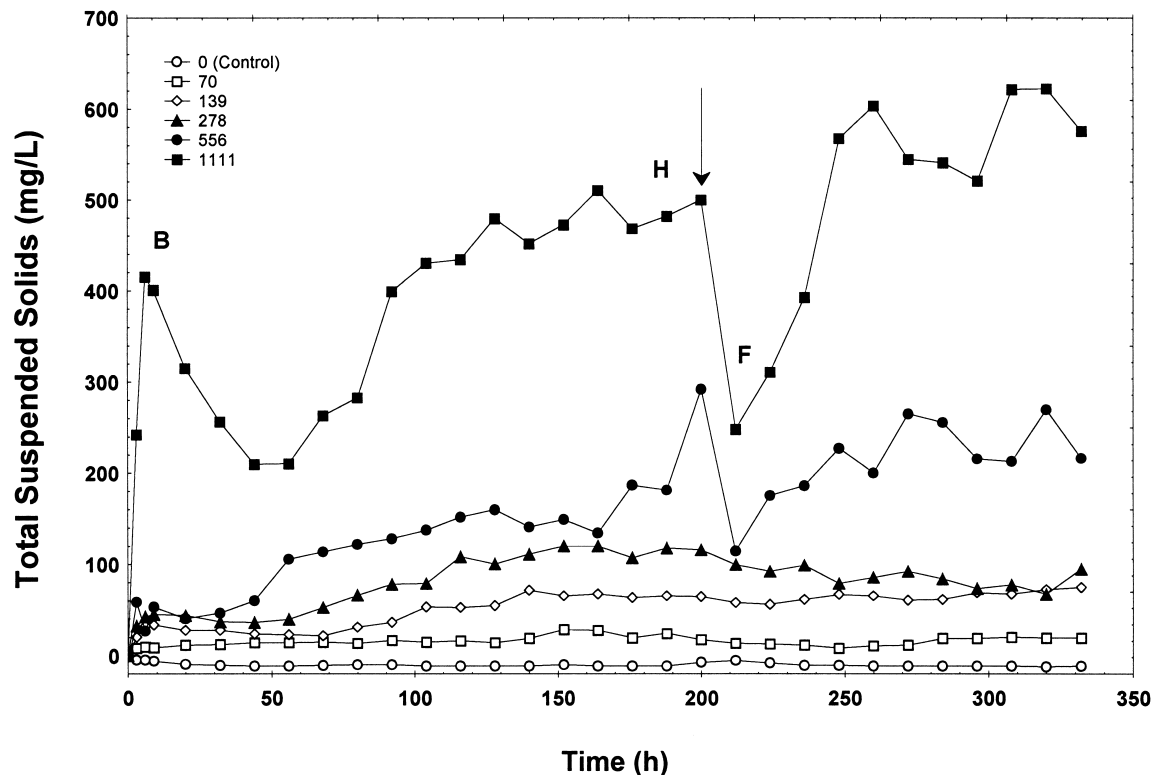


FIG. 3. Time course of Total Suspended Solids (TSS [mg/L]) during a single trial using 22 mm long larvae at 19°C and different densities. Letters indicate periods of initial burrow construction (B), hunger (H) and satiation following feeding (F). Arrow indicates time of feeding (200 h).

Size, Density, and Temperature Experiments

Bioturbation studies were conducted with five larval size classes (mean class [size range] mm: 12.5 [10–14], 17.5 [15–18], 20.5 [19–21], 23.0 [22–24], and 27.5 [25–30]), five larval densities (70, 139, 278, 556, and 1,111 larvae/m²) and five water temperature (10, 15, 19, 22, and 25°C) treatments whose values were based on the natural range of variation of these variables in the western basin of Lake Erie. The experiment was a 5×5×5 factorial design, with three replicate blocks, completed over a 2-y period. The 2 larvae/jar (139 larvae/m²) and 8 larvae/jar (556 larvae/m²) treatments for 17.5 mm larvae and for 23 mm larvae were left out of each temperature treatment due to space limitations. A control jar containing Lake Erie sediment and no larvae was part of each temperature treatment. Suspended sediment concentrations in each jar showed three distinct phases. We operationally describe these phases as representing periods of initial burrow construction, maximal bioturbation (larvae hungry) and minimal bioturbation (larvae recently

fed), each characterized by different sediment suspension rates (Fig. 3). These are delineated by distinctive peaks for initial burrow construction and maximal rates, and by a trough in the sampling period after feeding. The asymptotic TSS values for burrow construction, maximal, and minimal regions were used to determine the sediment suspension rates. Sediment suspension rates were estimated for each of these three phases during each trial—initial burrow construction (6–48 h), maximum, and minimum activity rates.

We used forward stepwise multiple regression to quantify the influence of size, density, and temperature on sediment suspension rates (B_{Bioturb}). All independent variables were Ln transformed prior to analysis. The independent variables' quadratic terms (values squared) and their interactions (products; e.g., Ln [size] × Ln [density] × Ln [temperature]) were also used in the analysis. To estimate the relative importance of among-trial variation, “block” was included in the analyses as two dummy variables. Except for “block” (trial), independent

variables whose slopes were statistically significantly different than zero ($p < 0.05$) were retained in the final regression equations. T-tests were performed on plots of the observed versus expected sediment suspension rates for each of the three sediment suspension phases to determine if the slopes differed significantly from a slope of one.

Variation in Sediment Suspension Due to Sediment Depth

A separate study used three size classes of larvae (lengths 10–14 mm, 16–20 mm, and 22–25 mm) and two sediment depths (3.5 and 10 cm) to determine if sediment depth in laboratory jars influenced larval sediment suspension rate. Five replicates of each larval size class and sediment depth combination, and one control bottle containing no larvae were set up at 22°C. Five larvae (577 larvae/m²) were added to polyethylene 2-L soft drink bottles with the tops cut off (19 cm tall × 10.5 cm inside diameter). Larvae were measured using a video camera and image analysis software to the nearest 0.01 mm. The textured bottom of the bottles was uneven in depth and was filled to a 4 cm depth with washed, fine silica sand (particle size < 500 μm) prior to adding experimental sediment to prevent larvae from burrowing into this portion of the bottles. *Hexagenia* larvae do not burrow into homogeneous sand (Lyman 1943). The appropriate depth of sediment placed on top of the sand, and aerated, dechlorinated water was added to a depth of 8.5 cm above the sediment. Food was added, and jars were allowed to clear as above. Water samples were collected at time intervals and duration as described above. Analysis of covariance (ANCOVA) was used to determine if sediment suspension rates differed between sediment depths using mean larval size per bottle as a covariate.

Variation in Flux Due to Sediment Source

Sediment collected from six locations (Fig. 1) in the western basin of Lake Erie was used to determine the influence of sediment type on suspension rates of *Hexagenia* larvae. Five replicate jars of sediment from each location and a reference jar, containing site L1 sediment but no larvae, were set up at 22°C. Sediment and water were added to 2-L jars as in the General Methods section. Medium sized (15–22 mm) larvae, measured to the nearest 0.01 mm using Mocha, were added to jars at a density of 8 larvae/jar (556 larvae/m²). An ANCOVA

was used to determine if sediment suspension rate was significantly influenced by sediment type. Mean larval size per jar was used as a covariate in the analysis. Methodology and analysis procedures were the same as in previously mentioned experiments.

RESULTS

Sediment Settling Rate

Sediment settling rates increased with increasing temperature. Settling rates ranged from 0.44 mg/L/h (10°C) to 1.04 mg/L/h (22°C) (Table 1). The settling rate for the 25°C treatment was lower (0.95 mg/L/h) than that for 22°C. Linear regression explained 88 percent of the variation in settling rate. The settling rate terms (B_{settle}) used in the non-linear regression equations for each temperature treatment to determine sediment flux were interpolated from this regression equation.

Size, Density, and Temperature Experiments

Total suspended sediments followed a characteristic time course, which was most pronounced in the high density and large larval size treatments. The TSS rose rapidly during the first 3–12 h likely as a result of larval burrow construction (Fig. 3 “B”). This was followed by a period of 10–20 h when TSS decreased. TSS then rose gradually and often exceeded levels observed during initial burrow construction (Fig. 3 “H”). Sediment concentrations fell abruptly and dramatically during the period following feeding (Fig. 3 “F”), but then gradually rose to reach or exceed previous levels. This was typical of most trials. The experiments may have ended prior to a steady state (maximum sediment concentration) being reached in the overlying water for high larval densities, potentially

TABLE 1. Sediment settling rates for Lake Erie site L1 as a function of temperature. The linear regression equation for these settling rates takes the form $B_{\text{Settle}} = 0.087 + 0.039 * T$, where T = temperature, $R^2 = 0.88$.

Temperature (°C)	Settling Rate ±SE(mg/L/h)
10	0.44 ± 0.11
15	0.66 ± 0.15
19	0.89 ± 0.04
22	1.04 ± 0.15
25	0.95 ± 0.23

TABLE 2. Summary of forward stepwise multiple regression for the effects of larval size, larval density and water temperature on initial burrow construction, maximum, and minimum sediment suspension rates. All variables are significant ($p < 0.001$).

Initial Burrow Construction Rate			
	Regression Coeff.	S.E.	R ²
Intercept	-5.21	2.00×10^{-1}	
Ln Size \times Ln Density \times Ln Temp	1.05×10^{-1}	7.04×10^{-3}	0.78
Ln Size \times Ln Density	5.91×10^{-2}	2.34×10^{-2}	0.01
Total			0.79
Maximum (Hungry) Rate			
	Regression Coeff.	S.E.	R ²
Intercept	-6.75	3.18×10^{-1}	
Ln Size \times Ln Density \times Ln Temp	1.04×10^{-1}	3.93×10^{-3}	0.78
Ln Temp	1.09×10^{-1}	1.29×10^{-1}	0.04
Total			0.82
Minimum (Fed) Rate			
	Regression Coeff.	S.E.	R ²
Intercept	-7.50	3.50×10^{-1}	
Ln Size \times Ln Density \times Ln Temp	9.40×10^{-2}	4.31×10^{-3}	0.73
Ln Temp	1.33	1.42×10^{-1}	0.07
Total			0.80

underestimating the maximum sediment concentrations and thus loading estimates.

Initial burrow construction, maximal, and minimal sediment suspension rates all increased with increasing larval size, larval density, and water temperature. Estimates for these three different sediment suspension rates were based on the TSS peak for initial burrow construction, the maximal TSS peak and the TSS valley observed 12 h after feeding the larvae, respectively (Fig. 3). The size, density, and temperature combinations varied with each of the three trials since there was often a shortage of large larvae. As a result some of the size, density, and temperature combinations have fewer than three replicates and some of the combinations that were to be omitted were actually used in some trials when the appropriate sizes of larvae were available. Because all treatment combinations were replicated at least twice within the three experimental blocks, these adjustments may have influenced the standard errors of regression coefficient estimates but not the coefficients themselves.

Regression analysis using trial as a dummy variable showed that trial explained a maximum of 1%

of the variation in the sediment suspension rates ($R^2 = 0.01$, $p < 0.001$). Initial burrow construction rates were best estimated by the variables Ln (size) \times Ln (density) \times Ln (temperature) interaction and Ln (size) \times Ln (density) interaction (total $R^2 = 0.79$, $P < 0.001$; Table 2). Maximal (hungry) sediment suspension rates were best estimated by the variables for Ln (size) \times Ln (density) \times Ln (temperature) interactions, and Ln (temperature) (total $R^2 = 0.82$, $p < 0.001$ for both independent variables; Table 2). Minimal (fed) sediment suspension rates were best estimated by the variables for Ln (size) \times Ln (density) \times Ln (temperature) interaction and temperature (total $R^2 = 0.80$, $p < 0.001$ for both independent variables; Table 2).

The observed sediment suspension rates were plotted against the sediment suspension rates predicted from the terms of the multiple regression analysis to test for biases in predicted sediment flux. A t -test of the slope relating observed vs. predicted sediment suspension rates for the initial burrow construction rate and the minimum (fed) rate did not differ significantly from 1.0 ($p > 0.05$). The slope for the maximum (hungry) sediment suspen-

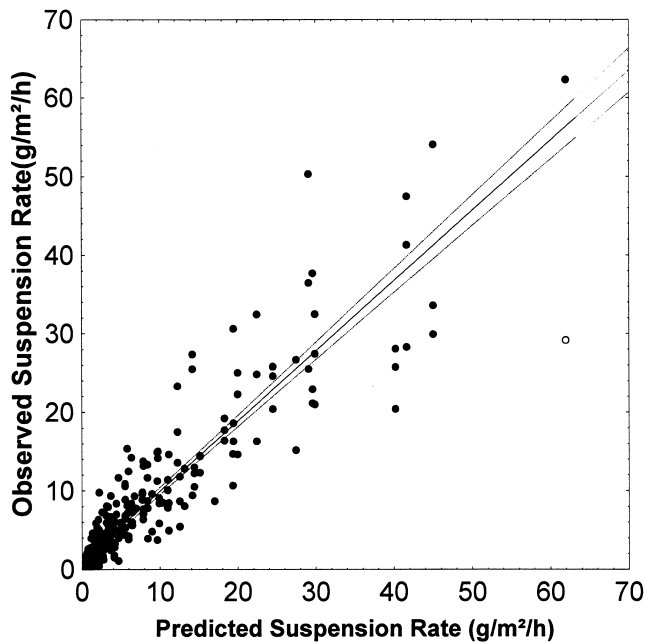


FIG. 4. Observed and predicted (from regression equation) sediment suspension rates for hungry larvae. Open circle represents an outlier excluded from analysis.

sion rate differed significantly from 1.0 ($p < 0.05$; Fig. 4), suggesting that the regression equation somewhat underestimated the maximal (hungry) sediment suspension rate.

Mean \pm SE maximum (hungry) sediment suspension rates were low in low temperatures for small larvae (12.5 cm), ranging from 0.23 ± 0.07 g/m²/h ($n = 3$) for 1 larva/jar at 10°C to 3.69 ± 1.35 g/m²/h ($n = 3$) for 8 larvae/jar. The high temperature (25°C) maximum (hungry) sediment suspension rates ranged from 0.36 ± 0.00 g/m²/h ($n = 2$) for small (12.5 cm) larvae at a density of 1 larva/jar to 39.02 ± 5.64 g/m²/h ($n = 3$) for large (27.5 mm) larvae at a density of 8 larvae/jar. Variation in sediment suspension rates for 19°C trials is shown in Figure 5.

Conversion of the regression-estimated suspension rates to a per larva basis suggests that synergistic interactive effects may occur among larger individuals. The sediment suspension rate per larva increased with increasing density for medium and large sized larvae during initial burrow construction and for large larvae during maximal sediment suspension (e.g., Fig. 6).

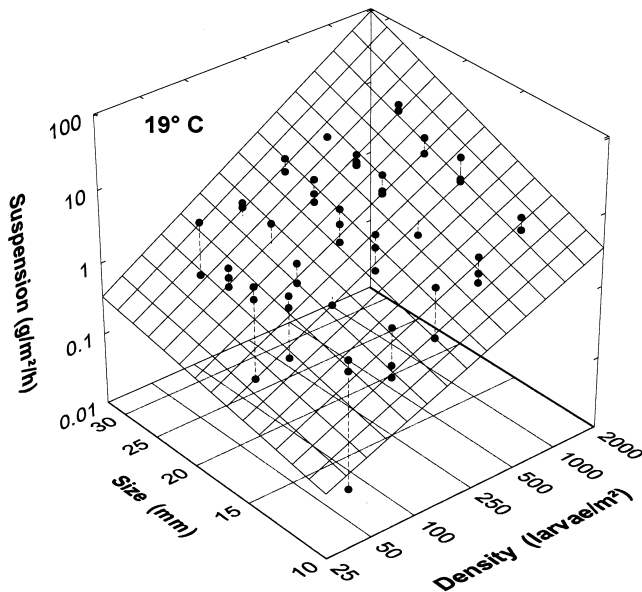


FIG. 5. Response surface of initial burrow construction sediment suspension rates (g/m²/h) estimated from the equation of the significant independent variables from the forward step-wise multiple regression analysis for 19°C. Dark circles represent actual data points upon which the regression analysis (Table 2) is based.

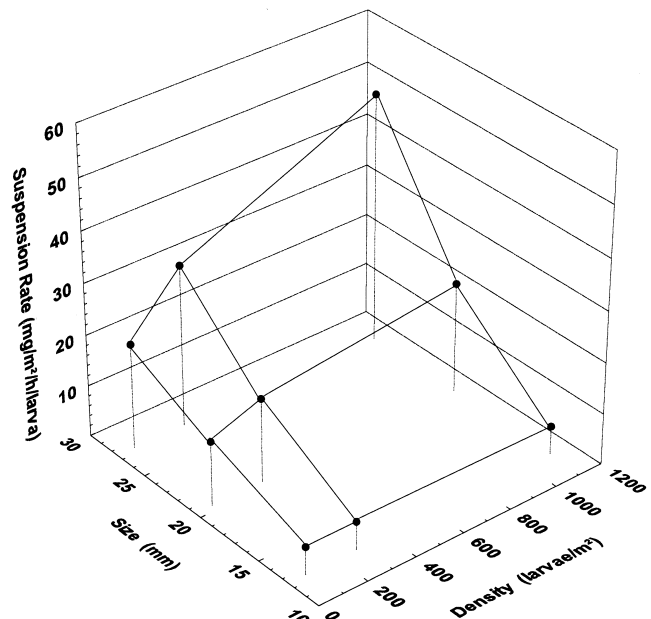


FIG. 6. Sediment suspension rates per larva (mg/m²/h/larva) at 25°C estimated from the equation of significant independent variables from the forward stepwise multiple regression (Table 2) for initial burrow construction rate.

TABLE 3. Analysis of covariance (ANCOVA) for the effects of sediment depth (3.5 cm or 10 cm) and larval size (small, medium or large) on sediment suspension rate (initial burrow construction and maximal rates). *** $p < 0.001$.

Initial Burrow Construction Rate				
	d.f.	SS	MS	F
Mean Larval Size	1	1,270.628	1,270.628	61.967***
Sediment Depth	1	83.391	83.391	4.067
Error	27	553.637	20.505	
Total	29	1,907.656		
Maximum (Hungry) Rate				
	d.f.	SS	MS	F
Mean Larval Size	1	1,029.200	1,029.200	39.065***
Sediment Depth	1	18.275	18.275	0.694
Error	27	711.340	26.346	
Total	29	1,758.815		

Variation in Sediment Flux Due To Sediment Depth

Sediment suspension rates during initial burrow construction by larvae in 10 cm of sediment were 18–20% greater than rates of equivalent-sized larvae in 3.5 cm of sediment. Maximum (hungry) sediment suspension rates for larvae in 10 cm of sediment were 4–14% greater than for larvae in 3.5 cm of sediment. However, these differences were not statistically significant ($p > 0.05$) and were much less than the differences observed among larval sizes. In contrast, larval size significantly affected both initial burrow construction and maximal sediment suspension rates for both sediment depths ($p < 0.001$) as had been observed in the size, density and temperature experiment (Table 3). Minimum sediment suspension rates were not analysed in this experiment since larvae began to emerge prior to the time point at which larvae were fed. Mean (\pm SE, $n = 5$) initial burrow construction rates for small larvae (10–14 mm) were 4.59 ± 0.58 g/m²/h and 7.51 ± 0.82 g/m²/h respectively, for the 3.5 and 10 cm sediment depth treatments. Mean (\pm SE, $n = 5$) initial burrow construction rates for large larvae (22–25 mm) were 18.97 ± 3.53 g/m²/h and 24.74 ± 2.46 g/m²/h for 3.5 and 10 cm sediment depths, respectively. The maximal (hungry) sediment suspension rates were 14.46 ± 0.88 g/m²/h and 15.83 ± 1.01 g/m²/h respectively, for 3.5 cm and 10 cm sediment depths for small larvae and 28.67 ± 2.89 g/m²/h and 30.01 ± 3.44 g/m²/h respectively, for 3.5 cm and 10 cm sediment

depths for large larvae (Fig. 7). No larval burrows were observed in the sand layer at the bottom of the bottles during the experiment or at the end of the experiment when larvae and sediments were removed from the jars.

Variation in Sediment Flux Due To Sediment Source

There were significant differences in both initial burrow construction and maximal (hungry) sediment suspension rates ($p < 0.001$) as a function of sediment type (Table 4). Mean (\pm SE, $n = 5$) suspension rates during initial burrow construction ranged from 7.47 ± 0.73 g/m²/h to 8.80 ± 1.23 g/m²/h for low larval density (L) sediments and from 3.19 ± 0.21 g/m²/h to 4.09 ± 0.42 g/m²/h for high larval density (H) sediment. During the maximal (hungry) period, mean (\pm SE, $n = 5$) sediment suspension rates ranged from 17.53 ± 0.91 g/m²/h to 21.10 ± 1.08 g/m²/h for low larval density sediments and from 9.75 ± 0.56 g/m²/h to 15.46 ± 2.49 g/m²/h for high larval density sediments (Fig. 8). A planned comparison test showed that the mean sediment suspension rates for both initial burrow construction and maximal (hungry) rates for the low larval density sediment sources were significantly different from the mean sediment suspension rates for the high larval density sediment sources ($p < 0.001$) (Table 4). Initial burrow construction rates for low larval density sediments were approximately double those for high larval density sediments. This ap-

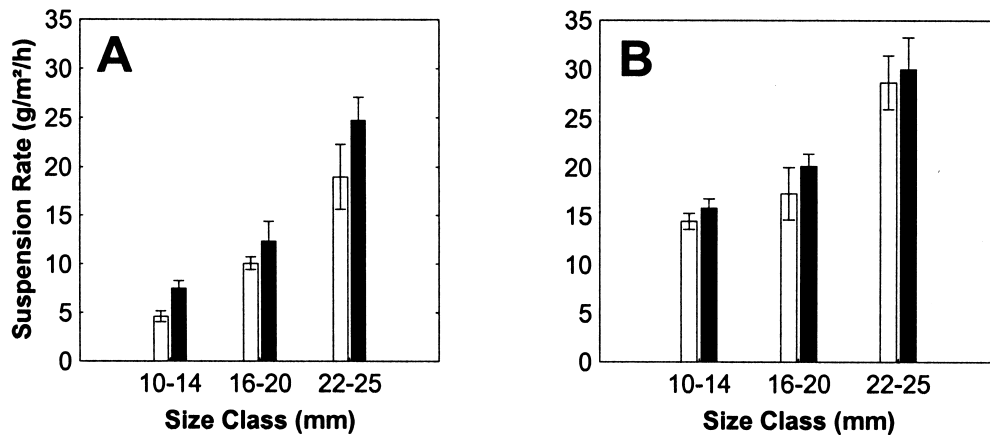


FIG. 7. Mean (\pm SE, $n=5$) sediment suspension rates of three size classes of larvae during initial burrow construction (A) and for maximal (hungry) (B) periods in containers with 3.5 cm (open bars) or 10.0 cm (filled bars) depth of sediment.

pears to be the case for some of the maximal sediment suspension rates also. The maximal (hungry) rates were approximately three times those observed for the initial burrow construction rates. Larval size did not significantly influence initial burrow construction or maximal rates ($p > 0.05$).

DISCUSSION

The findings that *Hexagenia* larval sediment suspension rates are a function of larval size, larval

density, and temperature are to be expected since larger larvae excavate larger burrows, which will displace larger volumes of sediment, and a larger amount of water will be pumped through the burrows. Higher densities mean that there are more larvae burrowing and feeding, hence a greater volume of sediment will be excavated per unit time. *Hexagenia* larval activity also increases with water temperature (Zimmerman and Wissing 1978), leading to increased bioturbation and sediment suspension. The interaction among size, density and tempera-

TABLE 4. Analysis of covariance (ANCOVA) for the effects of sediment source on sediment suspension rate (initial burrow construction and maximal rates) and planned comparisons for the effect of sediment larval density on sediment suspension rate. *** $p < 0.001$

Initial Burrow Construction Rate				
	d.f.	SS	MS	F
Sediment Source	5	140.028	28.006	8.137***
Larval Density	1	132.152	132.152	38.396***
Mean Larval Size	1	3.479	3.479	1.011
Error	23	79.162	3.442	
Total	29	222.669		
Maximum (Hungry) Rate				
	d.f.	SS	MS	F
Sediment Source	5	484.012	96.802	7.475***
Larval Density	1	353.003	353.003	27.257***
Mean Larval Size	1	1.423	1.423	0.110
Error	23	297.871	12.951	
Total	29	783.306		

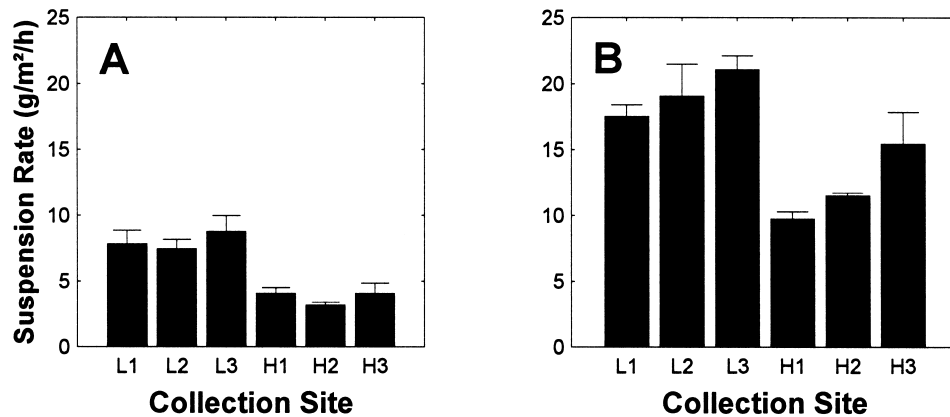


FIG. 8. Mean (\pm SE, $n=5$) sediment suspension rates during initial burrow construction and for maximal (hungry) rates for 15–22 mm long larvae in sediment collected at different locations in western Lake Erie. Sites L1, L2, and L3 are low larval density sites and sites H1, H2, and H3 are high larval density sites.

ture is by far the best predictor of sediment suspension rate for the three classes of sediment suspension rate estimates (initial burrow construction, maximum (hungry), and minimum (fed)). For initial burrow construction rates the size \times density interaction improved predictions of sediment suspension rate. For both maximal and minimal sediment suspension rates, temperature was also a significant predictor of sediment suspension rate. During initial burrow construction, the size and density of the larvae are likely more important than water temperature since *Hexagenia* larvae are obligate burrowers (Edmunds *et al.* 1976) regardless of water temperature. Once they have established their initial burrow, their respiratory and nutrient needs are strongly influenced by water temperature (Zimmerman and Wissing 1978, 1980).

This suggests that sediment flux due to *Hexagenia* bioturbation will likely be highest in late spring just prior to emergence when water temperatures are rising. Larvae are also largest (22–27 mm) and still present in large numbers (sometimes reaching 1,000 larvae/m²; typically 300–400, Schloesser *et al.* 2000) at this time. In contrast, during late fall and winter *Hexagenia* larvae will likely produce the least amount of suspended sediment through bioturbation since they are smaller and less active at low water temperatures despite their higher densities at this time. The sediment suspension rate for a high density of larvae (1,111 larvae/m²) in late spring is estimated to be approximately 45 times that in late fall.

There also appears to be a synergistic effect for large larvae at higher densities since the sediment suspension rate per larva appears to have increased with increasing density. Larvae share burrows (Henry *et al.* 1986) and aggregate in containers filled with sediment. Hanes and Ciborowski (1992) suggested that this may increase water flow through burrows, leading to increased oxygen and food availability. This increased current may explain the higher per larva sediment suspension rates at higher densities. Alternatively, high densities may leave insufficient space for larvae to maintain a burrow, or burrows may run into each other resulting in damage or collapse (Hanes and Ciborowski 1992). Excavation activity to repair damaged burrows is another possible reason for the increased sediment suspension rate per larva as larval density increases.

Sediment suspension rates varied with sediment collection locations within western Lake Erie. Suspension rates for sediment collected at sites supporting low larval densities in 2002 were approximately twice as high as in sediment collected from high density sites. This may be due to differences in sediment particle size, which affects larval burrowing ability (Eriksen 1963b) as well as determining settling rates of suspended particles. The cohesiveness of the different sediments may also influence sediment suspension rates since the larval burrow integrity will be affected. The positive water pressure generated when larvae irrigate their burrows helps maintain burrow integrity (Keltner and McCafferty 1986). Larvae in non-co-

hesive sediments may need to relocate burrows more often and may require greater ventilation activity to maintain burrow integrity. Sediments of appropriate particle size and cohesiveness are likely important in supporting high densities of larvae since larvae preferentially select sediment from certain locations (Hanes 1992).

Sediment organic richness and the sestonic content of overlying water may also influence sediment suspension rate since larvae may burrow and/or filter-feed more actively when sediment is nutrient-poor. The marked decrease in sediment flux observed 12 h after feeding suggests that larvae filter-feed first (Zimmerman and Wissing 1978) and resort to ingesting sediment to acquire food when seston concentrations in the water column are low. This suggests that sediment suspension rates may be lower in areas receiving high amounts of suspended organic material from river outflows or runoff since the larvae will likely be filter-feeding in these areas rather than actively excavating sediment for ingestion, and in offshore areas where allochthonous inputs of suspended material are less.

Hexagenia-induced bioturbation will vary among locations and times in western Lake Erie as larval density, larval size and water temperatures change. To assess the possible importance of sediment suspension relative to other sources of turbidity, we compared our daily sediment suspension estimates with storm-event data (Lick *et al.* 1994), the annual suspended sediment contribution of rivers, and shoreline erosion to western Lake Erie (Kemp *et al.* 1977). The sediment suspension rates of 288 g/m²/d observed for large larvae at late spring temperatures (22°C) at a density of 400 larvae/m² (basin wide average) in these experiments are about half the sediment inputs of shoreline erosion in western Lake Erie (584 g/m²/d calculated from data of Kemp *et al.* 1977). Mayfly-induced sediment suspension rates are lower in summer when mature larvae have emerged, and in winter when the water is colder and larvae are less active. Bioturbation-related sediment flux is considerably less than suspended sediment inputs from storm events of 900 g/m² (300 g/m²/d) for a 3-d storm event (Lick *et al.* 1994) and from both the Detroit River (1,168 g/m²/d) and the Maumee River (1,502 g/m²/d) (Kemp *et al.* 1977). Although shoreline erosion and river inputs are likely integrated over the entire depth of the water column, these contributions don't diffuse throughout the basin. In contrast, *Hexagenia* bioturbation contributes sediment mainly to the epibenthic water

layer over soft sediments throughout much of the western basin offshore.

Hexagenia burrowing behaviour may also increase the water content of the sediment (McCall and Tevesz 1992), making it is less cohesive and more likely to be disturbed by waves, thus indirectly inducing sediment suspension. In areas where biogenic sediment suspension is high, the sediment that settles out of the water column onto the sediment surface will also be less compact and be re-suspended at a lower shear stress. Marine subsurface deposit feeders can reduce the shear strength of sediment up to 5 cm below the sediment water interface (Rhoads and Boyer 1982).

Hexagenia sediment suspension will be greater than that of tubificid worms or chironomids in western Lake Erie. Although they occur at comparatively higher densities than mayflies (Manny and Schloesser 1999), tubificids are conveyor-belt feeders that deposit pelletized sediment at the sediment water interface (McCall and Fisher 1979) rather than suspending it into the water column. Some chironomids, most notably *Chironomus plumosus* irrigate their burrows with water and suspend particles directly into the water column. However, chironomids are much smaller than *Hexagenia* and typically more tolerant of hypoxia. Consequently, chironomid larvae will pump less water through their burrows than *Hexagenia* (Matisoff and Wang 2000).

Hexagenia bioturbation is likely most important close to the sediment-water interface, where it may influence other benthic organisms. *Hexagenia*-induced sediment suspension in late spring is markedly greater than the amount that can be filtered by zebra mussels. *Dreissena polymorpha* can filter approximately 200 mL/h at a suspended sediment (clay) concentration of 11 mg/L at 22°C (Diggins 2001). This is the equivalent of 4.4 g/m²/h for a population density of 2,000 mussels/m². In comparison, 400 large (25 mm) *Hexagenia* larvae/m² at a water temperature of 22°C suspend sediment at a rate of 12 g/m²/h. The filtration rate of *D. polymorpha* is also influenced by suspended sediment concentration. For example, filtration rate decreases exponentially from 1,900 L/1,000 animals/d to 800 L/1,000 animals/d with an increase of suspended sediment concentration from 0 to 25 mg/L (Reeders *et al.* 1993). Zebra mussel pumping rate also appears to decrease with increases in clay concentrations between 25 and 250 mg/L (MacIsaac and Rocha 1995).

Hexagenia bioturbation has been suggested as a

source of sediment associated nutrients, solutes (Matisoff and Wang 1998), and contaminants (Bartsch *et al.* 1999) in western Lake Erie. Phosphorus is presently the main nutrient of interest in Lake Erie. Despite the significant amount of sediment suspended by *Hexagenia* bioturbation, the amount of soluble phosphorus entering the water column is likely inconsequential. Oxygenated sediment contains ferric oxyhydroxides, which adsorb phosphorus. This appears to be what occurs in *Hexagenia* burrows since experimental containers containing *Hexagenia* larvae do not significantly increase the amount of total phosphorus (TP) in the overlying water compared to jars without *Hexagenia* larvae (Toot 2000). Experiments with *Chironomus plumosus*, which also irrigate their burrows, also show a decrease in the concentration of phosphorus in sediment pore water (Matisoff 1995, Soster *et al.* 2001) and no significant increase in phosphorus flux into the overlying water (Matisoff 1995). Consequently, the possible exclusion of dreissenids resulting from the increased turbidity produced by *Hexagenia* bioturbation may help in keeping western Lake Erie less eutrophic, since *Hexagenia* likely generate less TP than dreissenids.

Bartsch *et al.* (1999) found *Hexagenia* bioturbation caused cadmium concentrations in unfiltered overlying water of test cells to reach an average of 0.02% of the total mass of Cd initially spiked into the sediment. This suggests that sediment-bound contaminants can be resuspended and made available to the pelagic environment by *Hexagenia* sediment suspension. Since burial of contaminated sediments by deposition of clean particles is the most important part of the natural recovery of contaminated sediments (Thibodeaux and Bierman 2003), bioturbation by *Hexagenia* and other organisms will play an important role in the recovery process. Bioturbation may thus explain the slow recovery traditionally attributed to instability of bed sediment at sites that receive clean sediment layers through natural deposition (Thibodeaux and Bierman 2003). Release of these sediment-bound contaminants is likely greatest in late spring when larvae are largest and water temperatures are increasing, since large, active larvae burrow deeper, thus suspending sediment from greater depths.

Our laboratory studies suggest that *Hexagenia* mayflies are likely one of the major bioturbators in shallow mesotrophic systems, such as western Lake Erie. Their distribution and production on a local scale can influence epibenthic processes such as sediment shear strength, sediment suspension, pore

water solute content, and contaminant flux. Although the net production of sediment is small by comparison with allochthonous inputs, their continuous contribution to epibenthic, offshore turbidity has potential to significantly influence the base of the food web. Further research, especially *in situ* direct observation, is warranted.

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