BIOTURBATION BY *HEXAGENIA* LARVAE (EPHEMEROPTERA: EPHEMERIDAE) AND ITS IMPLICATIONS FOR SEDIMENT SUSPENSION IN LAKE ERIE

by

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ABSTRACT

Burrowing activities of aquatic benthic organisms can influence sediment suspension and nutrient cycling. The burrowing mayfly *Hexagenia* is a dominant benthic organism in western Lake Erie, and *Hexagenia* bioturbation can potentially influence water quality and other benthic organisms. Using laboratory experiments, I determined bioturbation-induced sediment suspension rates of fine Lake Erie sediment caused by *Hexagenia* larvae of varying body lengths (13 – 28 mm) at densities of 70 – 1,111 larvae/m² and water temperatures ranging from 10 – 25°C. Bioturbation rates (sediment suspension, g/m²/h) were estimated by nonlinear regression from measurements of suspended sediment concentrations in jars, taken twice-daily for 14 d. Sediment settling rates were also estimated from twice-daily measurements of suspended sediment concentrations collected for an additional 18 d in the surface water from the bioturbation experiments.

Multiple regression of suspension rate against the individual and combined independent variables indicated that the interaction (synergy) among logarithmic transformations of size, density and temperature was the best predictor of sediment suspension rates for three periods of sediment suspension (during initial burrow construction, when larvae are hungry [maximal], and just after feeding [minimal]). Sediment suspension rates were significantly influenced by sediment depth in laboratory jars and by the sediment collection location, but these factors were inconsequential compared to the other factors.

Hypothetical sediment suspension rates for western Lake Erie were estimated from larval density data previously collected in different years and seasons. Spatial variation was mapped using Geographic Information System (GIS) analysis. Estimated *Hexagenia*-induced sediment suspension is greatest in late spring (early June) prior to mass emergence of imagos, approaching daily sediment inputs for large storm events and contributions from shoreline erosion in locations where larval densities are high (> 1,000 larvae/m^2). Overall, *Hexagenia*-induced sediment suspension in western Lake Erie likely contributes a small fraction of the basin-wide annual sediment load. However, bioturbation may be great enough to have important effects on nutrient dynamics, suspension of sediment-associated contaminants, and other benthic organisms. Late-spring populations of *Hexagenia* in portions of the basin likely generate enough suspended sediment to interfere with dreissenid filter-feeding activity, possibly preventing mussels' establishment.

To my family, the insects and the uniform lattice-like structure, without whom none of this would have been possible

...A scientist must also be absolutely like a child. If he sees a thing,
he must say that he sees it, whether it is what he thought he was
going to see or not. See first, think later, then test. But always see
first. Otherwise you will only see what you were expecting.

Wonko the Sane
(The Hitch Hiker's Guide to the Galaxy)

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CHAPTER 1: GENERAL INTRODUCTION

Bioturbation

Bioturbation is the process by which the activities of aquatic organisms modify the physical and chemical properties of the substrate in which they live (Fisher et al. 1980). Bioturbation includes sediment reworking, solute flux (Matisoff 1992) and suspension of sediment into the water column (Matisoff and Wang 2000). I will use the term bioturbation to refer primarily to sediment suspension. In freshwater aquatic systems, bioturbation is caused by many types of organisms including oligochaete worms (Fisher et al. 1980, McCall and Tevesz 1982), chironomid midge larvae (Charbonneau et al. 1997, Charbonneau and Hare 1998, Matisoff and Wang 2000), amphipods (freshwater shrimp) (de Deckere et al. 2000), conchostracans (clam shrimp) (Luzier and Summerfelt 1997), mayfly larvae (Charbonneau et al. 1997, Charbonneau and Hare 1998, Bartsch et al. 1999, Matisoff and Wang 2000) and fish (Havens 1991, Wu et al. 1997, Lougheed et al. 1998). My research addresses bioturbation by burrowing mayflies of the genus *Hexagenia* spp. (Ephemeroptera: Ephemeridae).

Burrowing mayflies can be a dominant component of the zoobenthic community in shallow mesotrophic systems (Hunt 1953, Edmunds Jr. et al. 1976, Flannagan 1979). My research will determine how larval size, larval density and water temperature, and how different sediment collection locations and sediment depths influence the amount and rate of sediment suspension by the larval burrowing activities of *Hexagenia* using laboratory experiments. I will also estimate sediment suspension hypothetically attributed to *Hexagenia* across the basin based on annual population densities from historical and current sampling programs, and based on seasonal changes in larval density, water temperature and size frequency distribution. This will allow estimation of areas where *Hexagenia* larval sediment suspension has a major influence in western Lake Erie.

Biotubation by freshwater aquatic organisms can greatly influence aquatic environments. Oligochaetes mix sediment layers to a depth of up to 10 cm, although most of the sediment mixing occurs at depths of 6-8 cm (Fisher et al. 1980). Oligochaetes are "conveyer belt" feeders whose activites produce a pelletized layer on the sediment surface, but do not pump large amounts of water through their burrows (McCall and Fisher 1979). As a result, their burrow and feeding behaviours do not directly contribute to the turbidity of the water column. Chironomid larvae play an important role in sediment mixing also, but no large increases water turbidity are reported due to their burrowing activity as compared to *Hexagenia* (Matisoff and Wang 2000). Aquarium experiments using larvae of the marine amphipod *Corophium volutator* produced suspended sediment values ranging from 35 to 130 mg/L for densities ranging from 1,000 to 100,000 amphipods/m^2 (de Deckere et al. 2000). Clam shrimp (conchostracans) increased turbidity in 500-mL glass experimental containers from 0 to 750 nephelometric turbidity units (NTU) at densities of 4,488 individuals/m^2 (Luzier and Summerfelt 1997). These densities are typical of those observed in fish ponds (Luzier and Summerfelt 1997).

Hexagenia mayfly larvae in experimental vessels containing cadmium-spiked sediment produced turbidity in the water column ranging from 50 to 250 NTU at 22° C. *Hexagenia* larval sediment suspension in these experiments was significantly related to the larval size (Bartsch et al. 1999). Single larvae in 1,000-mL beakers containing western Lake Erie sediment produced turbidity values ranging from 2 – 18 NTU at 14° C (Toot 2000).

Carp activity also produces high turbidity in aquatic systems. Experiments with enclosures lacking carp and with low, medium and high carp densities show a 50 to 100 cm increase in Secchi depth when the enclosures lacking carp are compared to the enclosures with high densities of carp (biomass of 485 g/m^2) (Wu et al. 1997). Exclusion of carp from an area in Cootes Paradise Marsh in the Hamilton Harbour watershed at the west end of Lake Ontario reduced turbidity from mean open marsh value of 80 NTU to 45-60 NTU in the enclosures (a 25-45 % reduction in turbidity) (Lougheed et al. 1998).

Suspended Sediment

Suspended sediments are important in aquatic ecosystems because turbidity reduces light penetration and subsequently affects primary production, changes the algal community from green to blue-green, reduces the oxygen content of the water and reduces zooplankton populations (Luzier and Summerfelt 1997). Suspended sediments also affect invertebrate filtration rates (e.g., zebra mussels) (Reeders et al. 1993, MacIsaac and Rocha 1995) and reduce water clarity (Luzier and Summerfelt 1997). For this thesis, I define suspended sediments as the suspended solids > 0.45 μm in diameter. Suspended sediments also often have contaminants (Rosa 1985) and nutrients (Holdren and Armstrong 1980, Pettersson 1998) associated with them, which can re-enter the water column from the sediment layer. Thus, biologically mediated changes in suspended sediment concentrations can have profound effects on aquatic systems. For example, reductions in suspended sediment concentrations ascribed to the establishment of dreissenid mussels have been argued to have fundamentally changed the energy flow patterns in the Laurentian Great Lakes (Klerks et al. 1996). Zebra mussels have been shown to increase water clarity in biobox flow-through experiments (Klerks et al. 1996). In Lake Erie, increases in water clarity attributed to zebra mussels are most prominent in the near shore area (Charlton 2001). Zebra mussels also increase sedimentation rates, and the mucus secreted by mussels during the formation of feces and pseudofeces increases the organic content of the material deposited by the mussels (Klerks et al. 1996). This biodeposition may be increasing the food supply and contaminant transfer from pelagic areas to benthic food webs (Dobson and Mackie 1998) since the bottom of the lake may be considered a sink for seston (Ackerman et al. 2001).

Physical Sediment Suspension Processes

The major physical processes responsible for water turbidity in the west basin of Lake Erie include wind induced wave action, currents (Lick et al. 1994), shoreline erosion and the sediment plumes from both the Detroit River and the Maumee River (Kemp et al. 1976, Kemp et al. 1977). A major three-day storm event is capable of producing suspended sediment concentrations of 1,000 mg/L especially in near shore areas while the effects of current are a small correction in the determination of sediment suspension (Lick et al. 1994). Shoreline erosion in western Lake Erie contributes 0.7 million metric tons per year of fine grained material to western Lake Erie from the Detroit River to Point Pelee on the northern shore and from the Michigan and portions of the Ohio shoreline on the southern shore (Kempet al. 1977). The Detroit and Maumee rivers contribute an estimated 1.4 million and 1.8 million metric tons, respectively, to Lake Erie (Kempet al. 1977), which result in significant sediment plumes originating at the mouths of these rivers. Lake Erie exhibits two turbidity pulses, one in the spring and one in the fall, when most of the sediment suspension occurs (Kemp et al. 1976). This probably occurs since most of the storm events occur at these times. The spring pulse also likely occurs due to spring run-off into the rivers.

Bioturbation Effects on Benthic Organisms

The burrowing, feeding and respiratory activities of benthic organisms can alter basic processes of aquatic systems, such as sediment reworking, sediment suspension and nutrient cycling (McCall and Tevesz 1982, Matisoff and Wang 2000). Sediment transport due to benthic organism activity can also play a role in egg bank dynamics both in terms of burial (Kearns et al. 1996, Gerlofsma 1999) and upward transport (Kearns et al. 1996) of insect eggs and the resting stages of copepods, cladoceran and rotifers that remain in the sediment until the correct cues for hatching occur (Hairston Jr et al. 1995). Different organisms influence egg bank dynamics in different ways. For example, chironomid larvae produce a net downward transport of resting eggs, and tubificids produce a net upward transport (Kearns et al. 1996), affecting the vertical distribution of these resting eggs in the sediment. Suspended sediment from *Hexagenia* larval bioturbation that settles onto the sediment surface may also bury eggs and resting stages. The burial of eggs may isolate them from the oxygenated layer of the sediment and thus delay hatching or induce quiescence (Gerlofsma 1999). Upward transport may bring the eggs back to favourable conditions and allow them to hatch. Benthic organisms also live in close contact with the sediment and have the potential to make sediment bound-contaminants available to other organisms in the water column by sediment suspension (Bartsch et al. 1999) and biomagnification (Drouillard et al. 1996, Currie et al. 1997).

Study Organism

Habitat Requirements and Distribution

Burrowing mayflies of the genus *Hexagenia* (Ephemeroptera: Ephemeridae) are common in depositional zones where sediment consists primarily of silt and clay, in both lentic and lotic systems (Keltner and McCafferty 1986, Edmunds and Waltz 1996) since *Hexagenia* larvae can only survive in locations where cohesive substrate is present (Lyman 1943, Hunt 1953, Eriksen 1963a, Eriksen 1968). The western basin of Lake Erie is one such area (Bolsenga and Herdendorf 1993).

Species of *Hexagenia* are confined to the western hemisphere, occurring as far south as the Rio Negro of Argentina and as far north as Great Slave Lake in the Northwest Territories of Canada (Edmunds Jr.et al. 1976). *Hexagenia limbata* (Serville) is distributed throughout Canada and the USA and into northern Mexico. *Hexagenia rigida* McDunnough is found in eastern and central Canada and the United States (Edmunds Jr.et al. 1976). The populations of *Hexagenia* in the western basin of Lake Erie are a mixture of *Hexagenia limbata* and *Hexagenia rigida* (Corkum and Hanes 1992, Corkum et al. 1997b). They are functionally and ecologically similar (Edmunds Jr.et al. 1976, Flannagan 1979) and will be treated as a species group (*Hexagenia*).

Biological Importance

In areas where *Hexagenia* larvae are abundant they are an important part of the fish diet (Hunt 1953, Flannagan 1979, Edsall et al. 1999, Masteller and Obert 2000, Krieger and Toot 2001, Tyson and Knight 2001). They are found in the gut contents of yellow perch, bluegill, pumpkinseed and black crappie, in small Michigan Lakes (Hunt 1953) and in yellow perch in Lake Erie (Krieger and Toot 2001, Tyson and Knight 2001). *Hexagenia* larvae are also used as bait by anglers, and are harvested and sold commercially for this purpose (Hunt 1953; pers. obs.). *Hexagenia* adults are also food for birds, bats, cats, rats and other terrestrial organisms (Sweeney and Vannote 1982, Cochran and Kinziger 1997, L. D. Corkum University of Windsor, pers. comm.). *Hexagenia* larvae are also important in the epibenthic community since larval burrowing, feeding and respiratory behaviour (gill beats) all result in sediment suspension (Hunt 1953, Zimmerman and Wissing 1980, Keltner and McCafferty 1986). Suspended sediments can influence filtration rates in *Dreissena* mussels (Diggins 2001), so *Hexagenia* bioturbation may have a negative effect on *Dreissena* feeding and filtration, and may also affect *Dreissena* colonization ability.

Hexagenia in Western Lake Erie

Hexagenia larvae were once an abundant part of the benthic community in western Lake Erie (Hunt 1953, Britt 1955a, Carr and Hiltunen 1965, Reynoldson et al. 1989, Manny 1991). During a low oxygen event in 1953 *Hexagenia* larvae in western Lake Erie almost completely disappeared from the basin since they are intolerant of hypoxia (Hunt 1953, Eriksen 1963b). This hypoxic event was brought on by an unusually long period of calm weather associated with clear skies and high summer temperatures causing the western basin of Lake Erie to stratify (Britt 1955a). *Hexagenia* larvae were present the following year, but the population slowly declined after 1954 (Britt 1955b). By 1960, the number of larvae in the western basin of Lake Erie was very low (Carr and Hiltunen 1965). Mayflies were absent through the 1960s and 1970s (Reynoldson et al. 1989) and despite the implementation of pollution abatement programs in the late 1970s it was not until the early 1990s that signs of recolonization of the western basin of Lake Erie were observed (Krieger et al. 1996, Corkum et al. 1997a, Schloesser et al. 2000). This reappearance was associated with the appearance of the zebra mussel *Dreissena polymorpha* and an increase in water clarity and sedimentation in Lake Erie's west basin (Klerks et al. 1996, Krieger et al. 1996). As the population density and distribution of *Hexagenia* increases, sediment flux due to these organisms will also increase since *Hexagenia* have once again become a dominant benthic organism in Lake Erie after a 30-year absence (Schloesser et al. 2000).

Life Cycle

Adult female *Hexagenia* mayflies deposit eggs on the water surface in mid to late June. The eggs sink to the sediment surface at the bottom of the lake where egg hatching time depends on temperature and dissolved oxygen concentration (Gerlofsma 1999). In shallow, mesotrophic systems eggs hatch in two to three weeks (Hunt 1953). The larvae (approx. 1 mm long when newly hatched) immediately burrow into the sediment. The larval stage typically lasts for one to two years in Lake Erie (Manny 1991, Corkum et al. 1997a). The length of the *Hexagenia* larval stage, as well as larval survivorship and development, are influenced by water temperature (Hunt 1953, Wright and Mattice 1981, Wright and Mattice 1985, Corkum and Hanes 1992, Winter et al. 1996) and degree day (dd) accumulations (Sweeney 1984). However, the number of degree days required for *Hexagenia* emergence appears to decline with increasing latitude (Heise et al. 1987, Giberson and Rosenberg 1994). Other factors that affect larval duration, development and survivorship include the time of year eggs are deposited by adult females (Flannagan 1979), food supply (Hunt 1953, Giberson and Rosenberg 1992, Hanes and Ciborowski 1992) and oxygen concentration (Winter et al. 1996). In Lake Erie larvae begin to emerge when the water temperature reaches 20° C (J. J. H. Ciborowski and L. D. Corkum University of Windsor, pers. comm.). Emerging larvae, which are about 17 – 35 mm long (17-27 mm for males and 23-35 mm for females; (Hunt 1953), swim to the water surface where they moult into the opaque-winged, sexually immature subimago. The subimagos fly to the shore and rest overnight on vegetation. The following day, they moult into the imago stage, which is sexually mature. At dusk, male imagos form mating swarms. Females fly through these swarms and mate with a male. Gravid females then fly to the water, deposit their eggs and die (Hunt 1953). My research focuses on the sediment dwelling larval stages of these insects.

Burrowing Behaviour

Larvae burrow into the sediment (Hunt 1953) where they construct U-shaped burrows (Figure 1.1) (Charbonneau et al. 1997, Charbonneau and Hare 1998). The burrowing

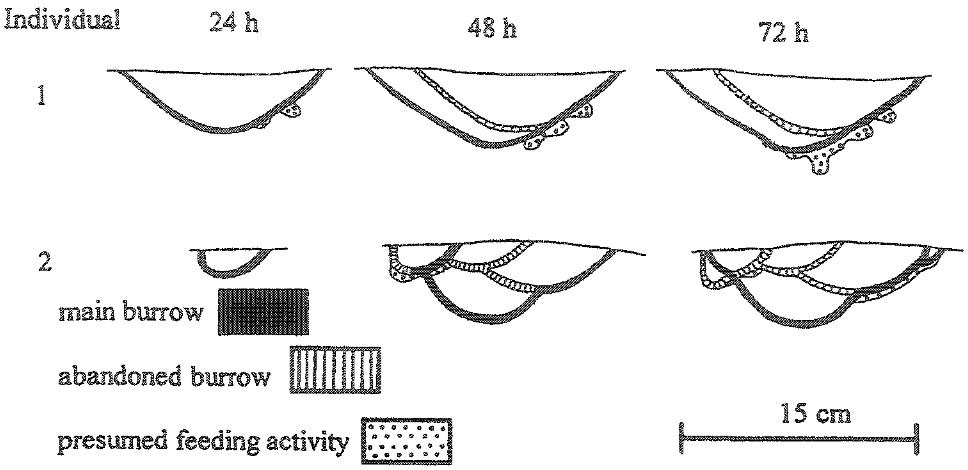

Figure 1.1: Side view of *Hexagenia* burrows at 24, 48 and 72 h. Modified from Charbonneau and Hare 1998.

activity, burrow irrigation and feeding behaviour of *Hexagenia* larvae contribute to sediment suspension (Bartsch et al. 1999) and solute flux (Matisoff and Wang 1998) from the lake bottom into the water column (bioturbation). Once a complete burrow is constructed, the abdominal gills continue to beat in metachronal waves. Sediment particles from in front of the larva are moved over the gills and out of the burrow (Lyman 1943) and are thus suspended into the water column. The beating of the gills serves to irrigate the burrows with oxygenated water (Wingfield 1939, Eriksen 1963b) which also brings suspended food particles towards the mouthparts (Zimmerman and Wissing 1980) and maintains burrow integrity (Keltner and McCafferty 1986). Larvae are thought to pump water almost continuously through their burrows (Wang et al. 2001). Individual larvae remain in a burrow for several hours and then construct new burrows in the sediment below the previous burrow and old burrows are blocked off and abandoned (Charbonneau et al. 1997, Charbonneau and Hare 1998). The larvae also feed directly on the sediment at the mouth of their burrows (Zimmerman and Wissing 1980), which can also lead to sediment suspension.

Rationale

The return of *Hexagenia* to the western basin of Lake Erie is an excellent opportunity to study the role of these organisms in a mesotrophic to oligotrophic environment. The sediment flux due to *Hexagenia* bioturbation will increase in the west basin of Lake Erie as the population increases. The objectives of this study are to determine the amount and relative importance of sediment flux due to *Hexagenia* larvae using laboratory studies. The ultimate goal is to estimate sediment flux due to *Hexagenia* larvae in the western basin of Lake Erie and hence the possible importance of *Hexagenia* bioturbation to the sediment budget of the basin.

Now that *Hexagenia* have returned to the basin (Krieger et al. 1996, Corkum et al. 1997a, Schloesser et al. 2000) after a prolonged absence from the 1960s to the early 1990s (Reynoldson et al. 1989, Krieger et al. 1996, Corkum et al. 1997a, Schloesser et al. 2000) there is a need to quantify how important *Hexagenia* bioturbation is compared to physical processes in the west basin of Lake Erie. The sediment flux due to *Hexagenia* will now be greater than during the early stages of recolonization since basin-wide mean larval densities have increased from being close to zero in 1990 to a low density in 1993 (10 ± S.E. 1.2 larvae/m^2) to higher densities in 1997 (430 ± S.E. 66.4 larvae/m^2) with a slight decline to 282 ± 43.7 larvae/m^2 in 1999 (Ciborowski et al. unpubl.). *Hexagenia*-induced sediment suspension will be especially important in areas where the highest larval densities occur such as the Maumee Bay region and the area near Colchester, Ontario (Chase 1998), Ciborowski unpubl.).

The large oligochaete populations (Reynoldson et al. 1989) present in the western basin of Lake Erie during the period when *Hexagenia* were absent likely contributed to sediment flux. Oligochaete mediated bioturbation is likely not as important as biotubation due to *Hexagenia*, even during times of high oligochaete density, since oligochaetes are conveyer belt feeders (Matisoff and Wang 2000). Conveyer belt feeders deposit sediment on top of the sediment in a pelletized layer (McCall and Fisher 1979) at the sediment water interface in contrast to burrow constructing insects (e.g. *Hexagenia*), which expel sediment into the overlying water column (Matisoff and Wang 2000).

Objectives and Expectations

This study will determine the effect of larval size, larval density and water temperature on *Hexagenia* larval sediment suspension. Larval densities in the west basin of Lake Erie as high as 1,000 larvae/m^2 now occur. The temperature near the sediment-water interface of the western basin of Lake Erie ranges from 0° C in the winter to 25° C in the summer (Chase 1998, J. J. H. Ciborowski University of Windsor unpubl.). Sediment suspension should increase as a function of larval size since larger larvae build larger burrows. Larger *Hexagenia* will displace more sediment during burrow construction, and burrows will be irrigated with a larger volume of water. Areas with higher larval densities should also display more bioturbation since there are more larvae present. Increased water temperature should also lead to increased bioturbation since larval activity, growth and development increase exponentially as temperature increases (Giberson and Rosenberg 1994). Thus, I expect that the greatest sediment suspension likely occurs in late spring prior to emergence when larvae are largest and the water temperature is high.

In the laboratory, I determined the amount and rate of sediment suspension by laboratory cultured *Hexagenia* larvae using five larval sizes, five larval densities and five water temperatures encompassing the natural range of variation in the west basin of Lake Erie (Chapter 2). The sediment suspension rates determined in Chapter 2 are applicable to *Hexagenia* larvae in most mesotrophic systems. I also conducted experiments to determine the effects of sediment depth and sediment collection location on laboratory estimates of *Hexagenia* sediment suspension rates (Chapter 3). In Chapter 4, sediment suspension rates were calculated for different locations based on *Hexagenia* larval densities using the regression equations derived in Chapter 2. These sediment suspension rates were mapped using Geographic Information System (GIS) analysis to delineate areas in the basin where sediment suspension is highest. Lastly, (Chapter 5, General Conclusions) I review the likely implications of *Hexagenia* bioturbation on nutrient dynamics and benthic ecology of biota in the western basin of Lake Erie.

CHAPTER 2: LABORATORY EXPERIMENTS TO DETERMINE THE EFFECTS OF *HEXAGENIA* LARVAL SIZE, LARVAL DENSITY AND WATER TEMPERATURE ON SEDIMENT SUSPENSION

INTRODUCTION

The purpose of this chapter is to determine the effects of *Hexagenia* larval size, larval density, water temperature and their interactions on the amount and rate of sediment suspension produced by the larval stage of *Hexagenia* in a laboratory experiment. These findings will ultimately be used to determine a basin wide estimate the amount of sediment suspended by *Hexagenia* larvae in western Lake Erie (see Chapter 4) based on the local distribution, population size structure and water temperatures, which vary temporally and spatially on a yearly and seasonal basis.

The magnitude and importance of aquatic invertebrate activity is affected by both biotic and abiotic factors including organism size (Rhoads 1967), organism population density, water temperature (Zimmerman and Wissing 1978, Sweeney 1984), food availability (Sweeney 1984), contaminant stress (Oseid and Smith 1974, Henry et al. 1986, Briggs et al. 2003) and dissolved oxygen concentration (Eriksen 1963b). Changes in any of these features can lead to increased bioturbation, which in turn can increase sediment flux, contaminant mobilization and nutrient flux.

Hexagenia larval feeding, respiration and burrowing activities suspend sediment into the water column, via bioturbation, leading to turbidity in the overlying water (Fremling 1967, Bartsch et al. 1999). *Hexagenia* larval size, larval density and water temperature may influence bioturbation, and thus sediment suspension rates. The influence of these factors will be considered in the context of the western basin of Lake Erie, but can be applied to any ecosystem where *Hexagenia* larvae occur.

Variation in Larval Population Density

Spatial Variation

Hexagenia larval densities vary across the western basin of Lake Erie (Chase 1998, Schloesser et al. 2000). Sites located near the Maumee Bay region and near Colchester, Ontario, Canada can contain up to 2,000 larvae/m^2. The Pigeon Bay area, west of Point Pelee, and sites near the centre of the basin contain low larval densities ranging from 0 to 200 larvae/m (Chase 1998, Schloesser et al. 2000), Ciborowski unpubl.). This phenomenon is likely the result of differences in substrate characteristics at some of these locations, especially those in the eastern portion of the basin, which consist of sand and fine gravel (pers. obs). *Hexagenia* larvae can only colonize locations where cohesive fine silt and clay substrate is present (Lyman 1943, Hunt 1953, Eriksen 1963a, Eriksen 1968). During 1991, early in the recolonization of western Lake Erie by *Hexagenia*, larvae appear to occur more frequently in nearshore areas (< 7.5 km from shore) than in offshore areas (> 7.5 km from shore). By 1993 *Hexagenia* larvae were again present in the offshore areas of the basin (Schloesser et al. 2000). Schloesser et al. 2000 suggest that the higher number of sites with larvae present in nearshore compared to offshore areas in 1991 occurs due to the establishment of sufficient populations in near shore areas which subsequently went on to populate the offshore areas (i.e. near shore areas act as a source for colonization of the offshore areas).

Annual and Seasonal Variation

Hexagenia larval populations also vary seasonally and interannually. Larval population densities varied markedly among years in western Lake Erie prior to the prolonged absence beginning in the mid 1950s (Reynoldson et al. 1989, Reynoldson and Hamilton 1993, Schloesser et al. 2000), during the subsequent recovery period beginning in the early 1990s (Schloesser et al. 2000, Schloesser and Nalepa 2001), J.J.H. Ciborowski, University of Windsor, unpubl.) and including the present (Ciborowski unpubl., pers. obs). Variation in consecutive years can be as high as 1,000 to 1,500 larvae/m² at a specific collection site (Schloesser et al. 2000, Schloesser and Nalepa 2001) and as high as 300 larvae/m² for the basin wide average (Ciborowski unpubl).

Larval populations also vary seasonally. Population densities just prior to emergence are about 60 % of the highest population density observed in late summer (Manny 1991). Seasonally, larval densities are generally lowest just after the mass emergence of sub-imagos (Manny 1991). About 1 month after this time the populations will begin to increase again after the recently deposited eggs begin to hatch (Hunt 1953, Manny 1991). As egg hatching continues over the summer, larval populations continue to increase until the late fall (Hunt 1953). Newly hatched larvae are small (approximately 1 mm in length) (Hunt 1953, Manny 1991) and contribute minimally to sediment flux, especially compared to half-grown larvae present at this time, which are larger and remained in the sediment during the mass emergence period (Manny 1991).

Variation in Larval Size

Hexagenia larval size also varies seasonally. Larvae are largest just prior to the mass emergence in late June to early July when female larvae are 25-30 mm long and males range from 20-25 mm in length (Manny 1991). Larvae > 5 mm long are observed in August or September and grow until about November when the water temperature decreases. Larvae begin to grow again in March or April of the following year (Manny 1991). Larvae that are in the second year of a semivoltine life cycle (Wallace and Anderson 1996) are likely to be larger (15-20 mm) than those just hatched in August of a particular year (5-10 mm) (Manny 1991). Larval growth is influenced by water temperature (Corkum and Hanes 1992, Giberson and Rosenberg 1992, Winter 1994, Winter et al. 1996), dissolved oxygen concentration (Winter 1994, Winter et al. 1996), food limitation (Giberson and Rosenberg 1992, Hanes 1992, Hanes and Ciborowski 1992) and larval population density (Giberson and Rosenberg 1992, Hanes 1992, Hanes and Ciborowski 1992).

Water Temperature

Water temperature in western Lake Erie ranges from a low of 0° C in January to a high of 25° C in August (Chase 1998, Ciborowski unpubl.). The western basin has a mean depth of 7.4 m with most of its bottom 8 to 11 m below the water surface (Bolsenga and Herdendorf 1993). The western basin is the Lake Erie's shallowest basin and wind induced mixing keeps the water column well mixed throughout almost the entire year (Bolsenga and Herdendorf 1993) resulting in virtually identical water temperatures at the surface and the sediment water interface.

Laboratory experiments were conducted using larval sizes (12.5 to 27.5 mm [length]), larval densities (70 to 1,111 larvae/m^2) and water temperatures (10 to 25 °C) that fall within the natural ranges observed in western Lake Erie. The lower limits used for these factors are greater than the lower limits observed in western Lake Erie, but are the limits where *Hexagenia* bioturbation will begin to be observable. Experiments were of a 5x5x5 factorial design and were used to determine the effects of the above factors on *Hexagenia* larval sediment suspension rate.

GENERAL MATERIALS AND METHODS

Study Organism

Hexagenia spp. eggs were collected from female imagos attracted to lights after sunset. Collections were made at a lighthouse at the head of the Detroit River, Windsor, Ontario, Canada (N 42° 20.20' W 82° 55.12') in 2001 and 2003, and at Colchester Harbour, Ontario, Canada (on the north shore of western Lake Erie) (N 41°59' W 82°56') in 2002. Gravid female imagos were placed in groups of 50 into 2-L polyethylene bags containing dechlorinated, aerated water, whereupon they immediately oviposited. Eggs were gradually cooled to 8° C and then stored refrigerated at 8 °C until required (Friesen 1981). At both collection locations, the *Hexagenia* population consists of a mixture of *H. limbata* (Serville) and *H. rigida* McDunnough (Corkum et al. 1997b). Both species are functionally and ecologically similar (Hunt 1953, Edmunds et al. 1976). *Hexagenia* cultures were started from first instar larvae hatched from eggs. Cultures were maintained in aquaria containing Lake Erie sediment and were fed weekly with a mixture of 4 g Nutrafin® fish food, 3 g alfalfa and 3 g yeast added to 100 mL of distilled water (Hanes and Ciborowski 1992).

Sediment Collection and General Methods

Sediment used for the size, density and temperature treatment experiment and for the sediment depth experiment was collected as needed from a location near the centre of western Lake Erie at Environment Canada's long term monitoring site No. 357 (N 41°48'51" W 82°59'17", Figure 2.1). *Hexagenia* larval densities were historically high at this location (Britt 1955a, Britt 1955b, Reynoldson and Hamilton 1993). Sediment was collected on three dates (10 October 2001, 5 September 2002, 13 June 2003). Sediment used in each experiment was from only one collection date. All sediment was stored in plastic 20 – 25 L buckets at 4° C until needed. Sediment was sieved though a 1-mm mesh sieve without the addition of water to remove any large resident organisms. Sieved sediment was returned to cold storage for at least 1 week prior to use.

Larval Removal from Culture Tanks

Larvae were recovered from culture tanks (aquaria) by passing the sediment through a 1-mm mesh sieve and agitating it partially submerged in a bucket of dechlorinated, aerated water. Larvae found in the sieve were anaesthetized in carbonated water (club soda) (Winter 1994), transferred into a Petri dish, and separated into size classes using a scale marked off with the boundaries of each five size categories. Size class of a larva was determined by length from the tip of the head to the end of the abdomen exclusive of the

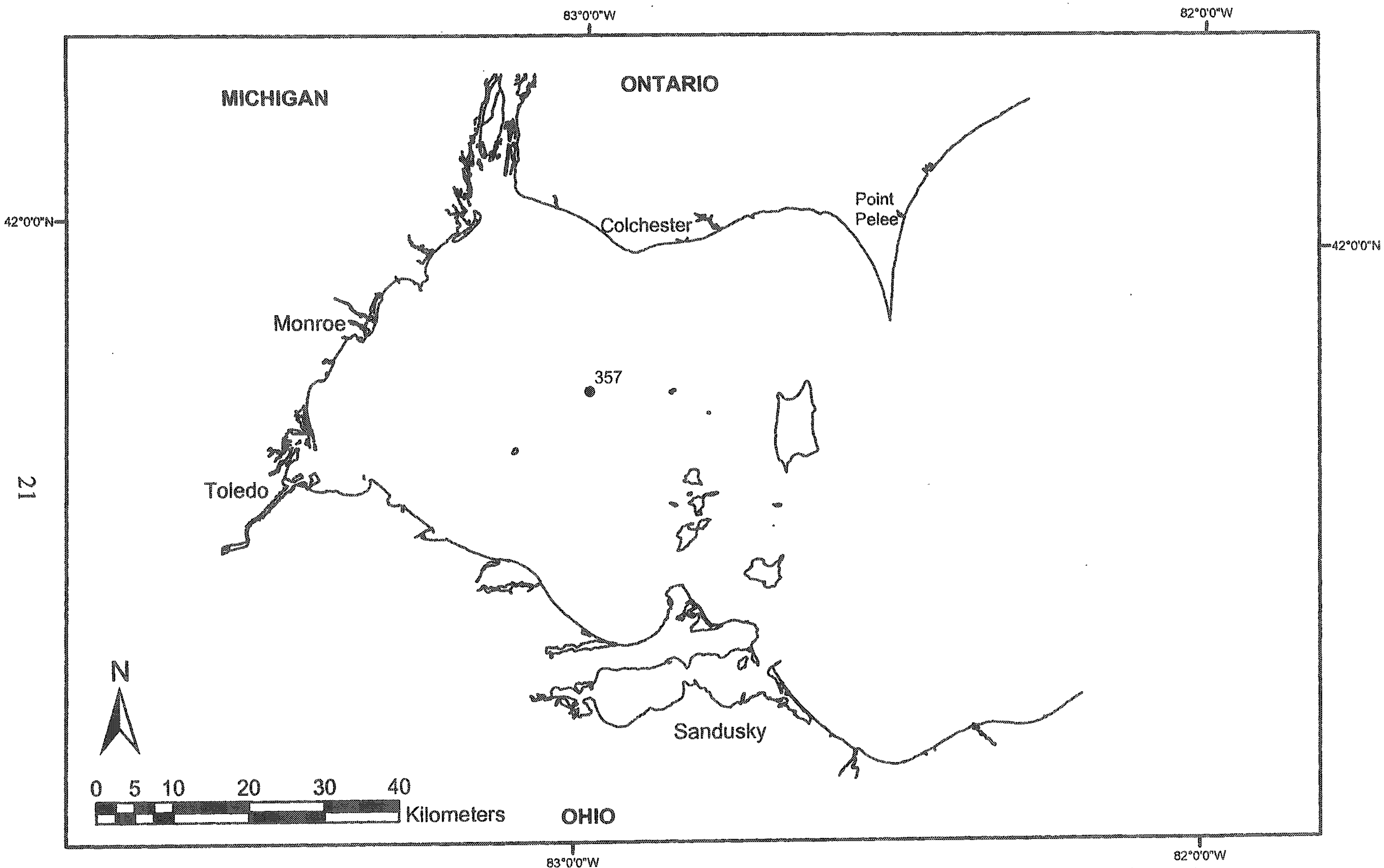

Figure 2.1: Sediment collection site (Environment Canada station 357) for sediment used in the size, density and temperature experiments.

cerci. Larvae assigned to size classes were placed into aerated, dechlorinated water to recover for 1 h prior to their transfer into experimental jars.

Sediment collected from the appropriate location(s) was removed from cold storage and added to 10 x 10 x 20 cm deep jars to a depth of 3.5 cm (340 mL) (Figure 2.2). The jars were topped up with 8.5 cm depth (1,220 mL) of dechlorinated, aerated water, 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. Jars were placed into either black Plexiglas water baths (128 cm L x 44 cm W x 40 cm H) whose temperature was regulated by circulating refrigerated water (Corkum and Hanes 1992) (treatments maintained below room temperature), or into cardboard boxes, painted black inside to simulate the light reflectance of the Plexiglas chambers, and placed into controlled-environment chambers (treatments at or above room temperature).

Jars were aerated using capillary tubing inserted through small holes in the lids and attached to the main air supply using hypodermic needles (Corkum and Hanes 1989). Size and density combinations were randomly assigned to each jar in a given temperature treatment and checked for appropriate interspersion. Food was added 48 h prior to the start of the experiment and again at 200 h. The amount of food added was based on larval density and was equivalent to 10 mg dry mass per larva, which is slightly higher

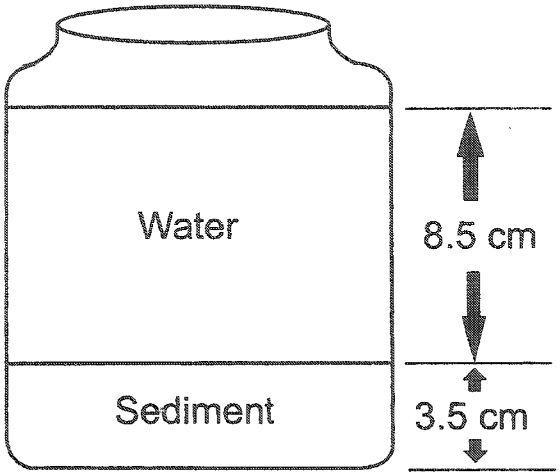

Figure 2.2: Sediment and water depths used in the size, density and temperature experiments.

than the 8 mg/larva of Hanes and Ciborowski (1992), to ensure that food was not limiting. A trial ran for a total of 332 h (14 d).

Larval Addition and Water Sample Collection

Prior to adding larvae to the experimental jars an initial water sample was collected (time = 0 h). 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 x 9 mm inside diameter) placed as close to the sediment water interface as possible without disturbing the sediment. The top of the tube was sealed with a fingertip, and the tube was removed from the jar. Two aliquots were collected from each jar during a given sampling period and emptied into a test tube.

Spectophotometry

Suspended sediment concentrations were estimated by spectrometry within 2 h of sample collection. Each test tube was agitated to resuspend any particles that may have settled. A 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. Two different spectrophotometers were used during the size, density and temperature experiment to allow two people to collect absorbance readings at the same time to decrease the time required to obtain turbidity readings. A standard curve was created for each spectrophotometer and water samples from a specific jar were measured on the same spectrophotometer for the entire duration of each experiment.

Standard Curve and Total Suspended Solids

Absorbance readings obtained for each jar at each sampling period were converted to Total Suspended Solids concentrations (TSS [mg/L]) using a standard curve created using sequential 1:1 dilutions of water containing suspended Lake Erie sediment from culture tanks. Culture tank water was diluted using distilled water. A standard curve was created for each of the spectrophotometers used. An absorbance reading was taken at 750 nm for each dilution. The water samples were then returned to the containers and a known volume of water from each dilution was vacuum filtered through a pre-ashed, preweighed Whatman GF/C glass fiber filter. The volume that could be 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.).

Linear regression was used to determine the relationship between TSS and absorbance at 750 nm. The equation for the regression line was rearranged to enable determination of the value of TSS (mg/L) from an absorbance reading (Sokal and Rohlf 1981).

Estimating Sediment Settling Rate

The settling rate of particles in water is affected by the water viscosity (which is affected by temperature) and possibly by 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 housing chamber from which the water was taken. Water samples were collected every 3 h for the first 12 h and every 12 h thereafter for 18 d. Water samples were collected as above, and total suspended sediment concentration was estimated for each time point from spectrophotometric readings. 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 among temperatures 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 :

$$TSS_t = (B_{Bioturb} / B_{Settle}) * (1 - \exp(-B_{Settle} * t)) \qquad \text{(eq. 1)}$$

where

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

$B_{Bioturb}$ is the rate of sediment suspension (mg/L/h),

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

t is time (h).

The terms for $B_{Bioturb}$ and B_{Settle} are both included in the equation since the amount of sediment in the water column at any given time is a function of both the amount of sediment suspended by mayfly activity and the amount of sediment settling out of the water column. This equation assumes that the amount of sediment in the water column will reach an asymtote (TSS_{∞}) after an indeterminate period of time (t).

SIZE, DENSITY AND TEMPERATURE EXPERIMENTS

Experimental Design

Bioturbation studies were conducted with five larval size classes, five larval densities and five water temperature treatments (Table 2.1) whose values were based on the natural range of variation of these variables in western basin of Lake Erie. The experiment was a 5x5x5 factorial design, with three replicate blocks, completed over a two-y period. The 2 larvae/jar (139 larvae/m^2) and 8 larvae/jar (556 larvae/m^2) 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. Thus, each temperature treatment consisted of 22 jars of different larval density and larval size combinations for a total of 110 jars per block, each containing sediment collected from Environment Canada sampling site 357. Suspended

Table 2.1: Number of *Hexagenia* larvae per jar and size categories for each of the five temperature treatments. The five temperature treatments are 10, 15, 19, 22 and 25° C. Densities (no./m^2) for each jar and the size ranges for each category are in parentheses. X indicates density and size combinations included in each temperature treatment. -- indicates density and size combinations not included in each temperature treatment.

Nominal Length (range – mm)	**Density** (larvae/Jar)					
	1 (70 /m^2)	2 (139 /m^2)	4 (278 /m^2)	8 (556 /m^2)	16 (1111 /m^2)	Control (0 /m^2)
12.5 (10 - 14)	X	X	X	X	X	X
17.5 (15 - 18)	X	--	X	--	X	
20.5 (19 - 21)	X	X	X	X	X	
23.0 (22 - 24)	X	--	X	--	X	
27.5 (25 - 30)	X	X	X	X	X	

sediment concentrations in each jar showed three distinct phases. I 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 (Figure 2.3). 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.

The influence of the independent factors on sediment suspension rates ($B_{Bioturb}$) was determined using forward stepwise multiple regression (STATISTICA v. 6.0 (StatSoft Inc. 2001)). All independent variables were Ln transformed prior to analysis. Independent variables were the three manipulated attributes (Ln [size], Ln [density], Ln [temperature]), their quadratic terms (Ln-transformed values squared) and their interactions (products of Ln-transformed values; e.g., Ln [size] x Ln [density] x Ln [temperature]). The quadratic terms were induced to determine if there was a nonlinear relationship between sediment suspension rates and the independent variables. 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. To test for systematic bias in predictions of the final

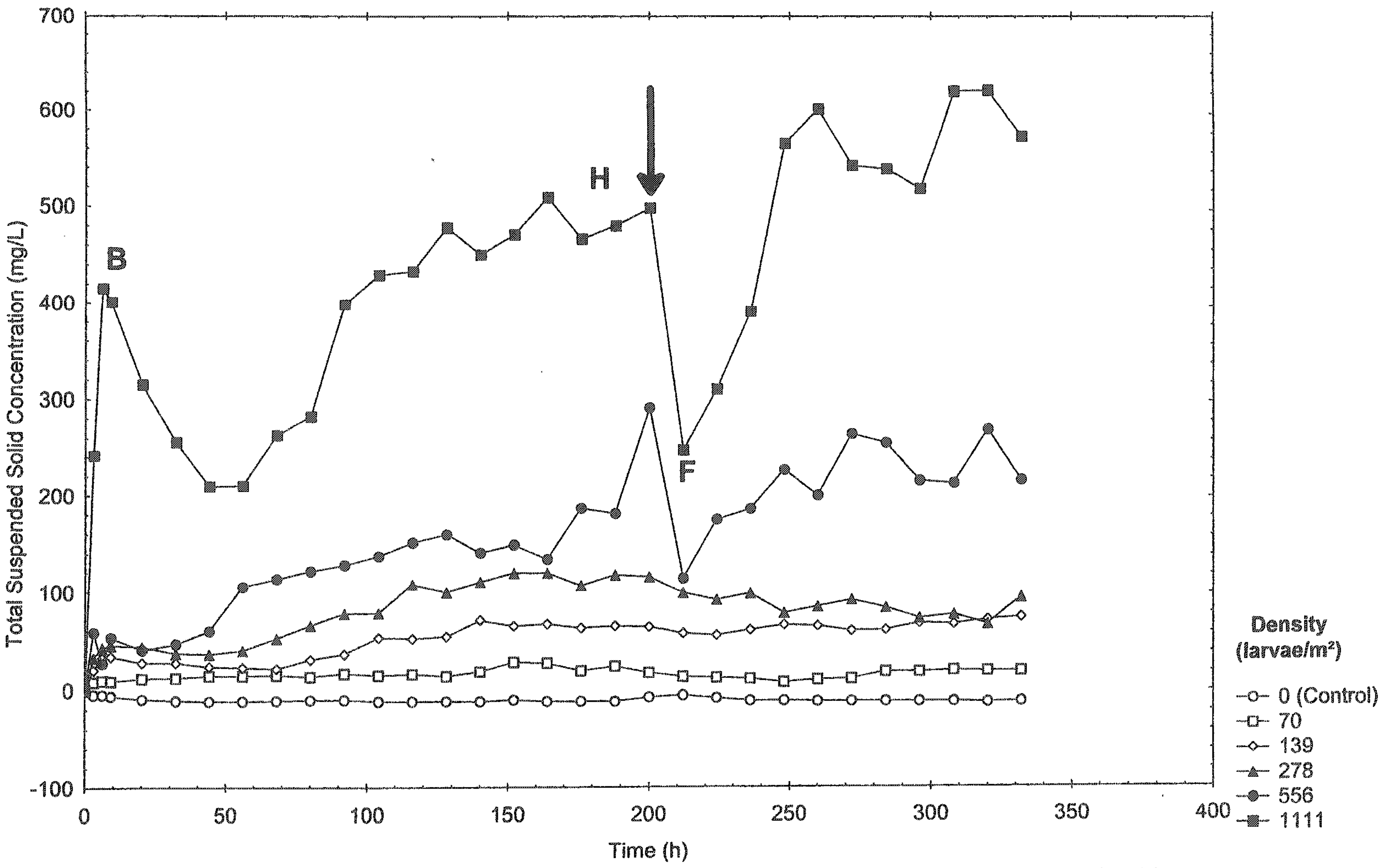

Figure 2.3: Time course of Total Suspended Solid concentration (TSS [mg/L]) during a single trial using 22 mm larvae at 19° C. Letters indicate periods of initial burrow construction (B), hunger (H) and satiation following feeding (F). Arrow indicates time of feeding (200 h).

model, regressions of the observed vs. predicted sediment suspension rates for each of the three sediment suspension phases was performed. A t-test was used to determine if the slopes differed significantly from a value of 1.0. Outliers were removed from slopes that differed significantly from zero and slopes were recalculated.

RESULTS

Sediment Settling Rate

Sediment settling rates increased as a function of increasing temperature. Settling rates ranged from 0.44 mg/L/h (10° C) to 1.04 mg/L/h (22° C) (Table 2.2). 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 (Figure 2.4). The lower sediment suspension value for the 25° C treatment was not removed as an outlier from the regression analysis since the values for the 19° C and 22° C treatments were calculated from a separate settling rate experiment. This was done since during the initial experiment these two values were uncharacteristically low due to low suspended sediment concentrations. Including the 25° C treatment will provide a more conservative estimate of the settling rate and thus *Hexagenia* sediment suspension. 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 sediment concentrations followed a characteristic time course, which was most pronounced in the high density and large larval size treatments. The TSS

Table 2.2: Settling rates for Lake Erie site 357 sediment as a function of temperature. The linear regression equation for these settling rates takes the form $B_{Settle} = 0.087 + 0.039 * T$, where T = temperature, R^2=088.

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]

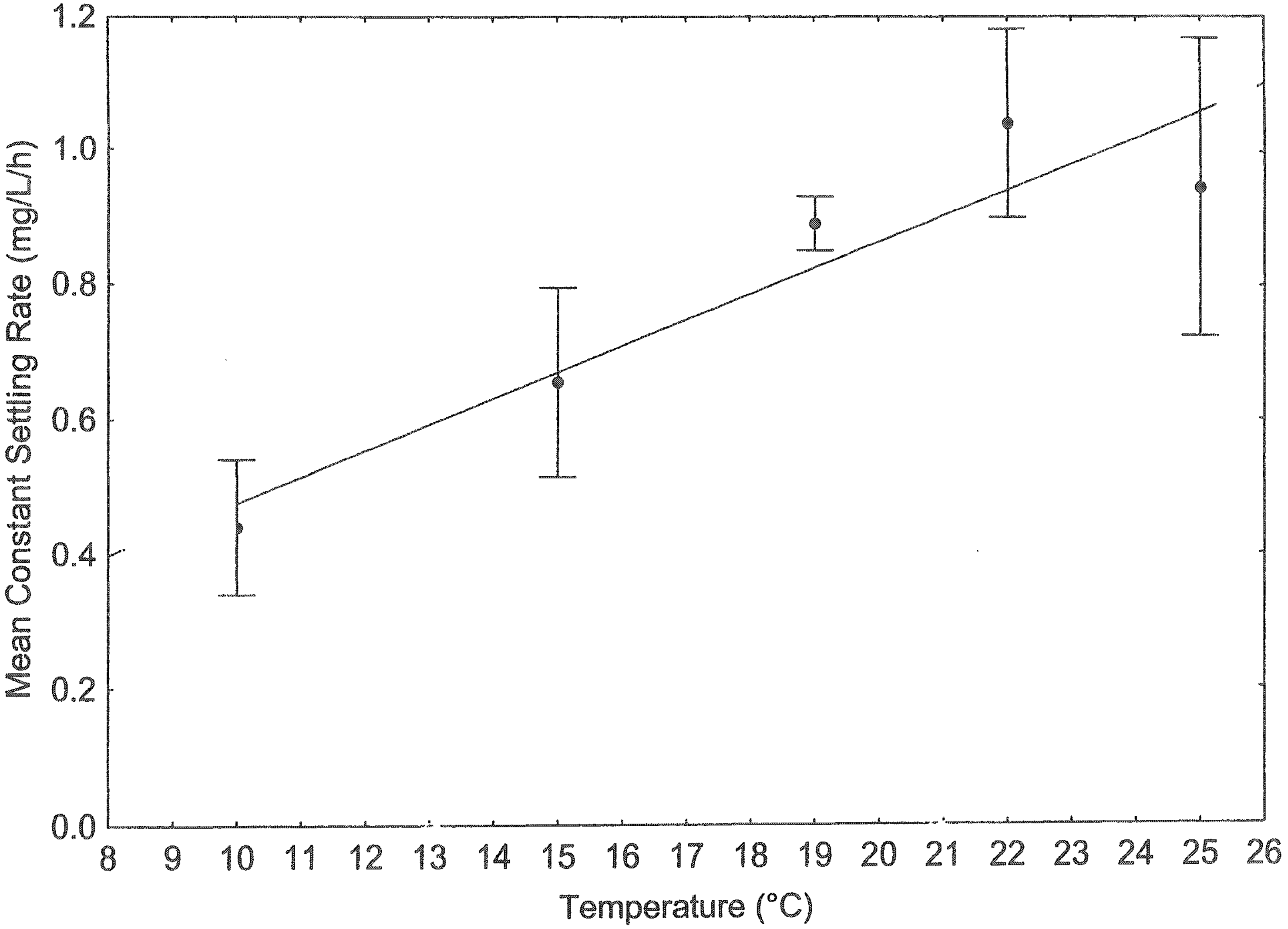

Figure 2.4: Sediment settling rates (mg/L/h) for Lake Erie site 357 sediment as a function of temperature. Regression equation takes the form $B_{Settle} = 0.087 + 0.039*T$, where T = temperature (°C) ($R^2 = 0.88$).

concentration rose rapidly during the first 3-12 h, likely as a result of larval burrow construction (Figure 2.3 'B') for the two highest larval densities. This was followed by a period of 12-48 h when TSS concentration decreased. TSS concentration then rose gradually and often exceeded levels observed during initial burrow construction (Figure 2.3 'H'). Sediment concentrations fell abruptly and dramatically during the period immediately following feeding (Figure 2.3 'F'), but gradually rose to reach or exceed previous levels. Similar patterns were observed for lower larval densities. However, the maximum and minimum TSS asymptotes for the lower densities were very close.

Initial burrow construction, maximal and minimal sediment suspension rates all increased with increasing larval size, larval density and water temperature. These three different sediment suspension rates were based on the TSS peaks for initial burrow construction and the maximal peak. The minimal rate estimate was based on the TSS valley that was observed 12 h after feeding the larvae (Figure 2.3). The size, density, and temperature combinations (see Table 2.1) used for this experiment 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 had fewer than three replicates and some of the combinations that were to be omitted (see Table 2.1) were actually used in some trials when the appropriate sizes of larvae were available.

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) x Ln (density) x Ln (temperature) interaction and Ln (size) x Ln (density) (total $R^2 = 0.79$, $P < 0.001$; Table 2.3). Maximal (hungry) sediment suspension rates were best estimated by the variables for Ln (size) x Ln (density) x Ln (temperature) interactions, and Ln (temperature) (total $R^2 = 0.82$, $P < 0.001$ for both independent variables; Table 2.3), and minimal (fed) sediment suspension rates were best estimated by the variables for Ln (size) x Ln (density) x Ln (temperature) interaction and temperature (total $R^2 = 0.80$, $P < 0.001$ for both independent variables; Table 2.3).

The independent variables for each of the three sediment suspension rates (burrow construction, maximum, and minimum) were used to create surface response curves estimating sediment flux due to the larvae, and the actual data points were overlaid on these response curves (Figures 2.5, 2.6, 2.7). The observed sediment suspension rates were plotted against the sediment suspension rates predicted from the terms of the multiple regression analysis (Figure 2.8 a-c) to test for biases in predicted sediment flux. A t-test of slopes for observed versus predicted sediment suspension rates for the initial burrow construction rate (0.97) and the minimum (fed) rate (0.96) did not differ significantly from 1.0 ($p > 0.05$). The slope for the maximum (hungry) sediment suspension rate (0.89) differed significantly from one ($p < 0.05$), suggesting that the regression equation somewhat underestimated the maximal (hungry) sediment suspension rate. The data points near the origin (low sediment suspension rates) are very close together indicating little systematic bias in estimation of sediment suspension rate.

Table 2.3: Forward step-wise 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 x Ln Density X Ln Temp	1.05×10^{-1}	7.04×10^{-3}	0.78
Ln Size X 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 x Ln Density x 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 x Ln Density x 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

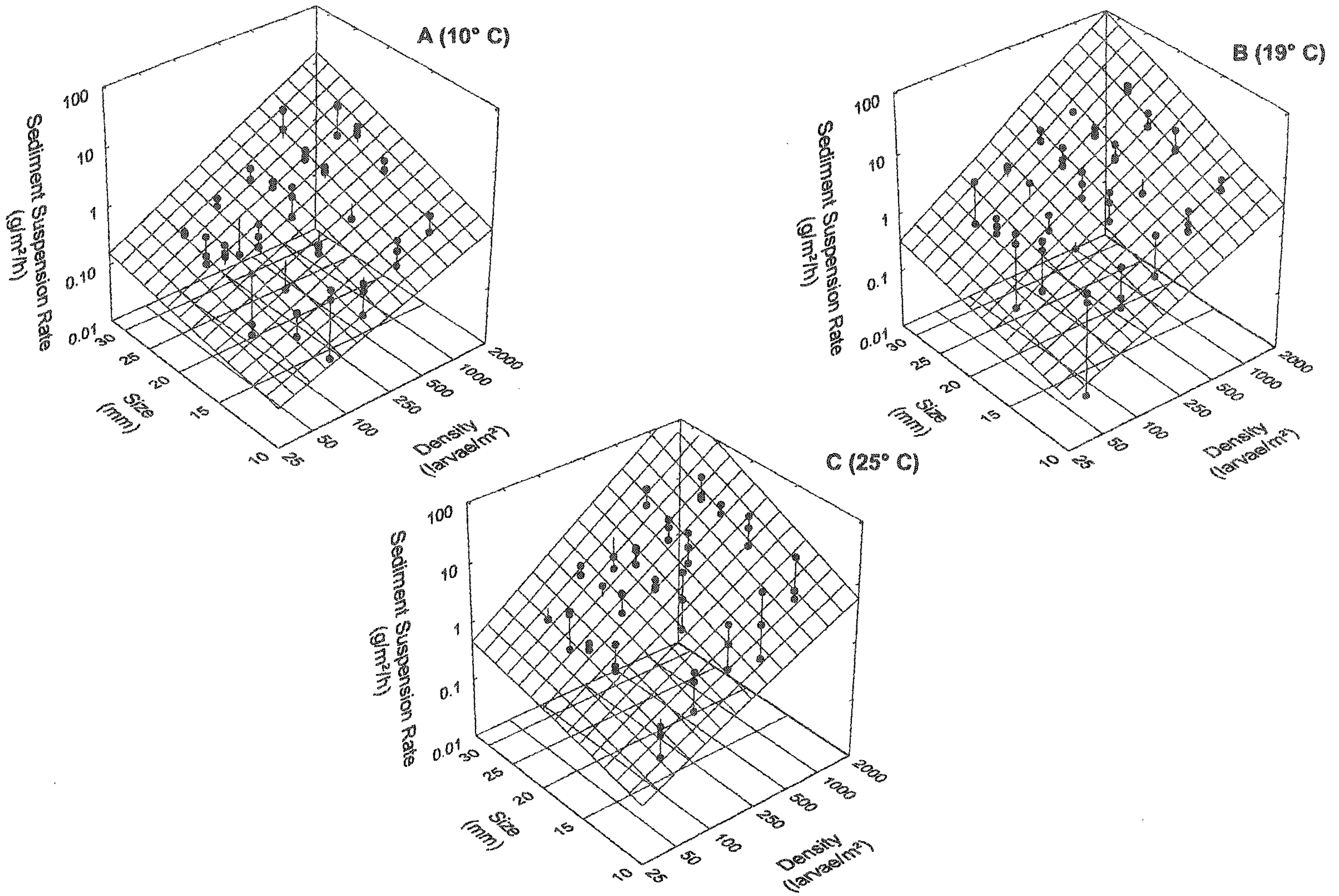

Figure 2.5: Response surface of initial burrow construction sediment suspension rates ($g/m^2/h$) estimated from the equation of the significant independent variables from the forward step-wise multiple regression analysis for (A) 10° C, (B) 19° C and (C) 25° C. Closed circles represent actual data points upon which the regression analysis is based.

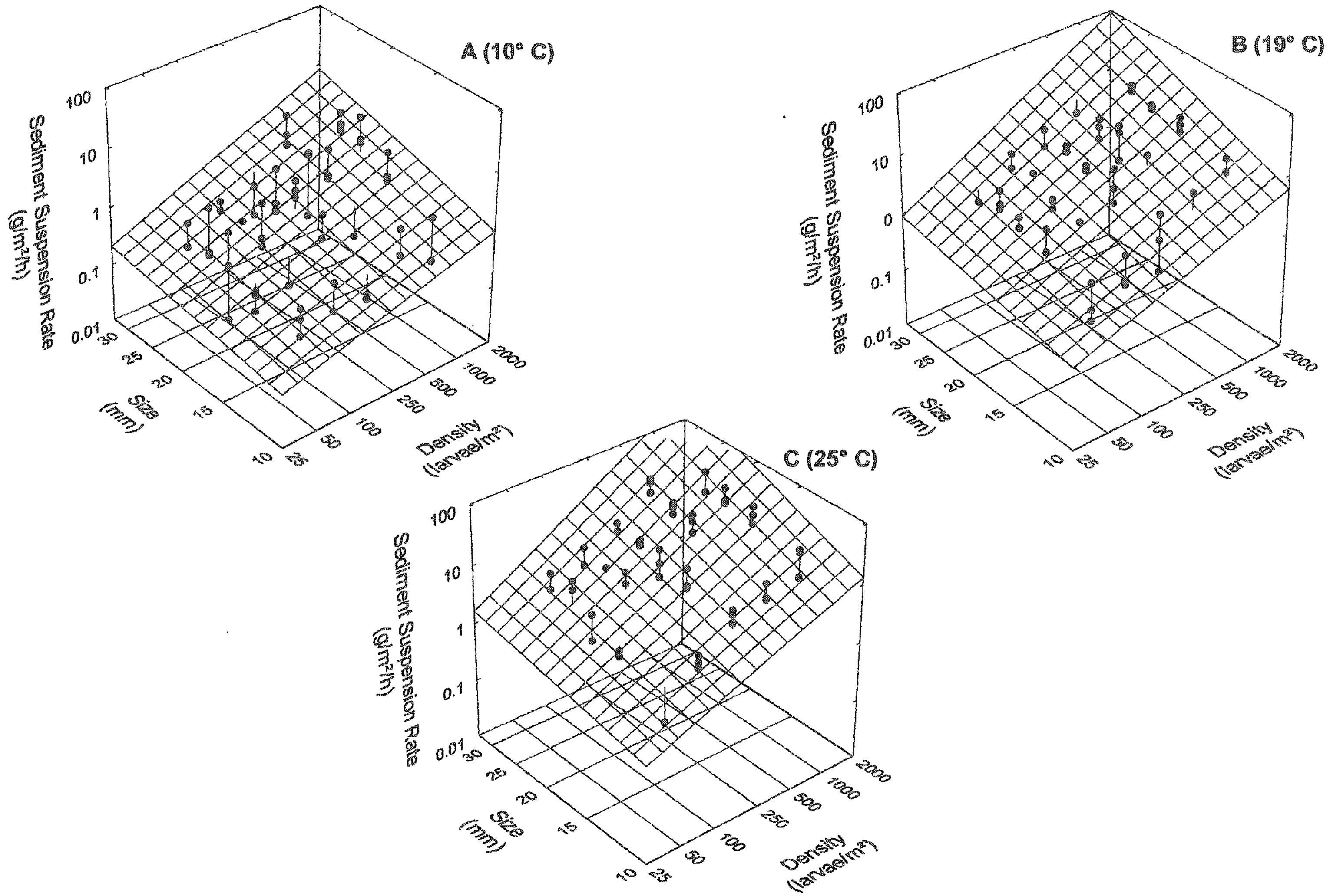

Figure 2.6: Response surface of hungry larvae (maximum) sediment suspension rates (g/m²/h) estimated from the equation of the significant independent variables from the forward step-wise regression analysis for (A) 10° C, (B) 19° C and (C) 25° C. Closed circles represent actual data points upon which the regression analysis is based.

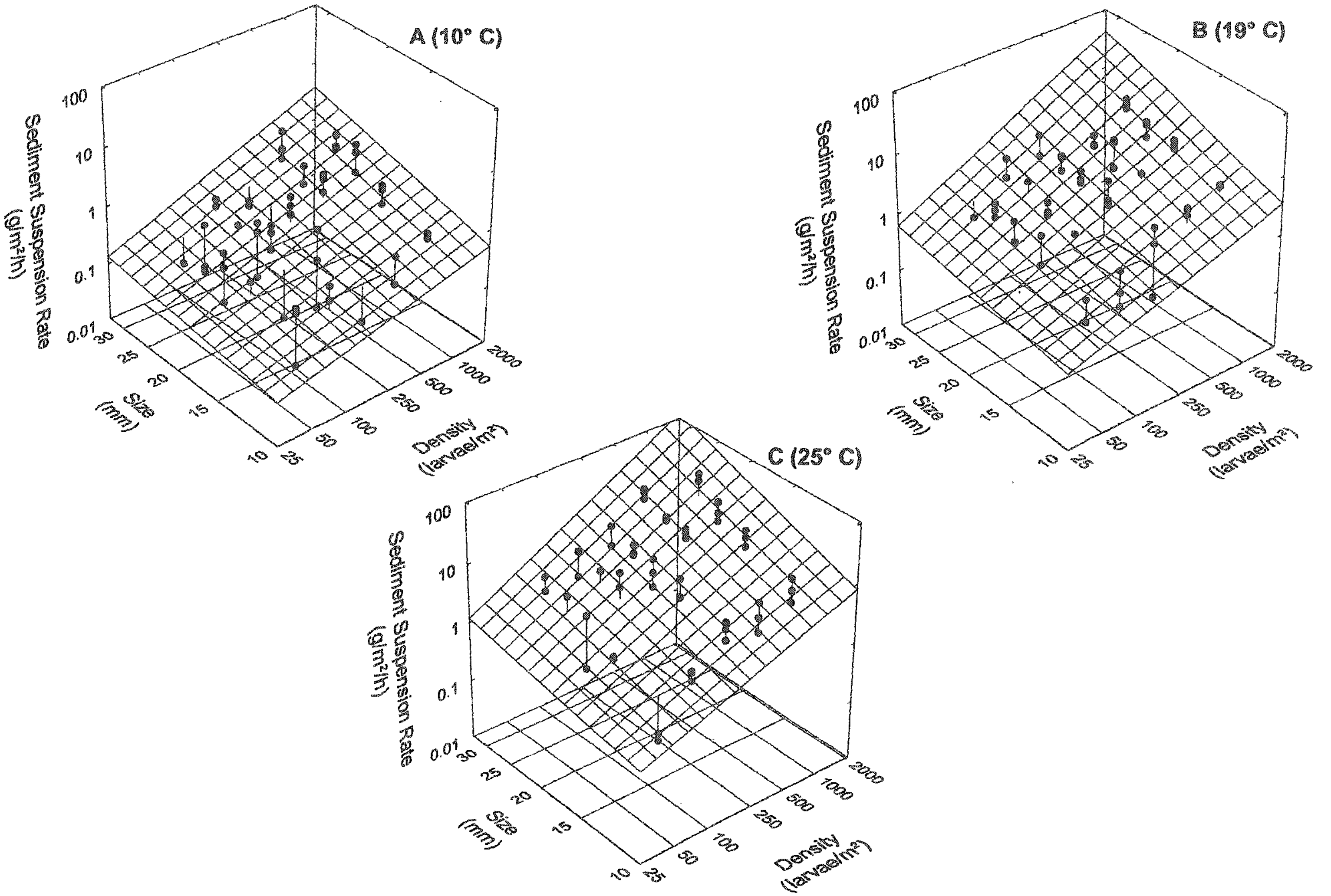

Figure 2.7: Response surface of fed larvae (minimum) sediment suspension rates (g/m²/h) estimated from the equation of the significant independent variables from the forward step-wise multiple regression analysis for (A) 10° C, (B) 19° C and (C) 25° C. Closed circles represent actual data points upon which the regression analysis is based.

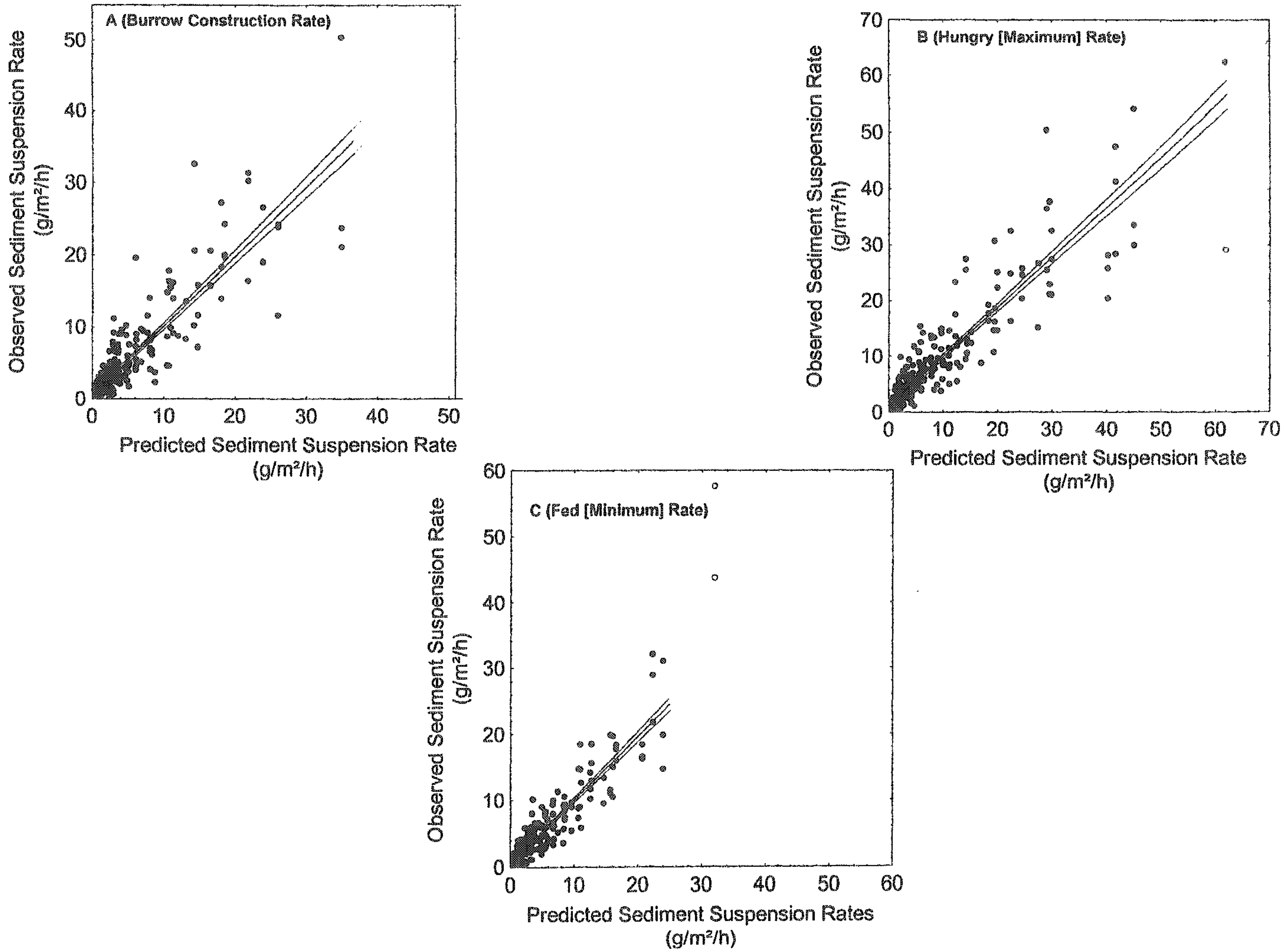

Figure 2.8: Observed and predicted (from regression equation) sediment suspension rates for (A) initial burrow construction, (B) Hungry larvae (maximum) and (C) fed larvae (minimum). Open circles represent outliers excluded from analysis.

Mean ± SE maximum (hungry) sediment suspension rates were low in low temperature treatments for small larvae (12.5 cm long), ranging from 0.23 ± 0.07 $g/m^2/h$ (n=3) for 1 larva/jar at 10° C to 3.69 ± 1.35 $g/m^2/h$ (n=3) for 8 larvae/jar. The high temperature (25° C) maximum (hungry) sediment suspension rates ranged from 0.36 ± 0.00 $g/m^2/h$ (n=2) for small (12.5 cm) larvae at a density of 1 larva/jar to 39.02 ± 5.64 $g/m^2/h$ (n=3) for large (27.5 mm) larvae at a density of 8 larvae/jar. When these rates are estimated using the regression equation and are converted to $mg/m^2/h$/larva there appears to be a synergistic effect occurring, since the sediment suspension rate per larva increased with increasing density, especially at the warmer temperatures (Figures 2.9, 2.10, 2.11).

DISCUSSION

Hexagenia larval sediment suspension rates increased as a function of increasing larval size, larval density and water temperature. This is 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 to provide oxygen. 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). In my experiments this was reflected by increased bioturbation and sediment flux. The interaction (synergy) among size, density and temperature was 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 x density interaction improved predictions of sediment suspension rate. For both maximal

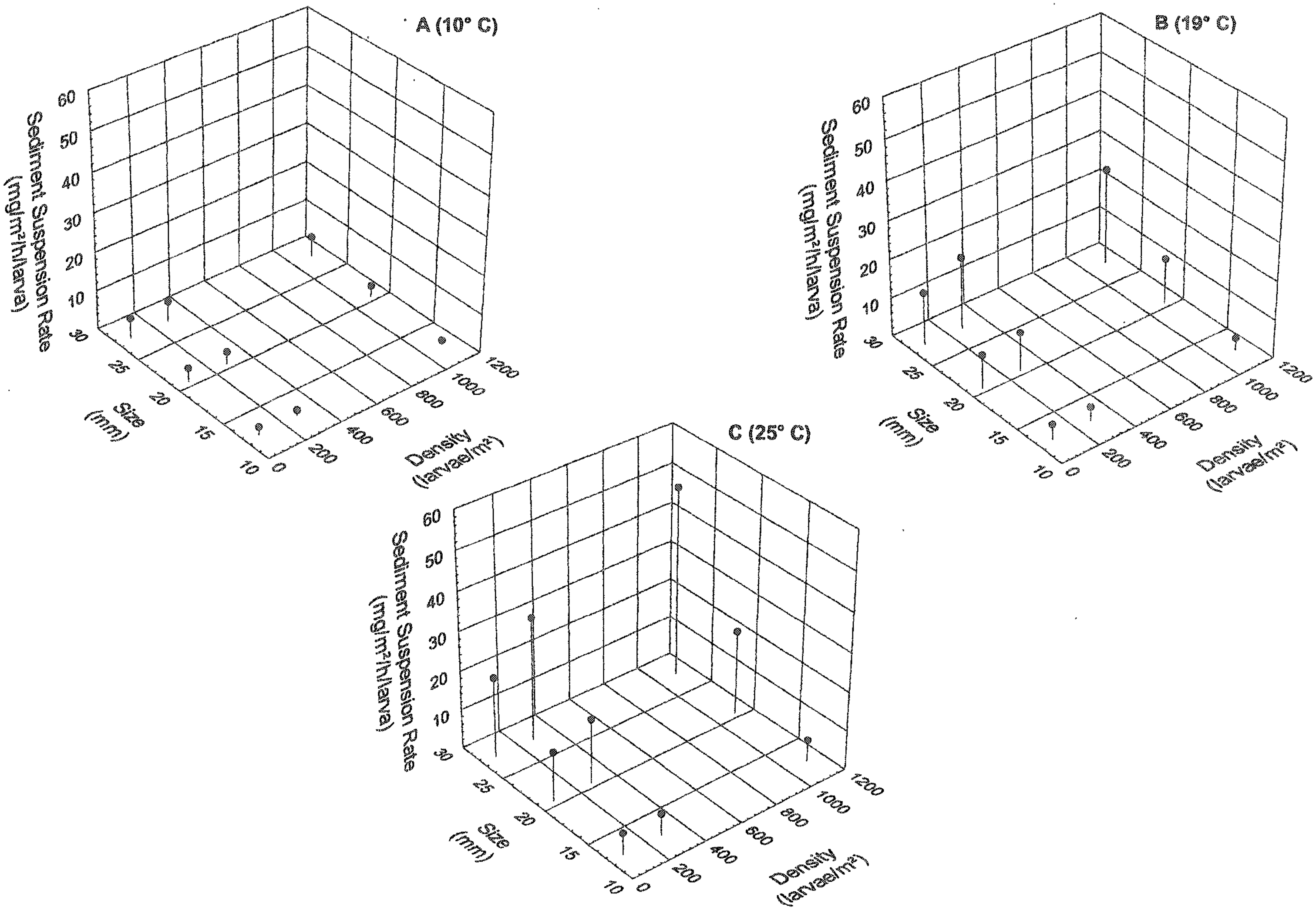

Figure 2.9: Initial burrow construction sediment suspension rate per larva (mg/m²/h/larva) estimated from the equation of significant independent variables from the forward step-wise multiple regression for (A) 10° C, (B) 19° C and (C) 25° C.

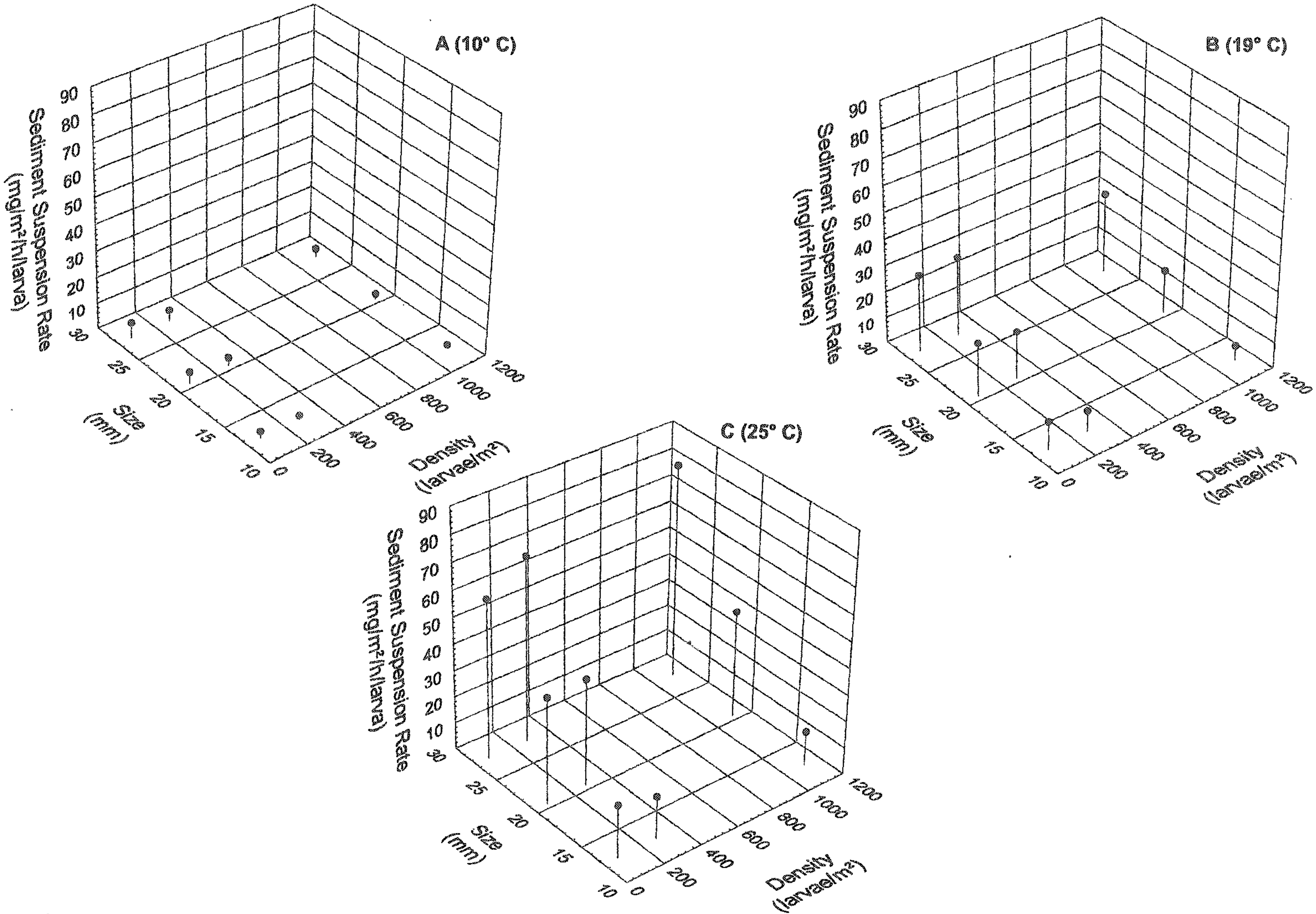

Figure 2.10: Hungry (maximum) sediment suspension rate per larva (mg/m²/h/larva) estimated from the equation of significant independent variables from the forward step-wise multiple regression for (A) 10° C, (B) 19° C and (C) 25° C.

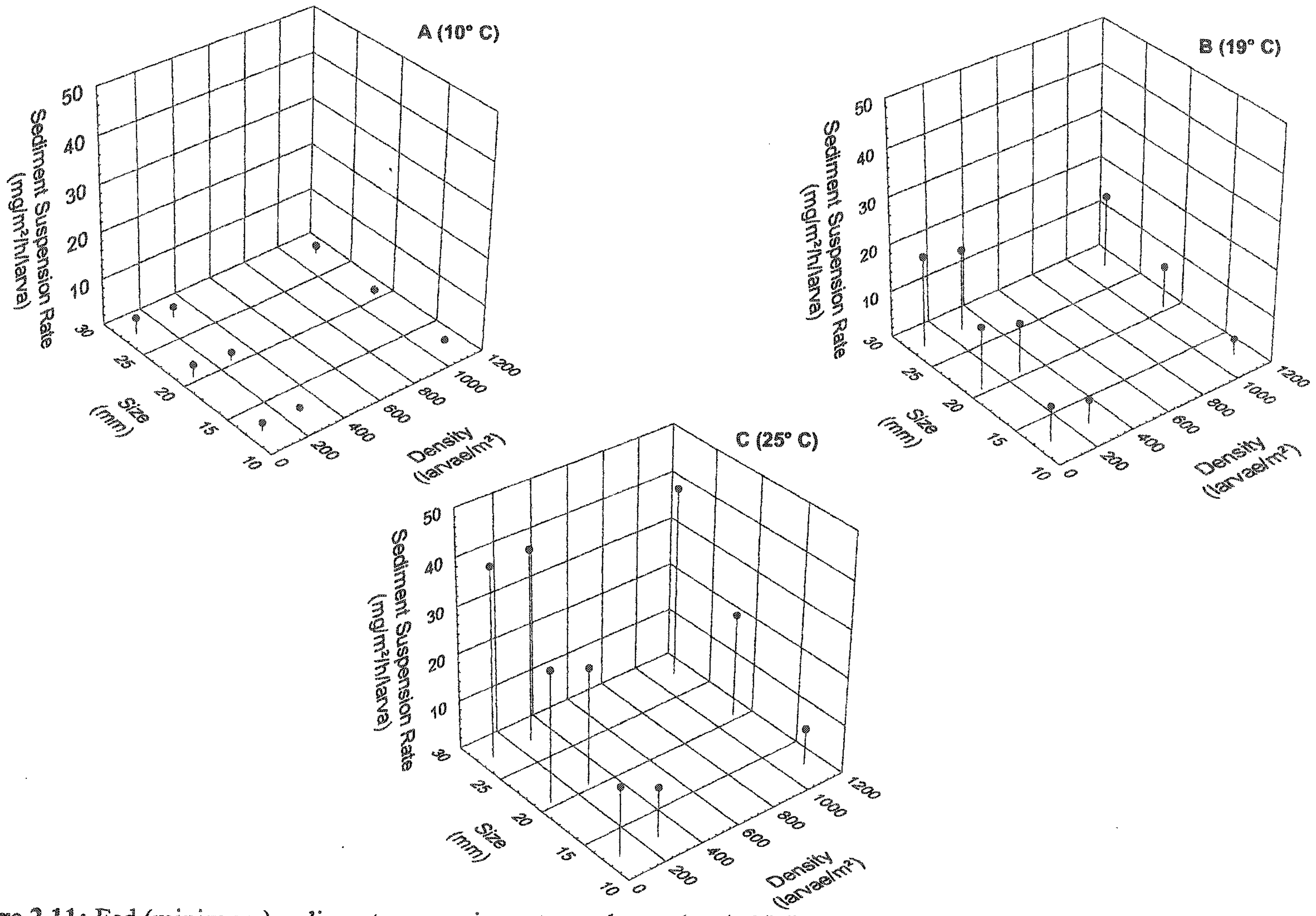

Figure 2.11: Fed (minimum) sediment suspension rate per larva (mg/m²/h/larva) estimated from the equation of significant independent variables from the forward step-wise multiple regression for (A) 10° C, (B) 19° C and (C) 25° C.

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, Zimmerman and Wissing 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 high (Chase 1998). Larvae are also largest (22 – 27 mm) and present in large numbers (greater than 1000 larvae/m^2) in late spring. 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 will be less active when the water temperature is low. The sediment suspension rate for a high density of larvae (1,111 larvae/m^2) in late spring approximately 45 times that in late fall when water temperature is low. The contribution of *Hexagenia* bioturbation will also be greatest in areas where there are traditionally high population densities, such as the Maumee Bay region and the area southeast of Colchester Harbour, Ontario.

There also appears to be a synergistic effect occurring at higher densities since the sediment suspension rate per larva appears to increases with increasing density. Larvae share burrows (Henry et al. 1986), and aggregate in containers containing sediment (Hanes and Ciborowski 1992). Hanes and Ciborowski (1992) suggested that this may increase the water current in the burrows, leading to increased oxygen and food availability. This increased current may explain the higher per larva sediment suspension rates observed at higher densities. At high densities, however, interference competition may occur since there may be 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 explanation for the increased sediment suspension rate per larva as larval density increases.

Sediment flux due to *Hexagenia* will vary among locations and times in western Lake Erie as larval density, larval size and water temperatures change. I used data from Lick et al. (1994) for a 3-day storm event and used the annual suspended sediment contribution of rivers and shoreline erosion to Western Lake Erie from Kemp et al. (1977) to compare the daily sediment suspension rates of these inputs to that of *Hexagenia* larval sediment suspension. The sediment suspension rates of 288 $g/m^2/d$ observed for large larvae at high temperatures (similar to what would occur in late spring) at a density of 400 larvae/m^2 (basin wide average) in these experiments approach the sediment inputs of shoreline erosion in western Lake Erie of 584 $g/m^2/d$ (Kemp et al. 1977). However, these high sediment suspension rates only occur during late spring and are considerably lower in the summer when mature larvae have emerged and in the winter when the water is colder and larvae are less active. Suspended sediment inputs from storm events 900 g/m^2 (300 $g/m^2/d$) for a 3-day storm event (Lick et al. 1994) and both the Detroit R. (1,168 $g/m^2/d$) and the Maumee R. (1,502 $g/m^2/d$) (Kemp et al. 1977) are considerably greater in western Lake Erie than *Hexagenia* bioturbation induced sediment flux. In terms of overall annual sediment loadings to western Lake Erie, *Hexagenia* bioturbation likely makes only a small contribution. However, shoreline erosion and river inputs are likely integrated over the entire depth of the water column, whereas the *Hexagenia* bioturbation contributes sediment mainly to the epibenthic water layer.

Hexagenia burrowing behaviour may also increase the water content of the sediment (McCall and Tevesz 1982) making it is less cohesive and more likely to be disturbed by wave induced 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 will likely become resuspended 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 reported for oligochaete worms, despite the worms' comparatively higher population densities in western Lake Erie (Reynoldson et al. 1989). Oligochaete worms are conveyer-belt feeders that deposit pelletized sediment at the sediment water interface (McCall and Fisher 1979). Thus, oligochaete feces are not suspended into the water column. *Hexagenia* larvae irrigate their burrows with oxygenated water (Keltner and McCafferty 1986) and in the process will convey suspended sediment particles directly into the water column. This is also true for chironomids. However, chironmids are much smaller and are more tolerant to anoxia than *Hexagenia* and thus will pump less water through their burrows than *Hexagenia*.

Hexagenia sediment flux 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/m^2/h for a population density of 2,000 mussels/m^2. In comparison, 400 large (25 mm) *Hexagenia* larvae/m^2 at a water temperature of 22° C suspend sediment at a rate of 12 g/m^2/h. Thus, the amount of sediment suspended by *Hexagenia* larvae is almost threefold greater than that which can be removed by *D. polymorpha*. This may lead to the exclusion of *Dreissena* from locations where *Hexagenia* densities are high.

The filtration rate of *D. polymorpha* is also influenced by suspended sediment concentration. For example, zebra mussels show an exponential decrease in filtration rate 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* are likely to suspend sediments to concentrations similar to those above during late spring in high larval density areas despite the increased dilution and mixing in the open water compared to the containers used in these laboratory experiments.

Hexagenia bioturbation has been suggested as a source of sediment associated nutrients, solutes (Matisoff and Wang 1998), and contaminants (Bartsch et al. 1999). Phosphorus is presently the main nutrient of interest in Lake Erie. Despite the significant amount of sediment suspended by *Hexagenia* bioturbation, the amount of biologically available phosphorus entering the water column is likely inconsequential. The oxygenated sediment in larval burrows contains ferric oxyhydroxides, which cause adsorption of phosphorus (Holdren and Armstrong 1980, Wetzel 1983). 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). As a result, 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* will generate less TP than dreissenids.

Bartsch et al. (1999) found that *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* bioturbation. 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 of natural recovery sites that receive clean sediment layers, traditionally attributed to instability of bed sediment (Thibodeaux and Bierman 2003). Release of these sediment bound contaminants is likely greatest in late spring when larvae are largest and water temperatures are high since larvae burrow deeper when they are larger and more active, thus suspending sediment from greater depths. *Hexagenia* 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, porewater solute content and contaminant flux.

CHAPTER 3: LABORATORY EXPERIMENTS TO DETERMINE THE EFFECTS OF DIFFERENT SEDIMENT DEPTHS AND SEDIMENT SOURCES ON SEDIMENT SUSPENSION BY *HEXAGENIA* LARVAE

INTRODUCTION

The purpose of this chapter is to determine the effects of different experimental sediment depths and different sediment collection locations on the rate of sediment suspension of *Hexagenia* larvae. These experiments determined if the sediment depth used in the size, density and temperature experiments allow for realistic predictions of *Hexagenia* sediment suspension in western Lake Erie and if there are differences in sediment suspension based sediment collected from different locations in western Lake Erie.

Hexagenia larvae burrow to an average maximum depth of 10 cm (Hunt 1953, Charbonneau et al. 1997, Charbonneau and Hare 1998). Since the sediment depth of 3.5 cm used in the size, density and temperature experiments is less than this burrow depth, it is possible that the sediment suspension rates from these experiments are either an over or under estimate of the sediment suspension rates that occur in western Lake Erie. Sediment depth can affect larval burrowing in a number of ways. In shallow (3.5 cm) sediment depths larvae may create burrows that are shallower and shorter in total length than burrows constructed in deeper sediment depths (10 cm). This would lead to a decrease in the total volume of sediment displaced during burrow construction compared to deeper sediment depths. However, in shallow sediment depths larvae may compensate by producing elongated burrows along the bottom of the experimental container. Hunt (1953) observed shallow, elongated burrows in areas of Big Silver Lake where the layer of suitable mud was shallow. This burrow elongation may allow for displacement of a similar volume of sediment as in the 10 cm sediment depth treatment. Burrow activity is constant thus the orientation of the burrow may not be relevant to sediment suspension rates. Sediment depth may also affect the amount of interference experienced from the burrows of other larvae, especially at higher larval densities and at larger larval sizes (Hanes and Ciborowski 1992). The shallow sediment depth of 3.5 cm will probably not affect the sediment suspension of small larvae (< 15 mm) since they are small and do not burrow as deeply into the sediment (Hunt 1953). Larger larvae (> 15 mm), however, burrow deeper into the sediment than small larvae (Hunt 1953) and thus the 3.5 cm of sediment used in the size, density and temperature experiments may affect sediment suspension rates for these larvae.

Sediment from different locations in western Lake Erie may also lead to differences in *Hexagenia* larval sediment suspension. Sediment collected from different locations in western Lake Erie may differ in particle size (MacFarlane 1998), organic content (Thomas et al. 1976) and contaminant load (Thomas et al. 1976, MacFarlane 1998, Marvin et al. 2002). Sediment in the central and western portions of the western basin of Lake Erie are composed mostly of silt and clay and become more sandy at the far eastern end of the basin, with some sand occurring along shoreline areas (Thomas et al. 1976, Bolsenga and Herdendorf 1993). These differences in particle size are influenced by river inputs (Kemp et al. 1977), wave induced sediment suspension (Lick et al. 1994) and lake geology (Sly 1976, Bolsenga and Herdendorf 1993). Sediment organic content at a given location is influenced by river inputs (runoff) (Wetzel 1983), presence of zebra mussel colonies, which increase the deposition of organic matter at the sediment water interface via the deposition of feces and pseudofeces (Klerks et al. 1996, Dobson and Mackie 1998), and pelagic (planktonic) and littoral (macrophytic) sources (Wetzel 1983). Sediment contaminant concentrations at specific locations in western Lake Erie are influenced by river inputs, industrial activities, atmospheric deposition, prevailing currents, sediment transport and deposition, remediation of contaminated sites and disposal of dredged material (Marvin et al. 2002). All of these local influences on sediment particles size, sediment organic content and sediment contaminant load will ultimately affect *Hexagenia* larval bioturbation and sediment suspension rates.

Hexagenia larval respiration (Eriksen 1963a) and burrowing ability (Lyman 1943), both of which influence sediment suspension rate, are influenced by sediment particle size. Larvae also preferentially select sediment of a particular particle size and organic content in which to construct burrows (Hanes 1992). Since *Hexagenia* larvae ingest sediment when feeding (Zimmerman and Wissing 1980) sediment organic content will influence how often and for how long larvae will feed. This in turn will influence the amount of sediment larvae excavate and ingest while burrowing thus affecting sediment suspension due to *Hexagenia* bioturbation. Sediment contaminant concentration also influences sediment suspension by *Hexagenia*. Sediment spiked with cadmium (Cd) led to decreased sediment suspension compared to control treatments containing no Cd (Bartsch et al. 1999). All of these factors may influence the physiology and behaviour of *Hexagenia* larvae. Differences in sediment particle size, sediment organic content or sediment contaminant load may influence larval feeding and burrowing activity, leading to changes in sediment suspension.

Two laboratory experiments were conducted to determine the effects of sediment depth and sediment collection location on *Hexagenia* larval sediment suspension. Plastic soft drink bottles containing sediment depths of 3.5 cm (as used in the size, density and temperature experiments [Chapter 2]) and 10 cm were used to determine the effects of sediment depth on larval sediment suspension of three size classes of larvae (small, medium and large larvae). Bottles of *Hexagenia* larvae containing sediment collected from 6 different locations in western Lake Erie were used to determine if sediment collection location effects larval sediment suspension for medium sized larvae.

MATERIALS AND METHODS

General Materials and Methods

The procedures for this chapter are described in the Materials and Methods section of chapter two. These methods include description of the study organism, collection and rearing of *Hexagenia* larvae, sediment collection methods, larval removal from rearing tanks, larval addition to experimental containers, water sample collection, spectrophotometery, determination of suspended solids from the standard curve, estimating sediment settling rates, determination of sediment flux and procedures for the size, density and temperature experiments. The procedures below describe the differences from the above mentioned methodology and analysis.

Variation in flux due to Sediment Depth

Three size classes of larvae (small [10-14 mm long], medium [16-20 mm] and large [22-25 mm]) and two sediment depths (3.5 cm and 10 cm) were used in a separate experiment to determine whether sediment depth influenced larval sediment suspension rate. Five replicates of each larval size class and sediment depth combination were set up. This experiment was conducted using polyethelyne 2-L soft drink bottles whose tops had been cut off (19 cm tall x 10.5 cm inside diameter). Five larvae (577 larvae/m^2) were added to each bottle. This experiment was conducted at a water temperature of 22° C. Prior to addition to the soft drink bottles the body lengths of larvae were measured using Mocha imaging software to the nearest 0.01 mm. One control bottle, containing no larvae, was set up for each sediment depth. A total of 32 bottles was used in this experiment. Because the bottom of the bottles was textured and of uneven depth, a 4 cm depth of washed, fine silica sand (particle size <500 um) was placed on the bottom of each bottle prior to adding experimental sediment. This prevented larvae from burrowing into the bottom of the pop bottles where the "feet" could interfere with burrow construction. *Hexagenia* larvae do not burrow into homogeneous sand (Lyman 1943). Sediment from site 357 (Figure 3.1) was placed on top of the sand to a depth of 3.5 cm or 10 cm. Aerated, dechlorinated water was added to a depth of 8.5 cm above the sediment (Figure 3.2 a). Food was added, and jars were allowed to clear while being aerated for 48 h as described in the general methods section of Chapter 2. Water samples were collected at time intervals and duration as described above. Independent variables were Ln transformed to equalize variances. An analysis of covariance (ANCOVA) was used to

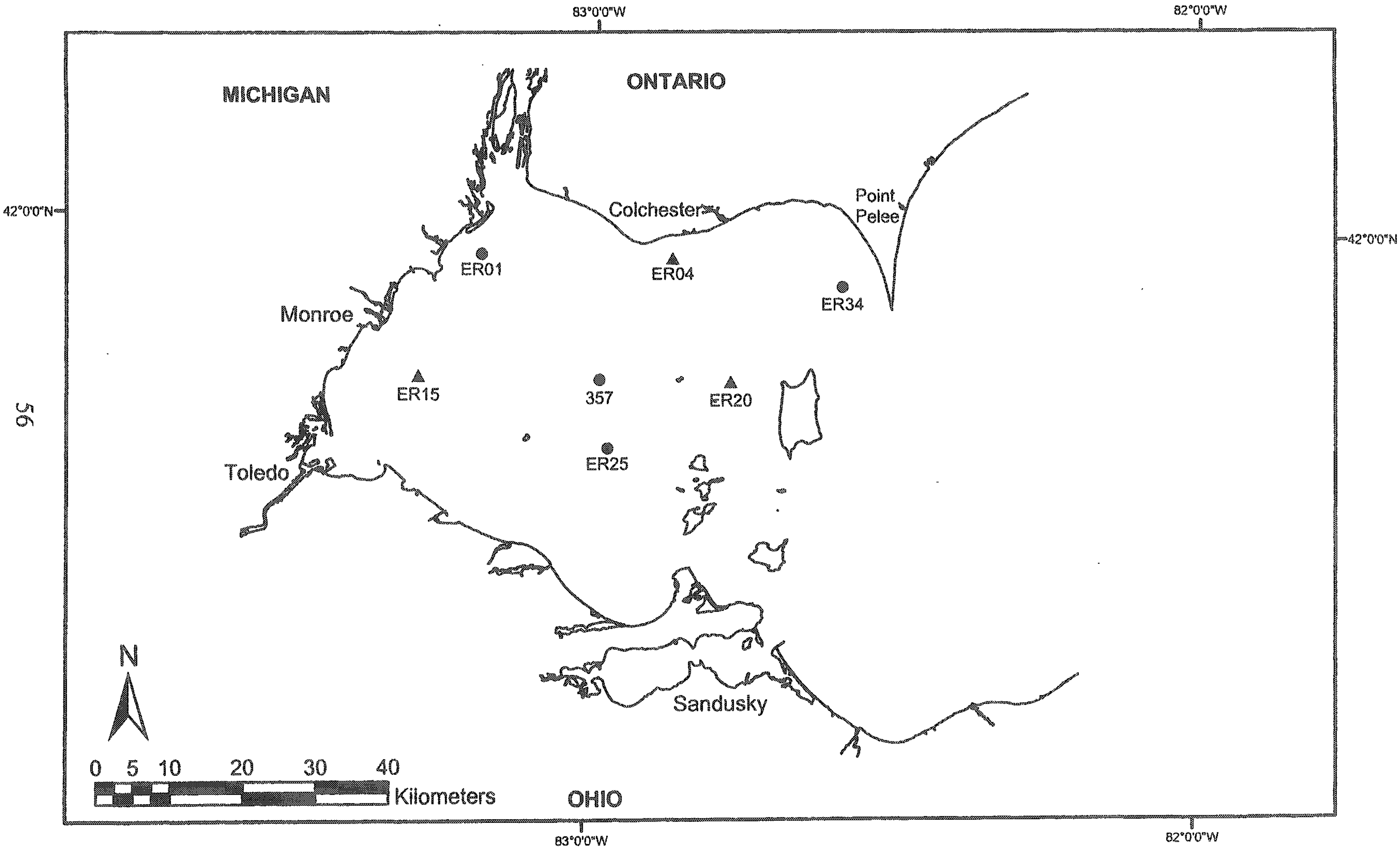

Figure 3.1: Sediment collection sites for sediment depth and sediment source experiments. Sites ER-01, ER-34, ER-25 and site 357 are low larval density sites (closed circles). Sites ER-04, ER-15 and ER-20 are high larval density sites (closed triangles). Site ER-01 was not used in any experiments since it was mostly sand and had an oily smell.

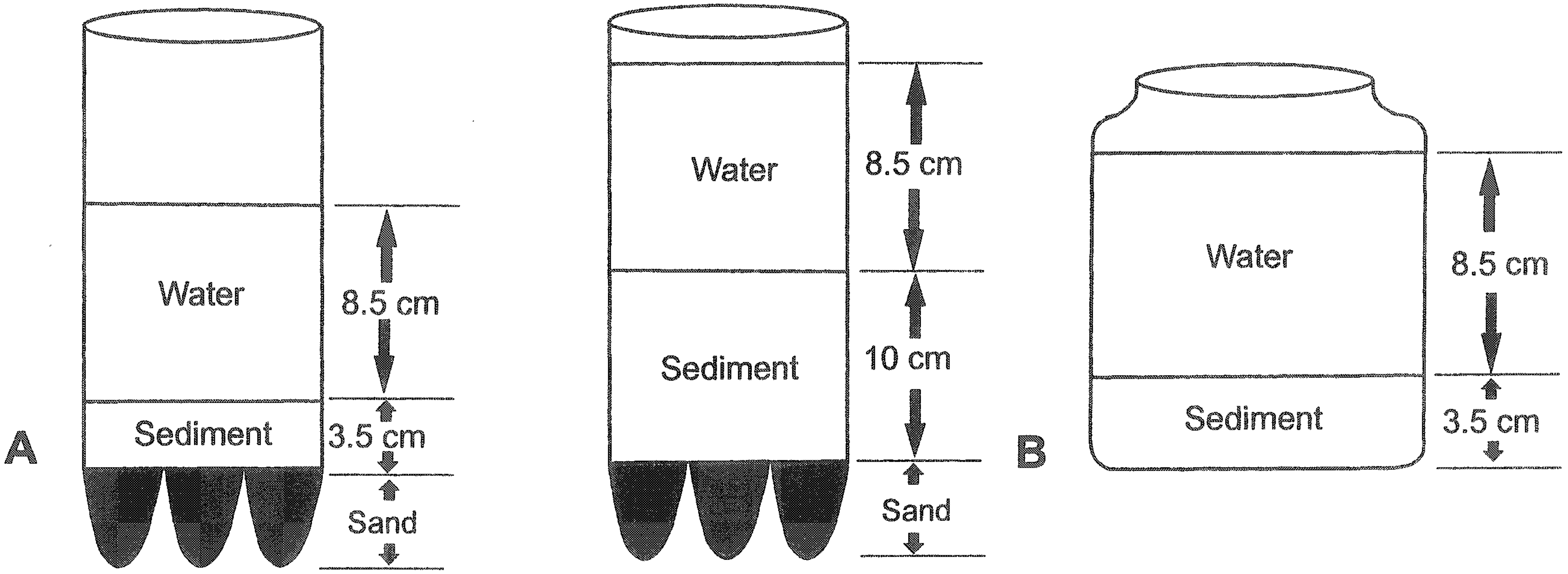

Figure 3.2: Sediment and water depths used in (A) sediment depth experiment (3.5 cm and 10 cm sediment depths) and the sediment site (B) experiment.

determine if Ln sediment suspension rates differed between sediment depths using Ln mean larval size per bottle as a covariate.

Variation in Flux due to Sediment Source

Experimental Setup

Sediment collected from 6 locations in western Lake Erie (3 high [> 300 larvae/m^2]and 3 low [< 200 larvae/m^2] larval population densities) (Figure 3.1) in the western basin of Lake Erie was used to determine the degree to which sediment type influenced suspension rates of *Hexagenia* larvae. Five replicate jars of sediment from each location and a reference jar, containing site 357 sediment but no larvae, were used. Sediment was added to 2-L glass jars to a depth of 3.5 cm, and dechlorinated aerated water was added to a depth of 8.5 cm (Figure 3.2 b). Medium sized larvae (15 – 22 mm) larvae were used at a density of 8 larvae/jar (556 larvae/m^2). This experiment was conducted at a water temperature of 22° C. Prior to the addition to jars digital images of anaesthetized larvae were measured to the nearest 0.01 mm using Mocha image analysis software. All other methodology was the same as in previous experiments.

Sediment Analysis

Sediment samples from each of the above locations were processed in the laboratory to determine moisture content, organic content (loss on ignition) and particle size distribution using methods based on ASTM designations D-2974-00 and C-136-01, with modifications for hand sieving.

Approximately 100 g of sediment from each site was spread on a sheet of aluminum foil and oven dried at 105° C for 24 h. The sample was removed from the oven and placed in a desiccator to cool and weighed to the nearest 0.01 g (dry mass). Water content of each oven dried sample was determined using the following equation:

$$\text{Water Content (\%)} = [(A - B) * 100]/A \qquad \text{(eq. 3.1)}$$

where

A = sample wet mass (g)

B = sample dry mass (g)

The oven dried samples were transferred to a crucible and incinerated in a muffle furnace at 440° C for at least 2 h until a constant mass was reached. Sediment samples were placed in a dessicator to cool and were weighed to the nearest 0.01 g. Loss on ignition was determined by calculating percent ash content using the following equation:

$$\text{Ash Content (\%)} = (C * 100)/B \qquad \text{(Eq. 3.2)}$$

where B = oven dried mass (g)

C = ashed sample mass (g)

To determine loss on ignition (LOI), ash content (%) is subtracted from 100.

The ashed sediment samples were used to determine particle size distribution for each sediment collection location. Samples were ground using a mortar and pestel and hand sieved through standard brass sieves. Mesh sizes used were 8.0, 4.0, 2.0, 1.0, 0.5, 0.25, 0.125 and 0.063 mm. Material was passed through the sieves using a side-to-side and up-down motion. Material retained on each sieve was re-ground and passed through the sieves again until all possible material passed through the sieves. Median particle size was determine by interpolation from a plot of cumulative sample mass (%) verses Wentworth scale (Phi). Conversion of sediment particle diameter to Phi scale was accomplished using the following equation:

$$(\text{Phi} = -\log_2 [\text{particle diameter}]) \text{ (Pye 1994).} \qquad \text{(Eq. 3.3)}$$

Statistical Analysis

Independent and dependent variables were Ln transformed to equalize variances. An ANCOVA was used to determine if Ln sediment suspension rate was significantly influenced by sediment depth. Ln mean larval size per jar was used as a covariate in the analysis. A planned comparison test was used to determine if Ln sediment suspension rate differed significantly between sediment collected at sites of high and low larval density. A separate ANCOVA and planned comparision test were used to determine if Ln sediment moisture content, Ln organic content, Ln particle size and sediment collection location significantly influenced sediment suspension rate. A planned comparison test was again used to determine if sediment suspension rate differed significantly between sediment collected at sites of high and low larval density.

RESULTS

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 only statistically significant ($p < 0.05$) for the sediment suspension rates during initial burrow construction and were not statistically significant ($p > 0.05$) for maximal sediment suspension (Table 3.1). These differences in sediment suspension 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 3.1). 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 (± SE, n=5) sediment suspension rates during initial burrow construction for small larvae (10-14 mm) were 4.59 ± 0.58 g/m^2/h and 7.51 ± 0.82 g/m^2/h respectively, for the 3.5 and 10 cm sediment depth treatments. Mean (±SE, n=5) sediment suspension rates during initial burrow construction for large larvae (22-25 mm) were 18.97 ± 3.53 g/m^2/h and 24.74 ± 2.46 g/m^2/h for 3.5 and 10 cm sediment depths, respectively (Figure 3.3 a). The maximal (hungry) sediment suspension rates were 14.46 ± 0.88 g/m^2/h and 15.83 ± 1.01 g/m^2/h respectively, for 3.5 cm and 10 cm sediment depths for small larvae and 28.67 ± 2.89 g/m^2/h and 30.01 ± 3.44 g/m^2/h respectively, for 3.5 cm and 10 cm sediment

Table 3.1: Analysis of covariance (ANCOVA) for the effects of Ln [sediment depth] (3.5 cm and 10 cm) and Ln [larval size] (small, medium or large) on Ln [sediment suspension rate] (initial burrow construction and maximal rates).

Initial Burrow Construction Rate

	d.f.	SS	MS	F	p
Ln Mean Larval Size	1	8.218	8.218	66.952	***
Sediment Depth	1	0.628	0.628	5.117	*
Error	27	3.314	0.123		
Total	29	12.160			

Maximum (Hungry) Rate

	d.f.	SS	MS	F	P
Ln Mean Larval Size	1	2.105	2.105	42.891	***
Sediment Depth	1	0.068	0.068	1.376	n.s.
Error	27	1.325	0.049		
Total	29	3.498			

* $p < 0.05$, *** $p < 0.001$, n.s. = not significant

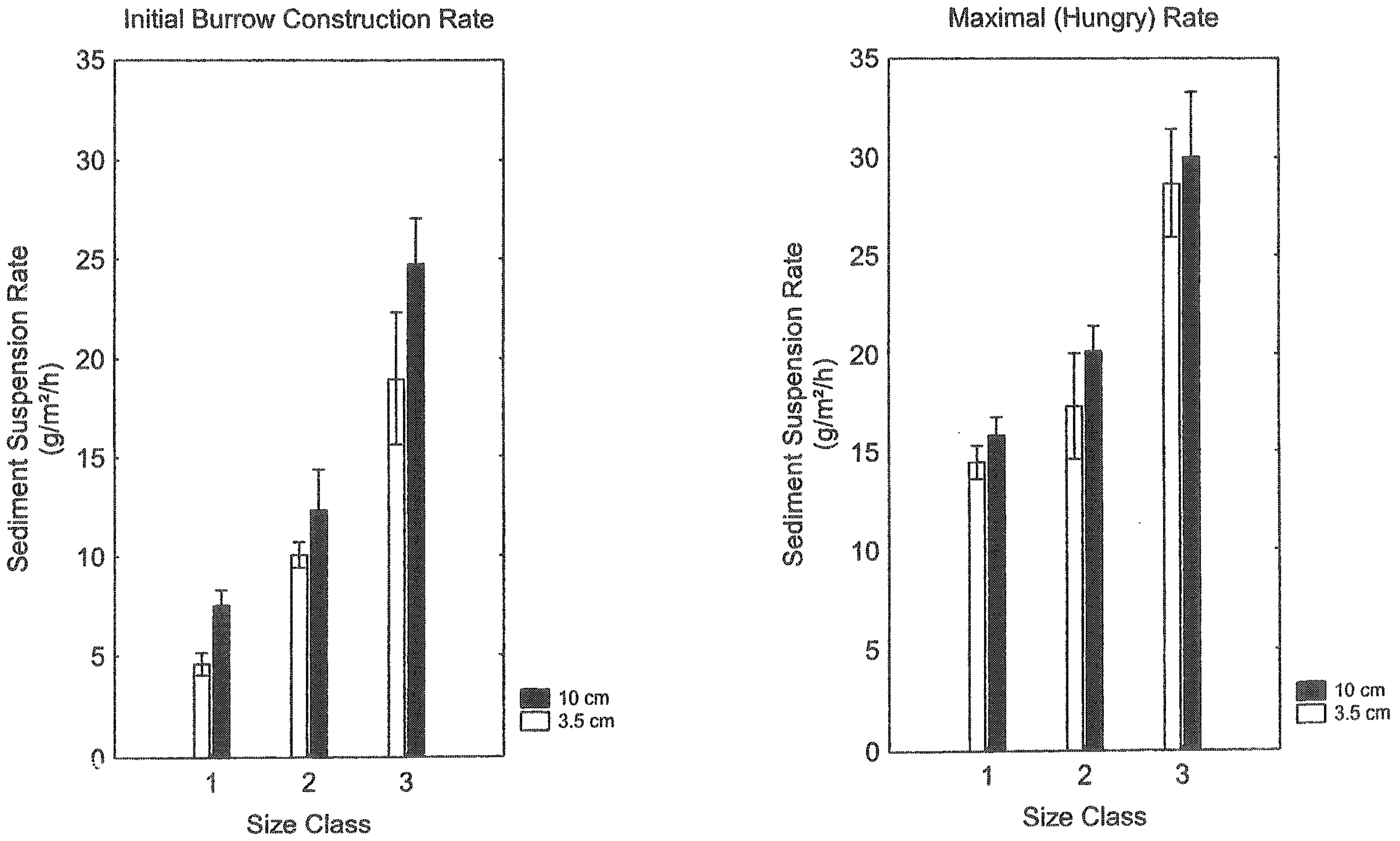

Figure 3.3: Mean (± S.E., n=5) sediment suspension rates at different sediment depths during initial burrow construction and for maximal (hungry) rates.

depths for large larvae (Figure 3.3 b). 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 the sediment suspension rate during both initial burrow construction and for the maximal (hungry) rates ($P < 0.001$) as a function of sediment type (Table 3.2). Mean (±SE, n=5) sediment suspension during initial burrow construction rates ranged from 7.47 ± 0.73 $g/m^2/h$ to 8.80 ± 1.23 $g/m^2/h$ for low larval density sediments and from 3.19 ± 0.21 $g/m^2/h$ to 4.09 ± 0.42 $g/m^2/h$ for high larval density sediment. Mean (± SE, n=5) sediment suspension during maximum (hungry) sediment suspension rates ranged from 17.53 ± 0.91 $g/m^2/h$ to 21.10 $g/m^2/h$ for low larval density sediments and from 9.75 ± 0.56 $g/m^2/h$ to 15.46 ± 2.49 $g/m^2/h$ for high larval density sediments (Figure 3.4). Using a planned comparsion test it was determined that the mean sediment suspension rates for both initial burrow construction and maximal (hungry) rates for two low density sediment sources were significantly different than the mean sediment suspension rates for the high larval density sediment sources ($p < 0.001$) (Table 3.2). Initial burrow construction rates for low density sediments are approximately double those for high density sediments. This appears 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 ($p > 0.05$).

Table 3.2: Analysis of covariance (ANCOVA) for the effects of sediment source on Ln [sediment suspension rate] (initial burrow construction and maximal rates) and planned comparisons for the effect of sediment larval density on sediment suspension rate.

Initial Burrow Construction Rate

	d.f.	SS	MS	F	p
Sediment Source	5	4.404	0.881	9.611	***
Larval Density	1	4.222	4.222	46.069	***
Ln Mean Larval Size	1	0.079	0.079	0.857	n.s.
Error	23	2.108	0.092		
Total	29	6.591			

Maximum (Hungry) Rate

	d.f.	SS	MS	F	p
Sediment Source	5	2.184	0.437	9.388	***
Larval Density	1	1.603	1.603	34.447	***
Ln Mean Larval Size	1	0.0003	0.0003	0.007	n.s.
Error	23	1.070	0.047		
Total	29	4.857			

*** $p < 0.001$, n.s. = not significant

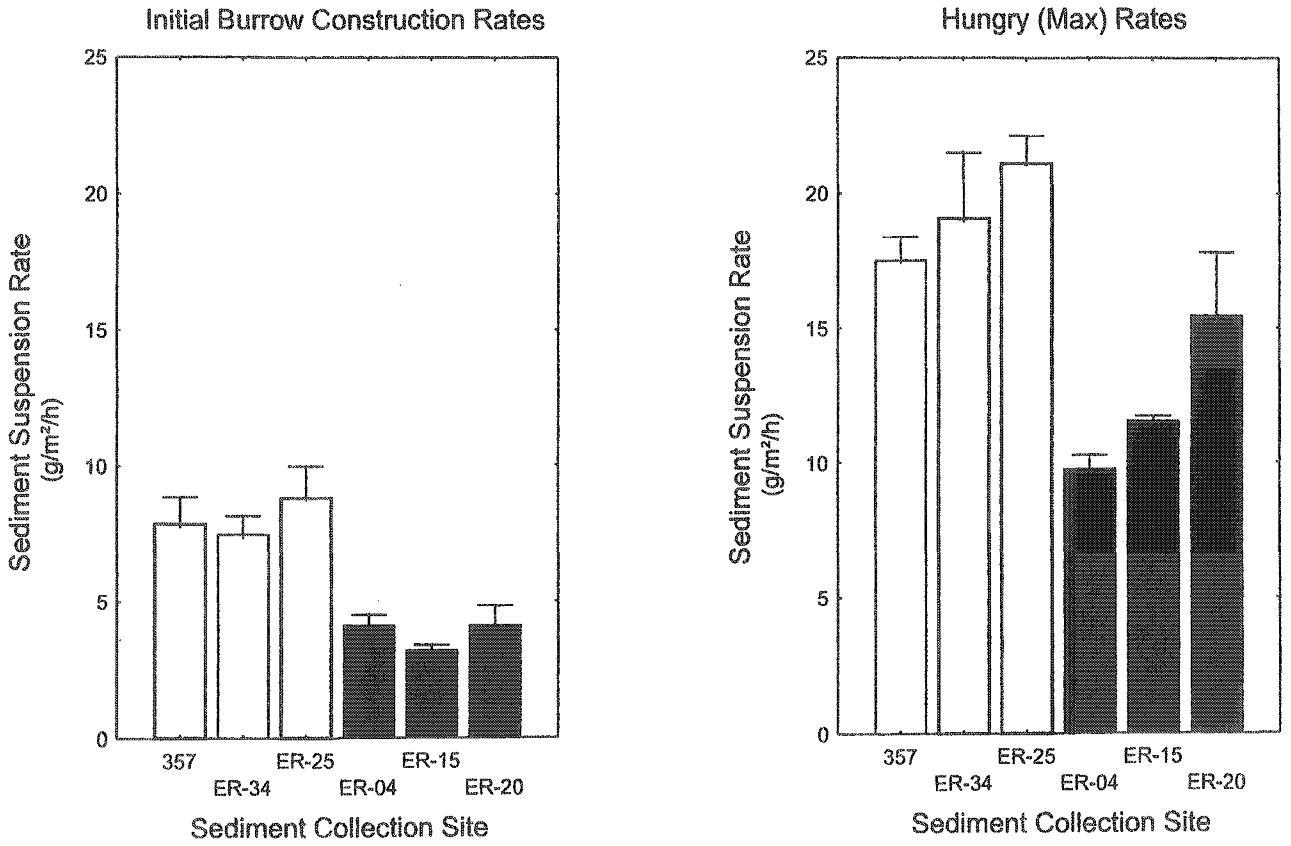

Figure 3.4: Mean (± S.E., N=5) during initial burrow construction and for maximal (hungry) rates for sediment collected at different locations in western Lake Erie. The white bars represent low larval density sites and the black bars represent high larval density sites.

The physical sediment characteristic varied between sediment collection locations (Table 3.3). The median particle size at site ER-04 (high larval density class site) and ER-34 (low larval density class site) were both in the silt and clay size range compared to all other sites which were in the fine sand range. Both sites ER-04 and ER-34 a lower moisture content and organic content compared to the other sites. This is due to the finer particle size which leads to smaller interstital spaces for water to reside and organic particles to adhere. An ANCOVA and planned comparison determined that sediment suspension rates for initial burrow construction were significantly influenced Ln organic content ($p < 0.001$), Ln particle size ($p < 0.001$) and sediment collection location ($p < 0.05$) (Table 3.4). For the maximum sediment suspension rates were significantly influenced by Ln moisture content ($p < 0.001$), Ln moisture content ($p < 0.001$), Ln particle size ($p < 0.001$). Sediment collection location did not significantly influence maximum sediment suspension rate (Table 3.4). For the planned comparison tests for both of these analyses high or low larval density at collection locations did not significantly influence sediment suspension rates.

DISCUSSION

Sediment Depth

Sediment suspension rates varied statistically based on the two sediment depths (3.5 cm and 10 cm) for the initial burrow construction, with the sediment suspension rate being greater in the 10 cm sediment depth. No significant differences were detected between

Table 3.3: Physical characteristics of sediment used in the sediment type experiment collected at different locations in western Lake Erie. All particle sizes (median particle size) fall within the fine sand range except those marked with an asterisks, which are in the silt and clay fraction.

Site	Larval Density	% Moisture	% Organic Content	Particle Size (μm)
ER-04	High	45.00	3.98	0.053*
ER-15	High	63.70	6.87	0.080
ER-20	High	65.04	6.20	0.084
357	Low	64.90	5.96	0.085
ER-25	Low	68.32	6.90	0.110
ER-34	Low	54.74	3.94	0.053*

Table 3.4: Analysis of covariance (ANCOVA) for the effects of Ln [moisture content], Ln [organic content], Ln [particle size] and sediment collection location on sediment suspension rate (initial burrow construction and maximal rates). Planned comparison for the effect of larval density class was also performed.

Initial Burrow Construction Rates

	d.f.	SS	MS	F	p
Sediment Source	2	0.763	0.381	4.162	***
Larval Density	1	0.377	0.377	4.113	n.s.
Ln Moisture Content	1	0.347	0.347	3.791	n.s.
Ln Organic Content	1	1.701	1.701	18.562	***
Ln Particle Size	1	1.593	1.593	17.380	***
Ln Mean Larval Size	1	0.785	0.381	0.857	n.s.
Error	23	2.108	0.092		
Total	29				

Maximum (Hungry) Rate

	d.f.	SS	MS	F	p
Sediment Source	2	0.082	0.041	0.885	n.s.
Larval Density	1	0.000	0.000	0.000	n.s.
Ln Moisture Content	1	0.904	0.904	19.439	***
Ln Organic Content	1	0.857	0.857	18.415	***
Ln Particle Size	1	0.340	0.340	7.315	*
Ln Mean Larval Size	1	0.0003	0.0003	0.007	n.s.
Error	23	1.07	0.047		
Total	29				

* $p < 0.05$, *** $p < 0.001$, n.s. = not significant

the two sediment depths for the maximal (hungry) sediment suspension rates. This suggests that the sediment suspension rates at the sediment depth (3.5 cm) used in the size, density and temperature experiment were comparable to what occurs in the western Lake Erie for the maximal sediment suspension rates, but an underestimate for the sediment suspension rates observed during initial burrow construction. However, the power of the experiment may not be strong enough to detect statistical differences between the constant differences observed. Some consistent differences were observed where the initial burrow construction rate was 18-20% greater in the 10 cm sediment depth experiments compared to that of the 3.5 cm sediment depth. This may occur since when larvae are first added to the containers they immediately burrow into the sediment when they come into contact with sediment surface (Hunt 1953, pers. obs). The length and depth of the burrows created may differ in the two sediment depth treatments. In the 10 cm sediment depth treatment larvae may be able to create burrows that are longer since they can burrow deeper into the sediment. This would lead to excavation of larger volume of sediment than would occur in the 3.5 cm treatment since burrow depth and length, and thus sediment volume excavated, would be restricted by the depth of the sediment. Larvae burrowing into the 10 cm sediment depth may also complete their burrows faster than those in the 3.5 cm sediment depth since they may not have to elongate their burrows along the bottom of the experimental container. This elongated shape may also decrease the water flow through the initial burrow leading to decreased sediment suspension since the burrow shape may not allow for optimum current flow.

Sediment Collection Location

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. Sediment organic content and particle size also influence sediment suspension rates during initial burrow construction along with sediment collection location. For maximal sediment suspension rates sediment moisture content, organic content and particle size also influence sediment suspension rate. For the maximal rates sediment type was no longer a significant predictor of sediment suspension rate since most of the variability explained by sediment collection location was explained by the physical attributes of the sediment.

Sediment suspension rates for sediments collected at different locations in western Lake Erie partly result from differences in sediment particle size since larval burrowing ability is affected by sediment particle size (Lyman 1943, Eriksen 1963a) and larvae preferentially select sediment from certain locations (Hanes 1992). Larval respiration is also influenced by sediment particle size (Eriksen 1963a), which will affect the sediment suspension rate. Sediment organic content also influences sediment suspension rate since *Hexagenia* larvae feed ingest sediment to feed (Zimmerman and Wissing 1980) and will feed more in sediments of lower organic content leading to increased sediment suspension. 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-cohesive sediments may need to relocate burrows more often and may require greater ventilation activity to maintain burrow integrity. As a result larvae in less suitable habitats may allocate more energy to burrow maintenance and feeding instead of growth. This will effect larval survival and thus the larval density at a given site.

Sediment suspension by *Hexagenia* larvae will vary at a specific location in western Lake Erie based not only on larval size, larval density and water temperature but, also on the suitability of the sediment for larval colonization. Some of the factors that are important in determining sediment suitability include sediment particle size (Lyman 1943, Eriksen 1963a, Hanes 1992), sediment organic content (Hanes 1992) and sediment water content (sediment cohesiveness). *Hexagenia* sediment suspension will likely increase as the sediment particle size changes above and below the optimum size required and as the cohesiveness of the sediment changes above and below the optimum required to maintain a burrow. It is also likely that *Hexagenia* larval sediment suspension will increase in areas where organic content is low since larvae will have to burrow more often to acquire food. Local sediment characteristics are also important in determining *Hexagenia* sediment suspension rates. Thus areas with sediments unsuitable for *Hexagenia* based on the increased energetic requirements resulting from increased sediment suspension will have lower larval densities.

CHAPTER 4: *HEXAGENIA* LARVAL-INDUCED SEDIMENT SUSPENSION IN WESTERN LAKE ERIE

INTRODUCTION

The purpose of this chapter is to estimate the mass of sediment suspended by activities of *Hexagenia* larvae in western Lake Erie using historical population densities prior to the prolonged absence of larvae from the 1960s to the 1990s (Carr and Hiltunen 1965, Reynoldson et al. 1989) and for population densities during the subsequent recolonization of *Hexagenia* in western Lake Erie (Krieger et al. 1996, Corkum et al. 1997a, Schloesser et al. 2000). Sediment suspension rates for different seasons for late spring 1997 (pre-emergence), summer 1997 (post-emergence), autumn 1997 and early spring 1998 are also calculated for western Lake Erie.

Hexagenia larvae were once a dominant zoobenthic organism in western Lake Erie (Hunt 1953, Britt 1955a, Carr and Hiltunen 1965, Reynoldson et al. 1989, Manny 1991). During a low oxygen event in western Lake Erie during the summer of 1953 *Hexagenia* larvae almost completely disappeared from the basin (Britt 1955a). *Hexagenia* population densities declined to near absence from the basin from the 1960s to the 1990s (Carr and Hiltunen 1965, Reynoldson et al. 1989). In the early 1990s *Hexagenia* larvae began to reappear in the western most portion of the basin. Range expansion continued eastward through to the late 1990s (Krieger et al. 1996, Corkum et al. 1997a, Schloesser et al. 2000). High population densities historically existed in the offshore areas of western Lake Erie, but greatest numbers have been observed in the southwest portion of the basin, relatively near shore in the late 1990s (Schloesser et al. 2000). If *Hexagenia* bioturbation contributes significantly to epibenthic suspended sediment concentrations, these spatial and temporal changes in the larval population may affect the distribution of suspended sediments at certain times of the year, and consequently the biota that are influenced by turbidity in western Lake Erie. In previous chapters I have shown that bioturbation results in significant sediment suspension as a function of larval density, larval size and water temperature. I will use current and historical data of the distribution, abundance and size of *Hexagenia* larvae in western Lake Erie to estimate sediment suspension rates throughout the basin.

Larval Life History Features

Seasonal changes in *Hexagenia*-induced sediment suspension are a function of larval densities, larval size frequency distribution and water temperature (Chapter 2). In western Lake Erie, larvae are largest just prior to emergence in June (Hunt 1953, Manny 1991). Water temperatures in western Lake Erie at this time rise to approximately 20 to 22° C (Chase 1998, J. J. H. Ciborowski unpubl.). Population densities then decrease immediately following the mass emergence of larvae in June when the large, mature larvae (≥ 16 mm body length) emerge (Hunt 1953, Manny 1991). Summer water temperatures are higher (reaching as high as 25° C) (Chase 1998, J. J. H. Ciborowski unpubl.). Autumn and early spring larval sediment suspension rates will be lower than the late spring (pre-emergence) and summer (post-emergence) rates primarily due to the low temperatures, approximately 14° C and 10 °C, respectively for autumn (October) and early spring (April) (Chase 1998, J. J. H. Ciborowski unpubl.). Larval sizes for these two times will also be smaller overall when compared to late spring larval sizes (Manny 1991).

I used records of western Lake Erie larval density distributions, larval size frequency distributions and water temperature data to estimate spatial distribution of sediment suspension rates. Sediment suspension rates were estimated for the month of June (just prior to emergence) using larval density data from 1930, 1951, 1993, 1995, 1997 and 1999. Also, data for four months (early June 1997, late July 1997, October 1997 and April 1998) over a 1y period in western Lake Erie were used to estimate sediment suspension rates based on changes in larval frequency distribution, larval density distributions and water temperature. The goal was to determine locations where *Hexagenia* sediment suspension is maximal in western Lake Erie. The sediment equations determined in Chapter 2 were used to calculate the minimum and maximum larval sediment suspension rates due to annual (year to year) variation in population density and for seasonal (month to month) changes in a given year for population density, size frequency distribution and water temperature.

MATERIALS AND METHODS

Population Density, Size Frequency and Water Temperature

Hexagenia population density data for the western basin of Lake Erie for 1930, 1951, 1993, 1995, 1997 and 1999 were compiled from benthic sampling programs conducted by the Ohio State University (Wood 1953, Wood 1973), U. S. Geological Survey, Heidelberg College (Tiffen, Ohio) and the University of Windsor (Chase 1998, Schloesser et al. 2000), K. Krieger Heidelberg College, unpubl., J. J. H. Ciborowski University of Windsor, unpubl.; See Appendix 2 for details about data sources, number of sites sampled, sample collection period, number of replicates per site and sampler type for each year). These density estimates were used in conjunction with water temperature data for western Lake Erie (Chase 1998, J.J.H. Ciborowski, University of Windsor, unpubl.) and size frequency data for *Hexagenia* larvae in western Lake Erie (1996; J.J.H. Ciborowski, Univ of Windsor, unpubl.) and substituted into the sediment suspension equations determined in Chapter 2.

In spring, the shallower westernmost and southern portions of the western basin warm more rapidly and are 1-2 °C warmer than the rest of western Lake Erie (K. Bedford et al. Ohio State University, unpubl.). However, epibenthic water temperatures in the present study were considered to be uniform throughout the basin to simplify the model.

Size frequency data was based on 11 sites sampled in 2 east-west transects that were 3 and 9 km south of the north shore of western Lake Erie in 1997. Sites were located at 6 km intervals along the length of the transects. Larvae had been collected in Petite Ponar grabs and were preserved in ethanol-formalin solution. They were measured to the nearest 0.1 mm using video images of the larvae and image analysis software. Data for all sites were pooled to produce size frequency distributions.

Water temperature data are monthly averaged data from Hydrolab Datasonde 3 measurements collected by the National Water Research Institute (NWRI) by T. B.

Reynoldson (Chase 1998) and from Greenspan DO300 logger and sensor at bottom -2 m by the University of Windsor (J. J. H. Ciborowski, unpubl.).

Sediment Suspension Rate Calculations

Equations used to estimate sediment suspension rate were from Chapter 2 of this thesis. The 'minimum sediment suspension rate' equation (Eq. 4.1) represents larval sediment suspension after food addition to experimental jars. The 'maximal sediment suspension rate' equation (Eq. 4.2) represents larval sediment suspension prior to food addition to experimental jars.

Minimum Sediment Suspension Rate

$$\text{Ln SedSusp} = -7.50182 + (0.09398*\text{Ln}[\text{size}]*\text{Ln}[\text{density}]*\text{Ln}[\text{temp}]) + (1.32688*\text{Ln}[\text{temp}])$$

(Eq. 4.1)

Maximum Sediment Suspension Rate

$$\text{Ln SedSusp} = -6.75440 + (0.10359*\text{Ln}[\text{size}]*\text{ln}[\text{density}]*\text{Ln}[\text{temp}]) + (1.08681*\text{Ln}[\text{temp}])$$

(Eq. 4.2)

where

SedSusp is the sediment suspension rate ($g/m^2/h$)

Size is the larval body length (mm)

Temp is the average water temperature (°C)

Density is the number of larvae at each collection location (larvae/m^2)

The densities for each site in western Lake Erie prior to the mass emergence (early June) for each the above mentioned years, the average water temperature for the month and the size frequency distribution of the larvae for the appropriate month were used to calculate the sediment suspension rate for each sampling site in western Lake Erie (Table 4.1). The number of sites for larval densities used in the calculations of sediment suspension rates varied among years (see Appendix 2 and Table 4.1). The size frequency distribution ranged from 8 mm to 28 mm (Figure 4.1). The 8 mm size class included larvae less than 8 mm and the 28 mm size class included larvae greater than 28 mm since the experiments conducted in Chapter 2 used larvae within this range. Thus, using sizes outside of this range would require extrapolation beyond the predictive range of equations 4.1 and 4.2.

Laboratory experiments to estimate larval sediment suspension rates were conducted using larvae of uniform sizes. In western Lake Erie, the size frequency distribution of natural *Hexagenia* larval populations is typically broad (Schloesser and Hiltunen 1984, Hanes and Ciborowski 1992, Figure 4.1). A macro was created in APL*Plus (APL*Plus STSC Inc. version 10) using the equations developed in Chapter 2 (Eq. 4.1 and 4.2) to calculate the sediment suspension rate for each size class in the size frequency distribution based on the total population density at the site. For example, if the population density the site was 400 larvae/m^2 then a sediment suspension rate was calculated for each size class as if there were 400 larvae of that size class present at the site. Then the total sediment suspension rate for each size class (e.g., 400 larvae of that size) was divided by 400 to express the estimate on a 'per larva' basis.

Table 4.1: Year, month and data used to calculate *Hexagenia* larval sediment suspension rates in western Lake Erie. Month of estimate indicates the month to which water temperature, larval density and size frequency distribution estimates pertain. The number of sites represents the total number of sites from which *Hexagenia* larval densities were available each year (see Appendix 2 for details on data sources and sampler type used). The maximum and minimum densities represent the upper and lower ranges of *Hexagenia* larval density for sites where larvae were present. Note that larval densities used for October 1997 and April 1998 (marked with "*") are based on samples collected in May/June 1998, which produces a conservative estimate for these sediment suspension rates.

Between Year Sediment Suspension Rate Estimates

Year	Month of Estimate	No. Sites	Min. Density (larvae/m^2)	Max. Density (larvae/m^2)	Water Temp. (°C)
1930	early June	67	2	692	20
1951	early June	184	48	500	20
1993	early June	47	6	38	20
1995	early June	21	5	115	20
1997	early June	58	9	2064	20
1999	early June	39	9	951	20

Seasonal Sediment Suspension Rate Estimates

Year	Month of Estimate	No. Sites	Min. Density (larvae/m^2)	Max. Density (larvae/m^2)	Water Temp. (°C)
1997	early June	58	9	2064	20
1997	end July	58	3	634	22
1997	October*	62	5	518	14
1998	April*	62	5	518	10

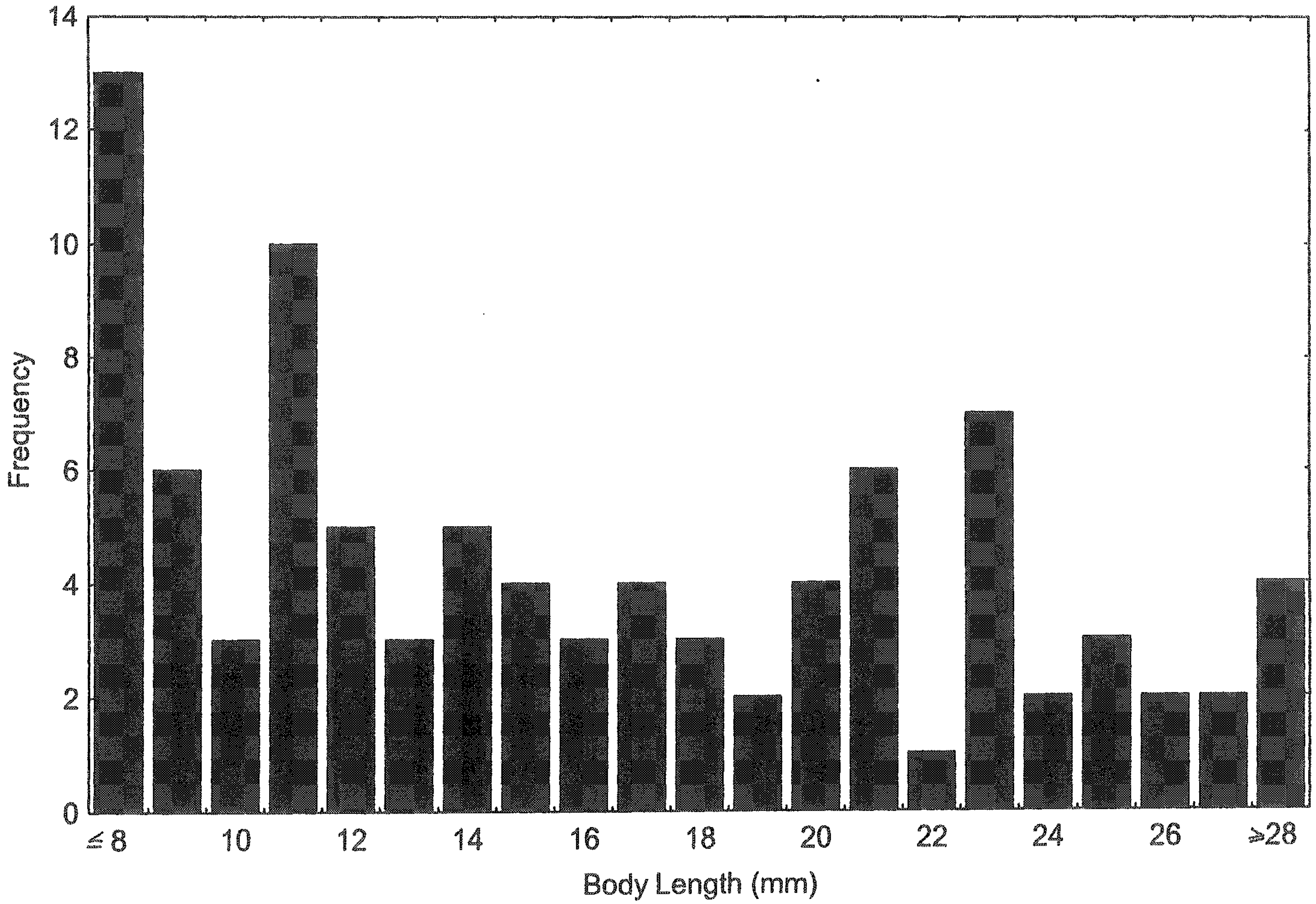

Figure: 4.1: Size frequency distribution of *Hexagenia* larvae prior to mass emergence in late spring 1996 and 1997 (Ciborowski unpubl.). Distribution is based on measurments of larvae collected from 3 high larval density sites in western Lake Erie in May of 1996 and 1997.

The contribution of each larval size class (i) to the site-specific estimate was determined by the equation

$$\text{Sedsusp}_{jTZ} = \text{D}_{jZ} \times \Sigma(l_{ijZ} \times sedsusp_{ijZ}) \qquad \text{(Eq. 4.3)}$$

where

Sedsusp_{jTZ} is the total sediment suspension rate at site j for a specific year or season Z (g/m^2/h)

D_{jZ} is the density of larvae at site j for a specific year or season Z(No./m^2)

L_{ijZ} is the proportion of larvae at site j in size class i for a specific year or season Z

$sedsusp_{ijZ}$ is the 'per larva' sediment suspension rate for a larva in size class i at site j for a specific year or season Z

and then multiplied by the proportion of the size frequency distribution represented by each size class. If 400 larvae/m² generate 20 g/m²/h, then one larva would generate 20/400 = 0.05 g/m²/h. If the 25 mm size class is 3% of the total size frequency distribution then there are 0.03 x 400 = 12 larvae/m² (25 mm long). Thus, the contribution of 25 mm long larvae would be 12 larvae x 0.05 g/m²/h = 0.6 g/m²/h. The contribution of each size class in the size frequency distribution was calculated in this way and the sum of the sediment suspension rates for each size class was the total sediment suspension rate for a particular site. These values were then multiplied by 24 to convert the sediment suspension rates from g/m²/h to g/m²/d.

Pre-emergent Sediment Suspension Among Years

Minimum and maximum sediment suspension rates were calculated for the 1930 and 1951 sampling locations as a historical reference for typical *Hexagenia* larval densities prior to the prolonged absence of larvae from western Lake Erie from the early 1960's to the early 1990's (Britt 1955b, Carr and Hiltunen 1965, Reynoldson et al. 1989). Sediment suspension rates were also calculated for all sampling locations for 1993, 1995, 1997 and 1999 to estimate the hypothetical amount of *Hexagenia* larval-induced sediment suspension during the period of range expansion of larval populations in western Lake Erie through the 1990's (Krieger et al. 1996, Corkum et al. 1997a, Schloesser et al. 2000).

Site-specific larval densities for each of the aforementioned years were input into equations 4.1 and 4.2 for each size in the size frequency distribution ranging from 8 mm to 28 mm using the macro described above. A water temperature average value of 20° C was used for these calculations because the temperature is attained by late May or early June (Chase 1998), J. J. H. Ciborowski unpubl.). This temperature is also the approximate threshold for the emergence of subimagoes of *Hexagenia* (Giberson and Rosenberg 1994, L. D. Corkum and J. J. H. Ciborowski, University of Windsor pers. comm.).

Variation in Sediment Suspension Rates Among Seasons - 1997

Sediment suspension rates were also calculated for late spring (early June) prior to mass emergence, summer (end of July) approximately 2 months (60 d) after mass emergence, autumn (October) and early spring (April) of the following year using population data from 1997 for all sampling locations in western Lake Erie (Table 4.1).

Late Spring (Pre-Emergence)

The population densities, size frequency distribution and water temperature for late spring 1997 were the same as those used for the yearly calculation of sediment suspension for 1997 above.

Summer (Post-Emergence)

The summer (end of July) densities were determined by assuming that all larvae ≥16 mm emerged and that no eggs from the next generation had hatched. The threshold length for emergence is deliberately conservative to produce the lowest reasonable estimate of sediment suspension. The larvae remaining in the lake after mass emergence (8 – 15 mm long) were multiplied by 1.15 to account for larval growth. This represents an estimated 15% increase in larval size over 60 days, based on data from Manny (1991). This led to a size frequency distribution ranging from 9 – 17 mm, which represents 53% of the original size frequency distribution. Therefore, the pre-emergence population density for each collection location was multiplied by 0.53 to approximate the larval density at each site remaining after emergence. To account for likely daily mortality, the post-emergence densities were further multiplied by a survival factor taken by converting the maximum 21-d survival rate from experiments (based on water temperature and dissolved oxygen concentration) conducted by (Winter 1994, Winter et al. 1996) to a daily survival rate and applying this over 60 d. This gave a survival rate of 0.58 for 60 d. Consequently, the number of larvae remaining post-emergence was multiplied by 0.58 to determine the population density for each site during the month of July. The size frequency distribution for this period included larvae ranging from 9 to 17 mm in length and the average water temperature used for the summer calculations was 22° C (Chase 1998).

Autumn

The larval densities used for the autumn sediment suspension calculation were those from the 1998 sampling year (Table 4.1). These densities are a conservative estimate of the number of larvae present after eggs deposited by ovipositing females hatched in late summer 1997 in that the number of larvae present in the autumn of 1997 (following completion of the hatching period) can have been no less than the number of larvae present during the subsequent late spring sampling in 1998. The size frequency distribution used was one that ranged in size from 8 – 20 mm assuming that no larvae greater than 20 mm were present. This was determined by multiplying the size frequency remaining in July by 1.20 (a 20% increase in larval size over 60 d). The size frequency distribution used was a truncated version of the pre-emergence (early June) size frequency distribution to take into account newly hatched larvae. The average water temperature for the month of October was 14° C estimated from lake bottom temperature probes (J. J. H. Ciborowski unpubl.).

Early Spring

Early spring sediment suspension rates were calculated using population densities from the 1998 sampling year to once again produce a conservative estimate for sediment suspension since the number of larvae present in early April 1998 would be no less than the number present during the May/June sampling period. The size frequency distribution used included larvae ranging from 8 – 25 mm, assuming no larvae greater than 25 mm were present. The average water temperature for the month of April was 7° C (J. J. H. Ciborowski unpubl.). However, a temperature of 10° C was used in the calculations since 10° C is the developmental threshold for *Hexagenia* larvae in the Lake Erie region (Hunt 1953) and it is also the lower temperature limit used in the development of the equations used to estimate sediment suspension (Chapter 2).

GIS Mapping and Interpolation

Point estimates of sediment suspension rates determined for each sample location above ($g/m^2/d$) were entered into a Microsoft Excel™ spreadsheet along with the latitude and longitude of the sample location. The spreadsheet was converted to Data Base IV™ (DBF IV) format. The DBF table was then converted into an ArcGIS™ version 8.3 shapefile using ArcCatalogue ™ and inserted as layer into a digital map of western Lake Erie obtained from Government of Michigan Centre for Geographic Information, Department of Information Technology. This placed all the sample locations in their appropriate position within the western basin of Lake Erie.

A raster layer of sediment suspension rate was created using the 'ordinary kriging' procedure in the *Spatial Analyst* module of ArcGIS (ESRI Inc. 2002). The appropriate sediment suspension rate (minimum or maximum) was selected as the Z value using a spherical semivariogram model with variable search radius (ESRI Inc. 2002). The search radius settings were set to the number of points (sites) in western Lake Erie where *Hexagenia* population density samples were collected and a maximum distance of 1.0. The output raster layer was overlaid onto the map surface and the contour interval was set to 25 g/m²/d for each map to show areas of differing sediment suspension. The kriging method of interpolating the response surface (raster layer) was used to create the raster surfaces instead of Inverse Distance Weighting (IDW) or Spline methods since kriging uses a statistical model that includes autocorrelation between sites that are located close to each other (ESRIInc. 2002). Maps showing the spatial distribution of the minimum and maximum sediment suspension rates were created for each year for the yearly sediment suspension rates and for late spring, summer, autumn and early spring for the seasonal sediment suspension rates. Basin wide means (± S.E.) for sediment suspension rates were calculated for each map contour surface based on the sediment suspension rates calculated in APL.

RESULTS

Pre-emergent Sediment Suspension Among Years

Sediment suspension rates determined for among-year comparisons were calculated for late spring just prior to emergence. Mean (± S.E.) basin wide minimum and maximum sediment suspension rates for 1930 were 32.6 ± 4.7 g/m²/d (n=67) and 56.2 ± 8.6 g/m²/d (n=67), respectively. The 1930 *Hexagenia*-induced minimum sediment suspension rate ranged from a low of 2.4 g/m²/d to a high of 129.6 g/m²/d, and the maximum sediment suspension rate ranged from 2.4 to 240.0 g/m²/d for sampling locations where larvae were present (Appendix 2, Table A2.2). In 1930, the highest larval densities and, thus the highest sediment suspension rates occurred in the eastern region of the basin near the Island area and the lower sediment suspension rates occurred in the western portion of the basin and in the near shore areas (Figure 4.2). The small number of sampling locations in the central and eastern portions of the basin for 1930 may make these estimates imprecise. However, the population densities reported by Wright and Tidd (1933) are similar to the pattern observed in 1951 (Wood 1973).

Mean (± S.E.) basin wide sediment suspension rates for 1951 are 46.9 ± 2.3 $g/m^2/d$ (n=184) and 80.7 ± 4.3 $g/m^2/d$ (n=184), respectively for minimum and maximum sediment suspension rates. The 1951 minimum sediment suspension rates ranged 14.4 to 98.4 $g/m^2/d$ and the maximum sediment suspension rates ranged from 21.6 to 177.6 $g/m^2/d$ at sites where larvae were present (Appendix 2, Table A2.3). The areas with the highest sediment suspension occur in the central and eastern portions of the basin (Figure 4.3) similar to the pattern observed for 1930. The contours for the map in Figure 4.3 are interpolated directly from the maps of Wood (1973) since no data were available for larval densities for each individual sampling location to be input into ArcMap^{TM}.

Mean (± S.E.) basin wide sediment suspension rates for 1993 were 3.5 ± 0.6 $g/m^2/d$ (n=47) and 4.9 ± 0.8 $g/m^2/d$ (n=47), respectively for minimum and maximum sediment suspension rates. The 1993 minimum sediment suspension rates ranged from 2.4 to 12.0 $g/m^2/d$ and the maximum sediment suspension rates ranged from 4.8 to 16.8 $g/m^2/d$ at sites where larvae were present (Appendix 2, Table A2.4). These sediment suspension

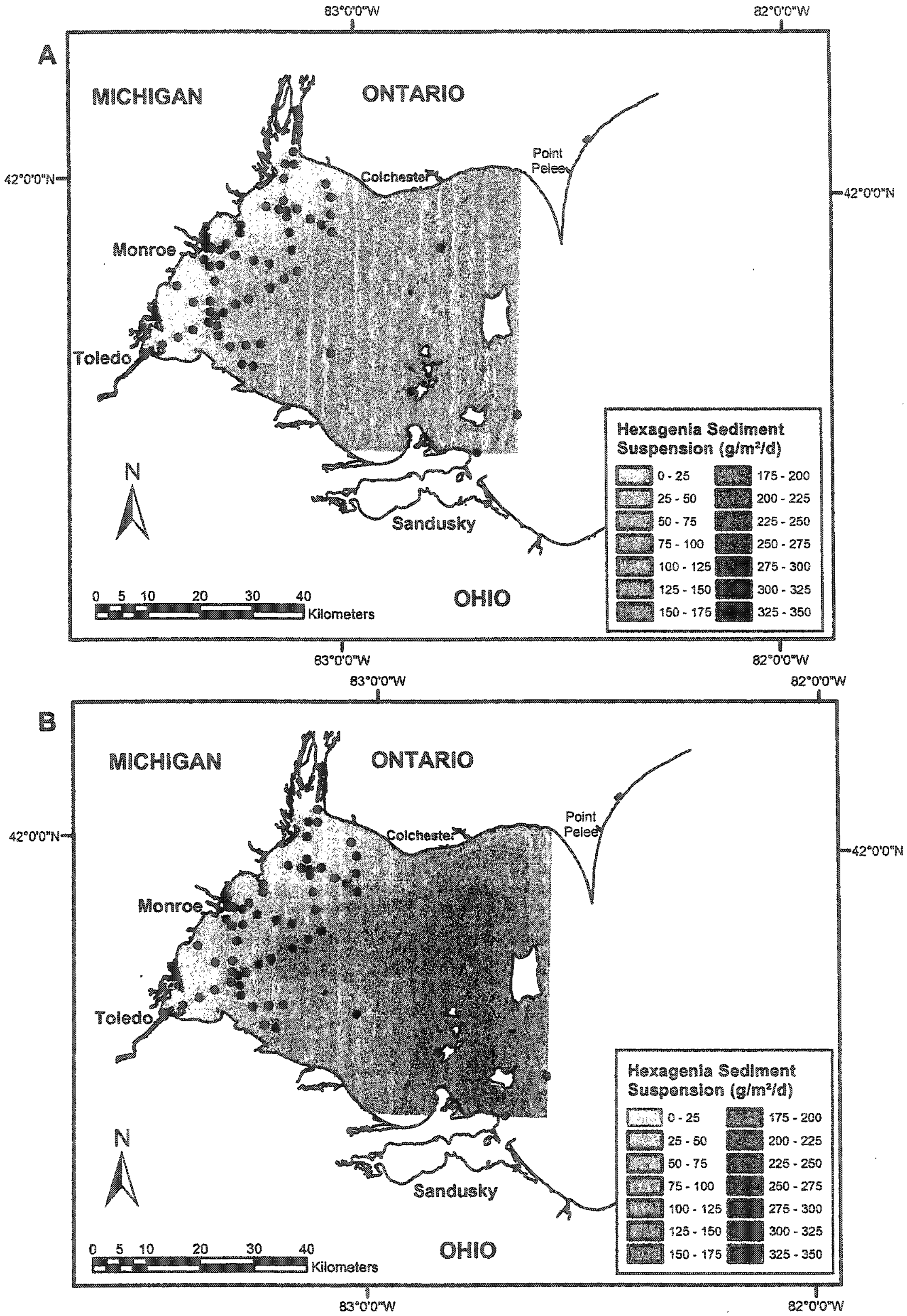

Figure 4.2: Estimated (A) minimum and (B) maximum Hexagenia larval sediment suspension in western Lake Erie for 1930. Contours are extrapolated from Hexagenia larval densities in 1930 at sites indicated by filled circles.

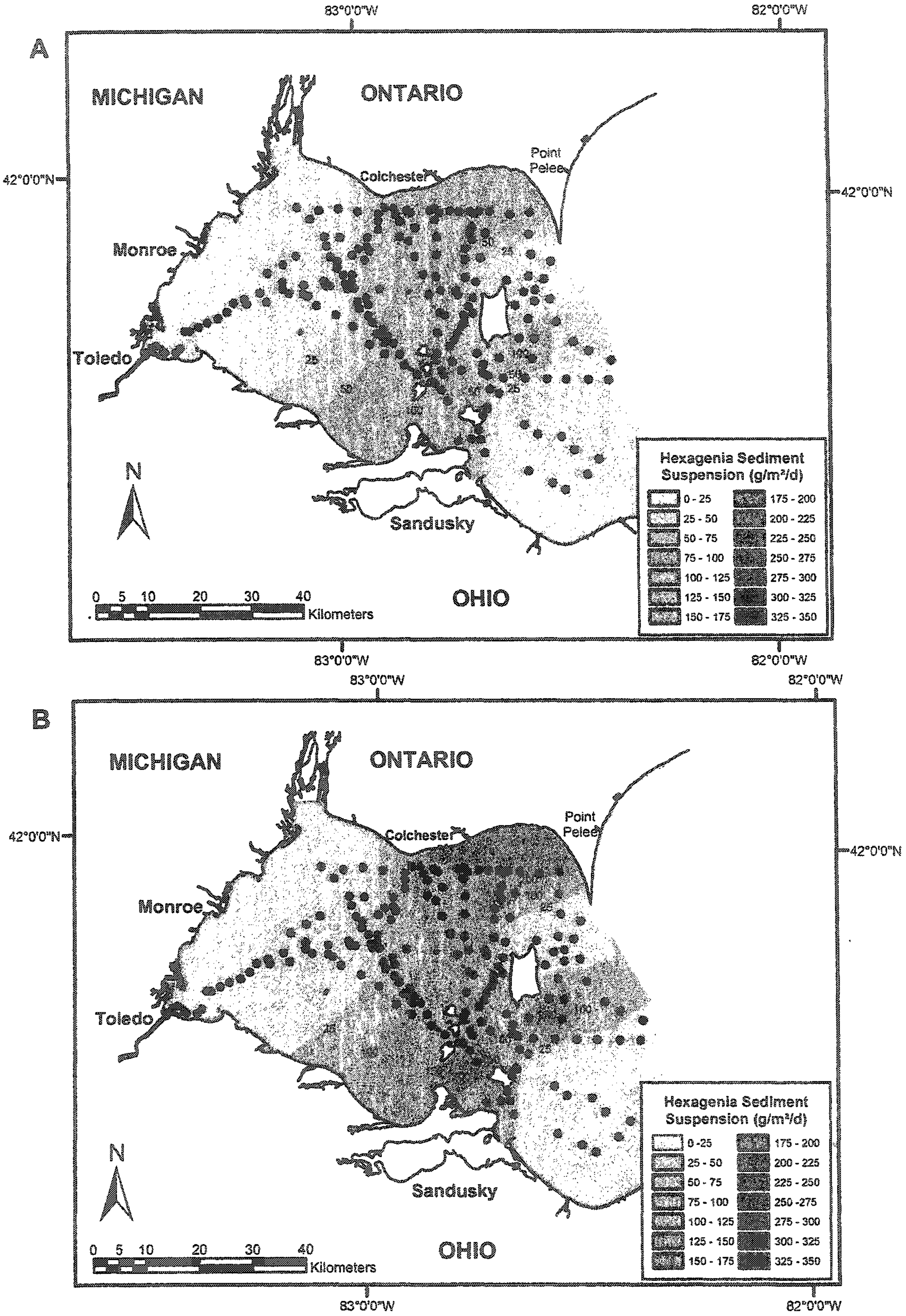

Figure 4.3: Estimated (A) minimum and (B) maximum Hexagenia larval sediment suspension in western Lake Erie for 1951. Contours are extrapolated from Hexagenia larval densities in 1951 indicated by filled circles.

rates were so low that the two contour maps produced using ArcMap 8.3 were identical since the first contour interval incorporates sediment suspension rates from 0 to 25 g/m²/d. The entire portion of western Lake Erie covered by the sample locations for this year falls within the 0 to 25 g/m²/d contour interval (Figure 4.4).

Mean (± S.E.) basin wide sediment suspension rates for 1995 were 10.1 ± 2.6 g/m²/d (n=21) and 15.2 ± 4.2 g/m²/d (n=21), respectively for the minimum and maximum rates. For 1995, the minimum sediment suspension rates ranged from 2.4 to 43.2 g/m²/d and the maximum sediment suspension rates ranged from 2.4 to 72.0 g/m²/d at sites where larvae were present (Appendix 2, Table A2.5). The minimum sediment suspension rates estimated for the map contour layer were between the 0 to 25 g/m²/d contour interval for the entire basin (Figure 4.5). The maximum sediment suspension rates were higher in the western end of the basin near the Maumee River area and Monroe, Michigan.

Mean (± S.E.) basin wide sediment suspension rates for 1997 were 68.0 ± 9.6 g/m²/d (n=58) and 124.7 ± 19.3 g/m²/d (n=58), respectively for the minimum and maximum rates. For 1997, the minimum sediment suspension rate ranged from 4.8 to 321.6 g/m²/d and the maximum sediment suspension rates from 4.8 to 660.0 g/m²/d at sites where larvae were present (Appendix 2, Table A2.6). Both the minimum and maximum sediment suspension rates were highest in the Maumee Bay region of the basin and lowest in the Pigeon Bay region (Figure 4.6). The highest population densities since *Hexagenia* recolonization of western Lake Erie began were estimated for this year, which results in the highest sediment suspension rates for this year as well.

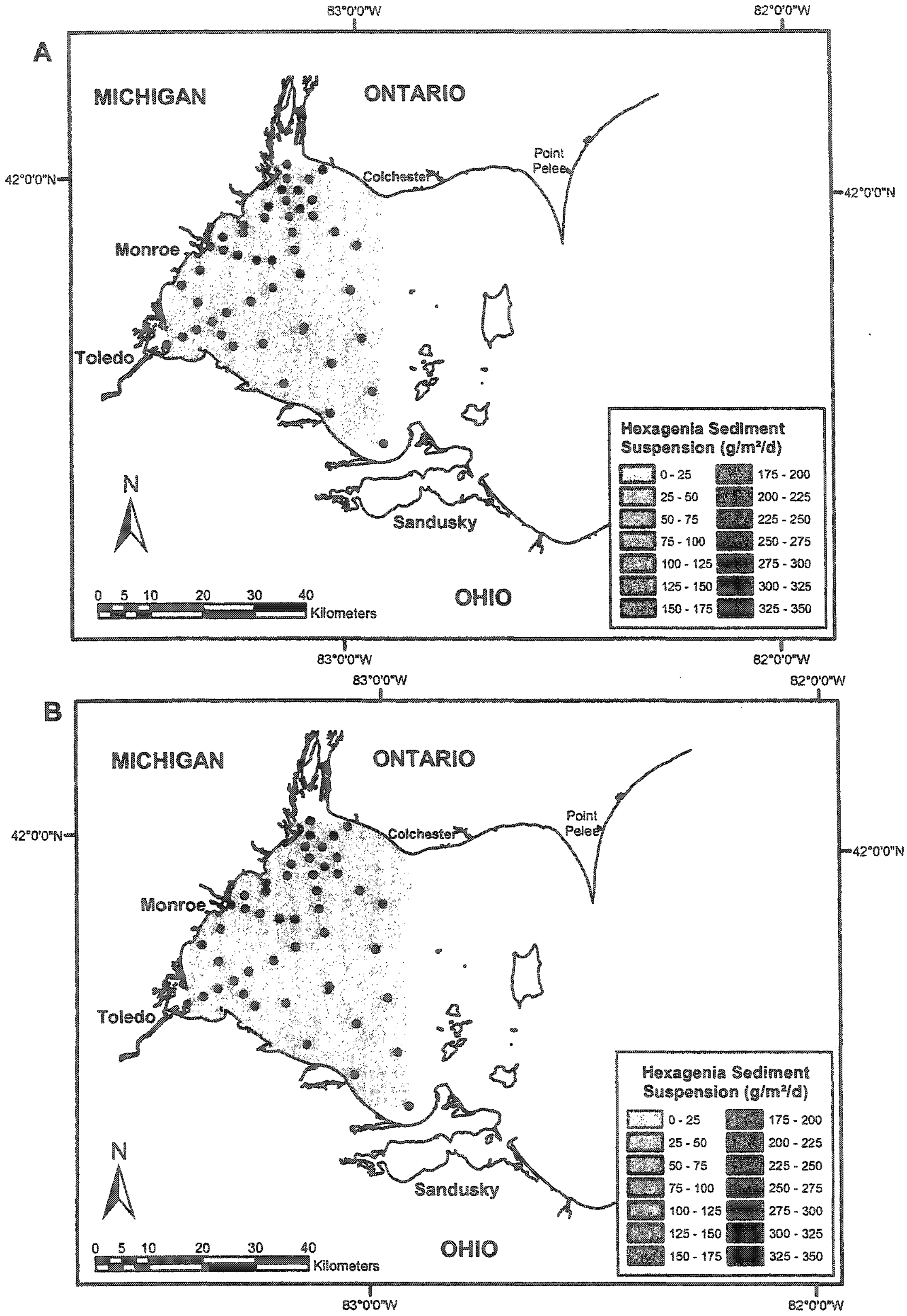

Figure 4.4: Estimated (A) minimum and (B) maximum Hexagenia larval sediment suspension in western Lake Erie for 1993. Contours are extrapolated from Hexagenia larval densities in 1993 indicated by filled circles.

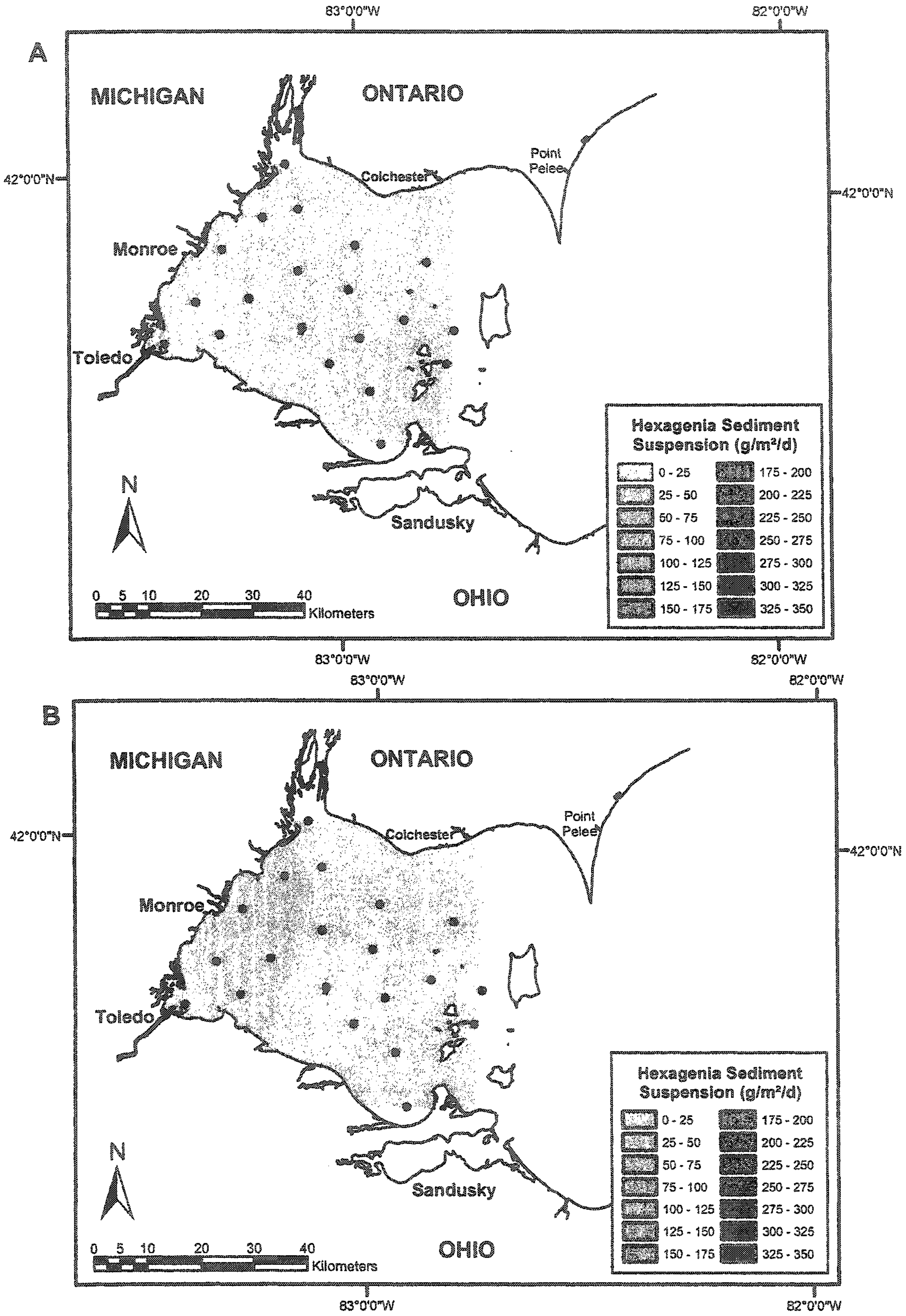

Figure 4.5: Estimated (A) minimum and (B) maximum Hexagenia larval sediment suspension in western Lake Erie for 1995. Contours are extrapolated from Hexagenia larval densities in 1995 indicated by filled circles.

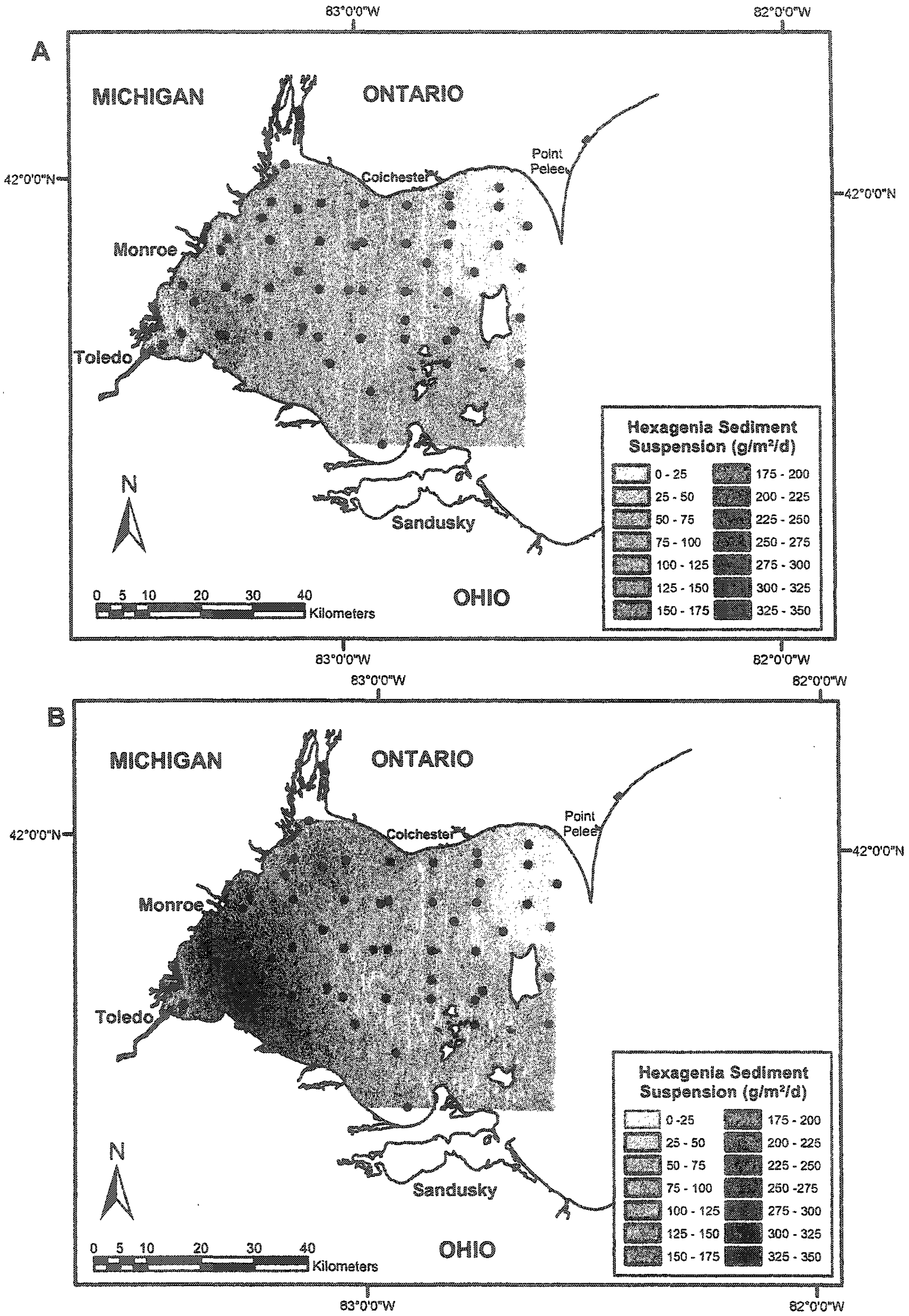

Figure 4.6: Estimated (A) minimum and (B) maximum Hexagenia larval sediment suspension in western Lake Erie for 1997. Contours are extrapolated from Hexagenia larval densities in 1997 indicated by filled circles.

Mean (± S.E.) basin wide sediment suspension rates for 1999 were 57.1 ± 7.5 $g/m^2/d$ (n=39) and 100.4 ± 14.3 $g/m^2/d$ (n=39), respectively for the minimum and maximum sediment suspension rates. Sediment suspension rates ranged from 4.8 $g/m^2/d$ to 153.6 $g/m^2/d$ for the minimum sediment suspension rate and from 4.8 $g/m^2/d$ to 290.4 $g/m^2/d$ for the maximum sediment suspension rate for sites where larvae were present (Appendix 2, Table A2.7). The highest values for both the minimum and maximum sediment suspension rates are in Maumee Bay region and near Monroe, Michigan and the lowest values occurred in the Pigeon Bay region west of Point Pelee (Figure 4.7).

The year to year changes in basin wide averages for the minimum and maximum larval sediment suspension rates varied with changes in larval density (Figure 4.8). These changes are most drastic between 1930 and 1951, when larval densities were at historic highs, and 1993, when larval densities are beginning to recover in western Lake Erie. Sediment suspension rates then increase up until 1997 and then a slight decrease is observed in 1999.

Seasonal Sediment Suspension Rates

Late Spring (Pre-Emergence)

Mean (± S.E.) basin wide sediment suspension rates for late spring 1997 (end of May to beginning of June) were 68.0 ± 9.6 $g/m^2/d$ (n=58) and 124.7 ± 19.3 $g/m^2/d$ (n=58), respectively for the minimum and maximum sediment suspension rates. For late spring

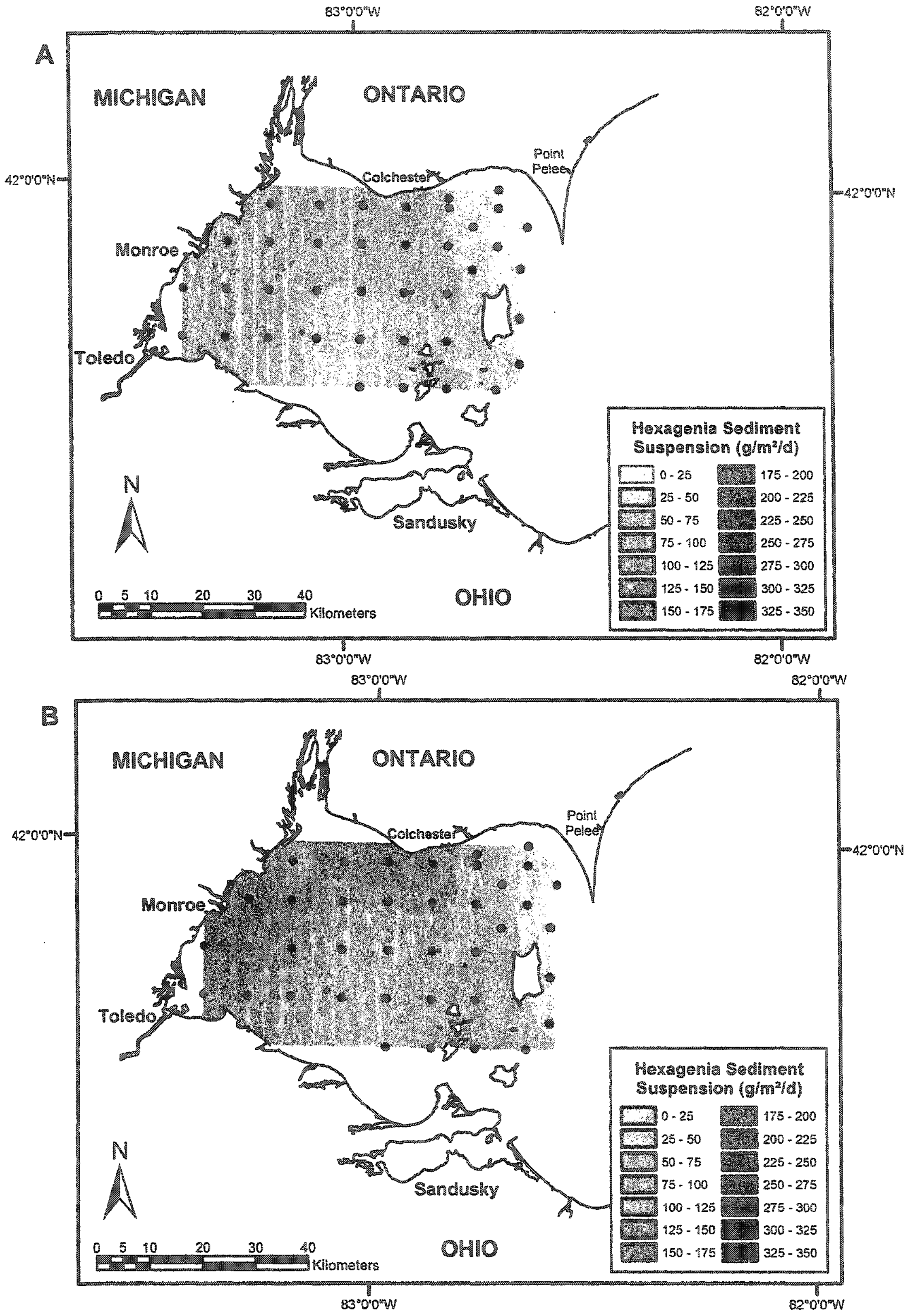

Figure 4.7: Estimated (A) minimum and (B) maximum Hexagenia larval sediment suspension in western Lake Erie for 1999. Contours are extrapolated from Hexagenia larval densities in 1999 indicated by filled circles.

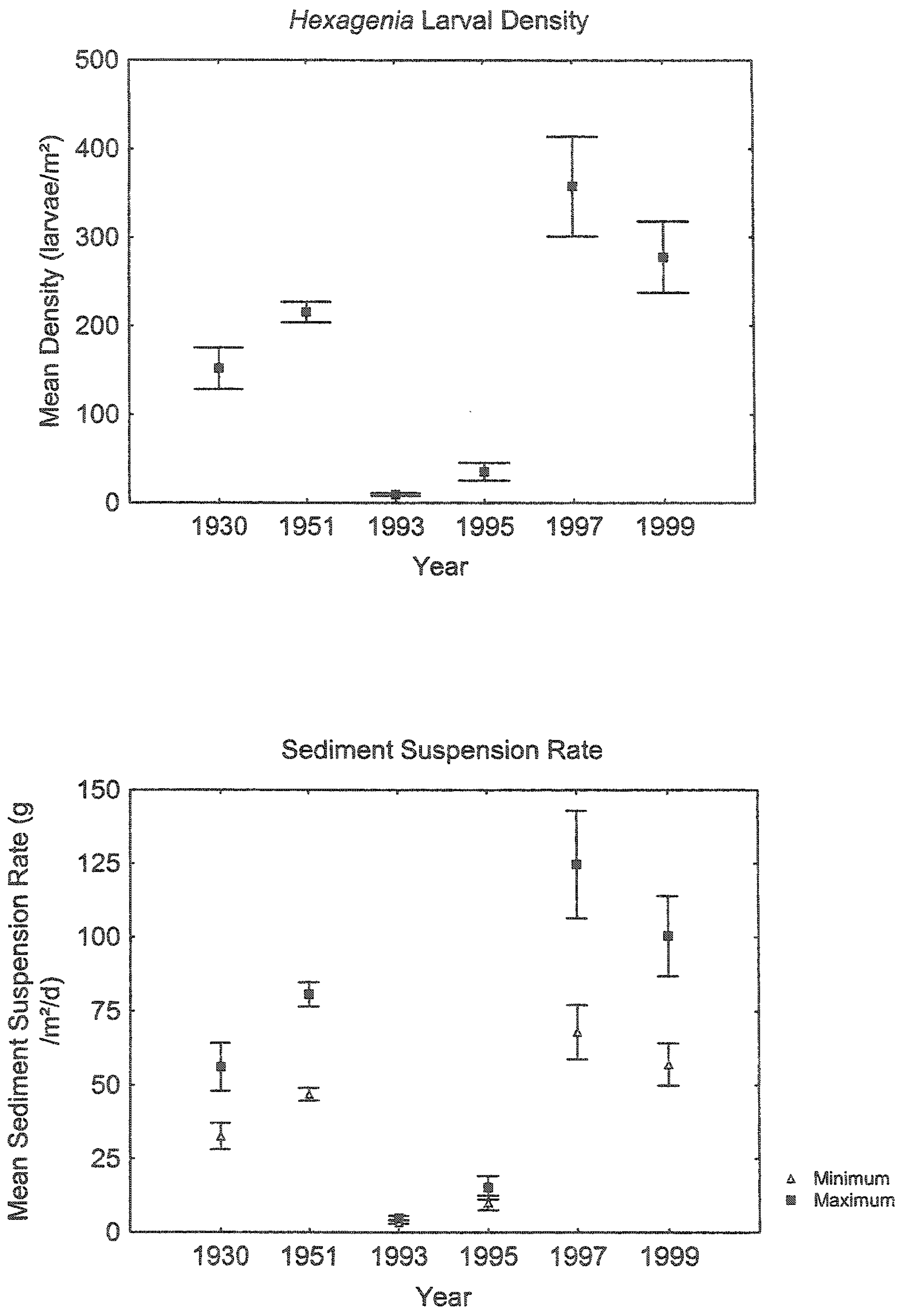

Figure 4.8: Mean basin wide among year variation for (A) *Hexagenia* larval density and (B) larval sediment suspension rate.

1997, minimum sediment suspension rates ranged from 4.8 g/m²/d to 321.6 g/m²/d and the maximum sediment suspension rates ranged from 4.8 g/m²/d to 660.0 g/m²/d at sites where larvae were present (Appendix 2, Table A2.8). Since the larval densities are highest in the Maumee Bay region and lowest in the Pigeon Bay region the sediment suspension rates are highest and lowest in these respective regions as well (Figure 4.9).

Summer (Post-Emergence)

Mean (± S.E.) basin wide sediment suspension rates for summer 1997 (end of July) were 21.4 ± 2.8 g/m²/d (n=58) and 32.8 ± 4.5 g/m²/d (n=58), respectively for the minimum and maximum sediment suspension rates. These sediment suspension rates are 25 to 30 % of the spring 1997 rates. For summer 1997, the minimum sediment suspension rates ranged from 2.4 g/m²/d to 88.8 g/m²/d and the maximum sediment suspension rates ranged from 2.4 g/m²/d to 151.2 g/m²/d at sites where larvae were present (Appendix 2, Table A2.9). The highest sediment suspension rates occurred in the Maumee Bay region for the summer of 1997 and the sediment suspension rate for the rest of the basin was low (Figure 4.10).

Autumn

Mean (± S.E.) basin wide sediment suspension rates for autumn 1997 (October) were 7.0 ± 0.7 g/m²/d (n=62) and 11.3 ± 1.2 g/m²/d (n=62) respectively, for the minimum and maximum sediment suspension rates. The autumn 1997 minimum sediment suspension rates ranged from 2.4 g/m²/d to 21.6 g/m²/d and the maximum sediment suspension rates ranged from 2.4 g/m²/d to 38.4 g/m²/d at sites where larvae were present (Appendix 2,

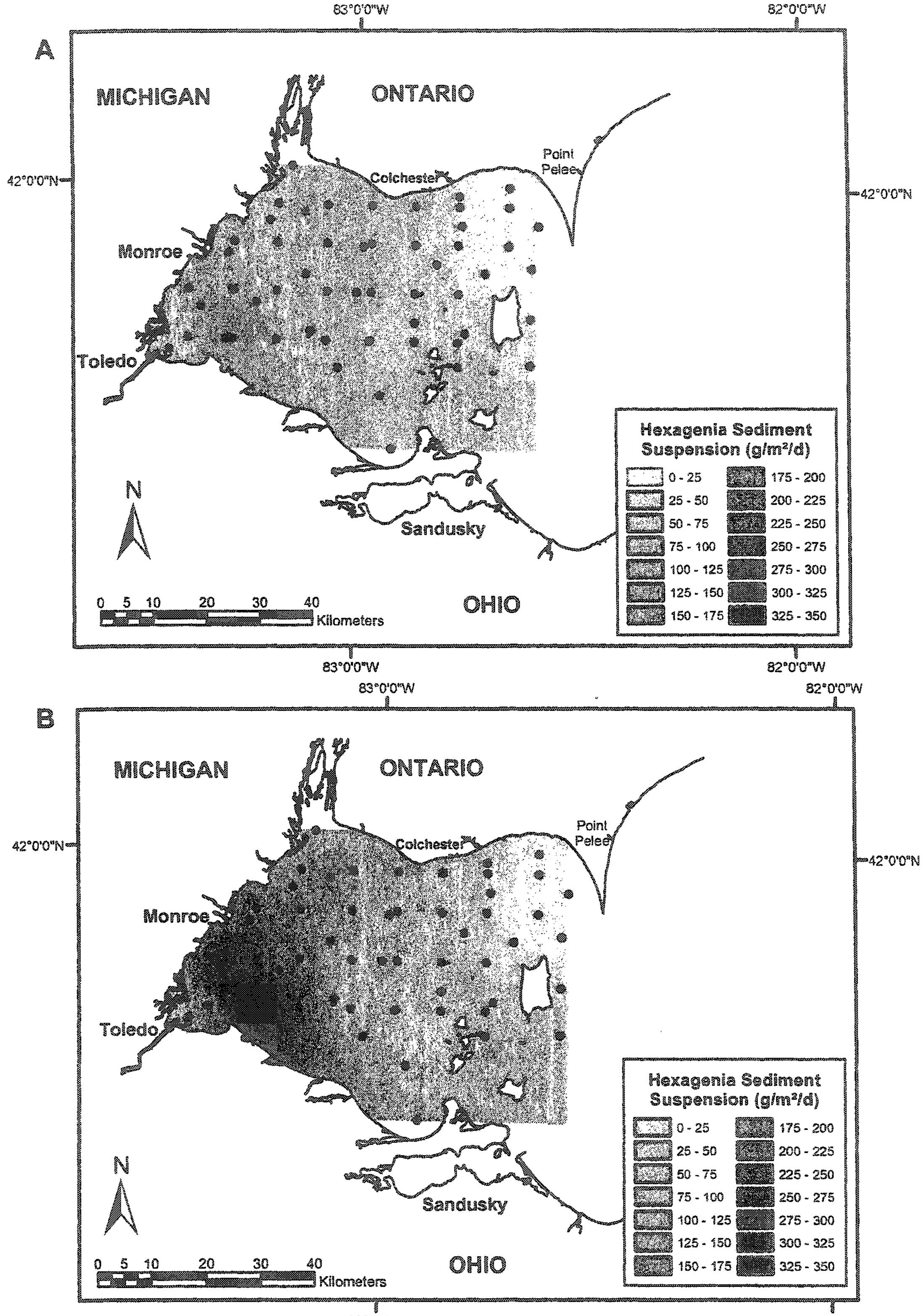

Figure 4.9: Estimated (A) minimum and (B) maximum Hexagenia larval sediment suspension in western Lake Erie early June (pre-emergence) 1997. Contours are extrapolated from Hexagenia larval densities in early June 1997 at sites indicated by filled circles.

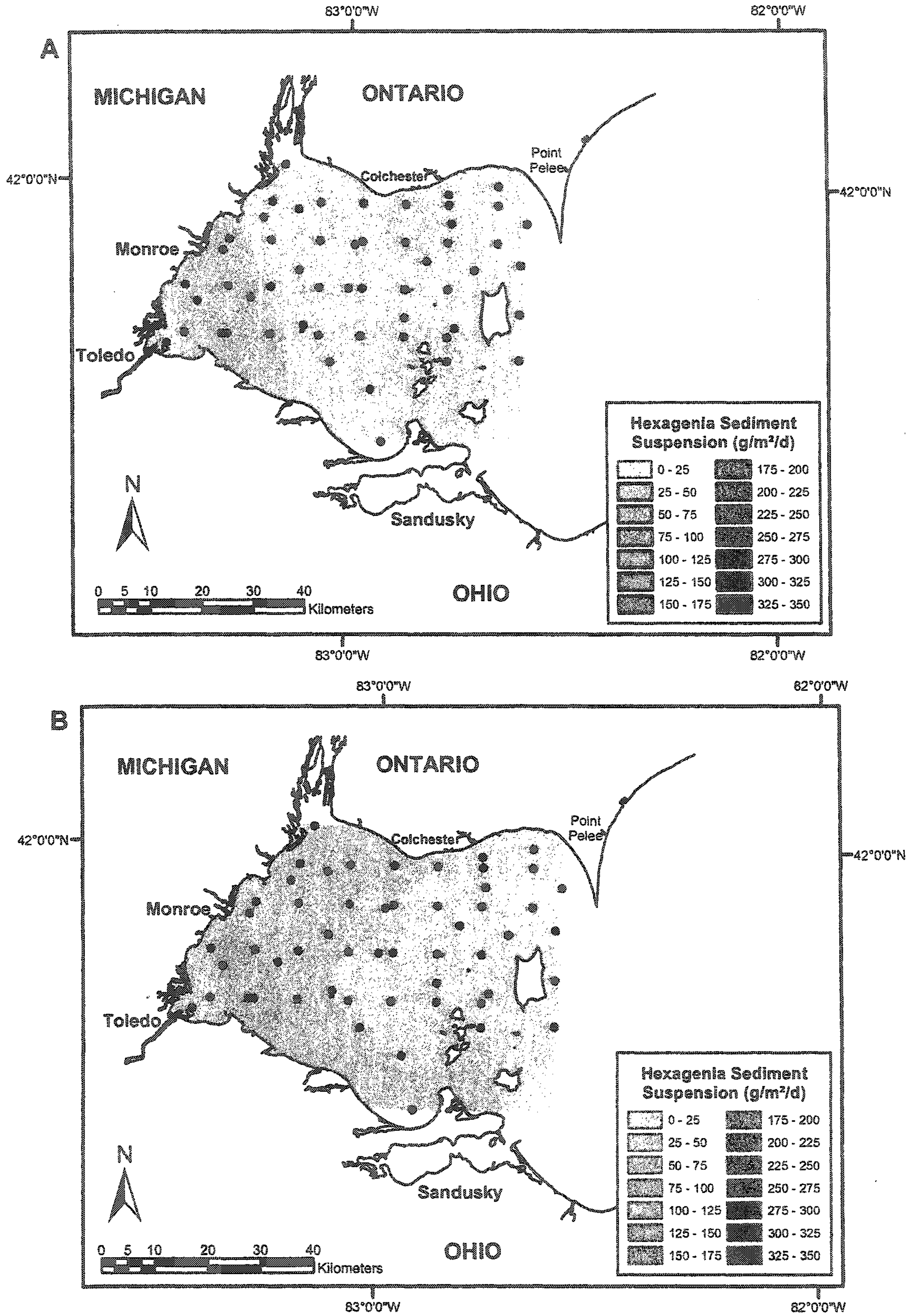

Figure 4.10: Estimated (A) minimum and (B) maximum Hexagenia larval sediment suspension in western Lake Erie for end of July (post-emergence) 1997. Contours are extrapolated from Hexagenia larval densities calculated after mass-emergence of imagoes and using survival rate equations from Winter et al. (1996) at sites indicated by filled circles.

Table A2.10). For autumn 1997, the minimum and maximum sediment suspension rates show a single contour for the entire basin, which ranged from 0 to 25 g/m²/d (Figure 4.11).

Early Spring

Mean (± S.E.) basin wide sediment suspension rates for the spring of 1998 (April) were 3.7 ± 0.4 g/m²/d (n=62) and 6.1 ± 0.7 g/m²/d (n=62), respectively for the minimum and maximum sediment suspension rates. The spring 1998 minimum sediment suspension rate ranged from 0.0 g/m²/d to 9.6 g/m²/d and the maximum sediment suspension rate ranged from 0.0 g/m²/d to 19.2 g/m²/d (Appendix 2, Table A2.11). Mapping the minimum and maximum rates produced a single contour for the entire basin, which ranged from 0 to 25 g/m²/d (Figure 4.12). This is to be expected since the water temperature at this time is 10° C and is close to the activity (Hunt 1953) and developmental (Giberson and Rosenberg 1992) threshold for *Hexagenia* larvae.

The monthly basin wide averages for larval sediment suspension rate, water temperature and larval density varied greatly over the course of the one year period examined above (Figure 4.13). The basin wide estimated minimum larval sediment suspension rates ranged from 68 ± 3.6 g/m²/d (n = 58) (early June 1997) to 3.7 ± 0.4 g/m²/d (n = 52) (April 1998). The basin wide maximum sediment suspension rate ranged from 124.7 ± 19.3 g/m²/d (n = 58) (early June 1997) to 6.1 ± 0.7 g/m²/d (n = 62) (April 1998). Water temperature ranged from a high 24.0 ± 0.9 °C (n = 2) in August to a low of 0.2 ± 0.03 °C in January (n = 31). The monthly average temperatures for May to September were

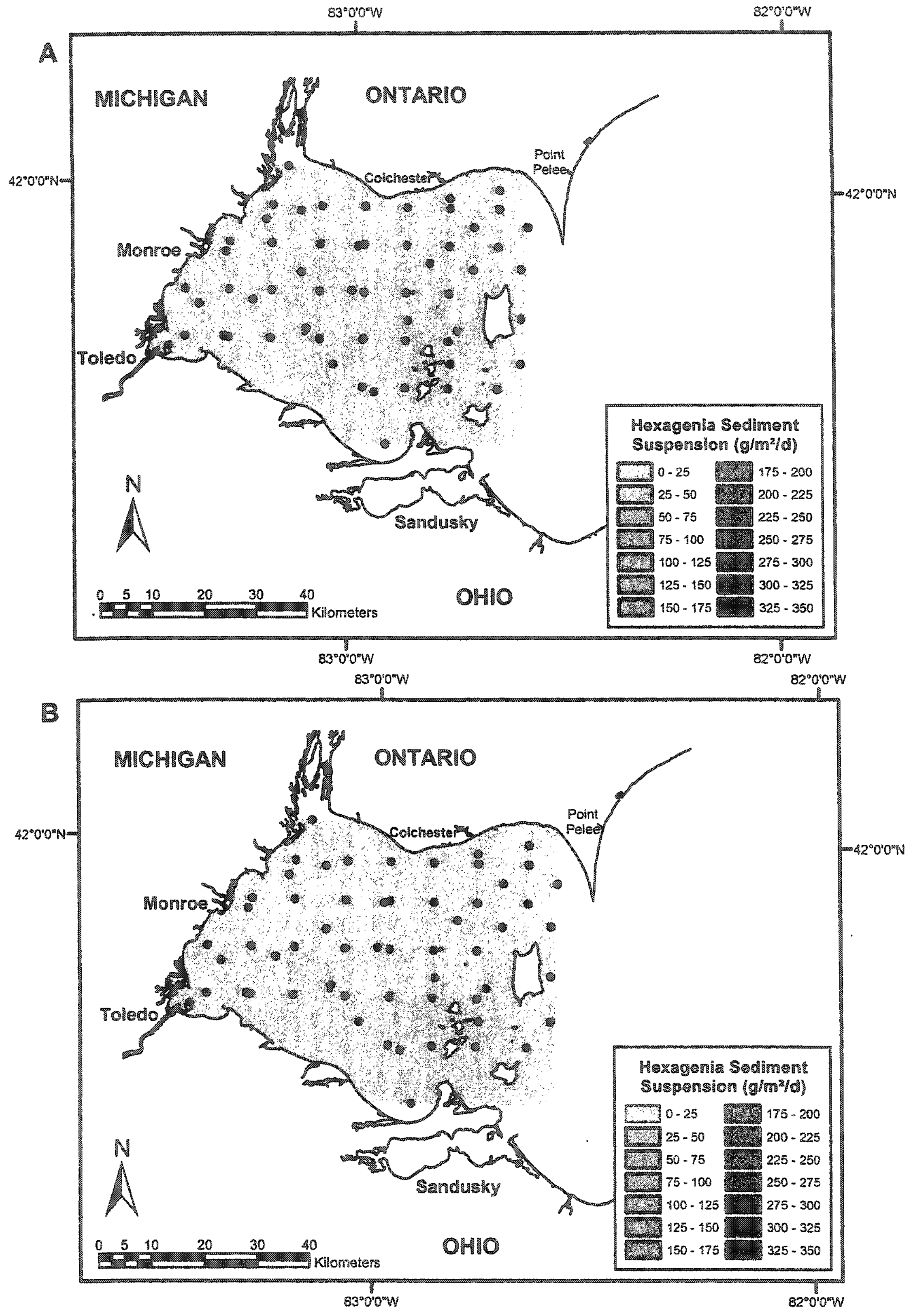

Figure 4.11: Estimated (A) minimum and (B) maximum Hexagenia larval sediment suspension in western Lake Erie for October 1997. Contours are extrapolated from Hexagenia larval densities in 1998 at sites indicated by filled circles.

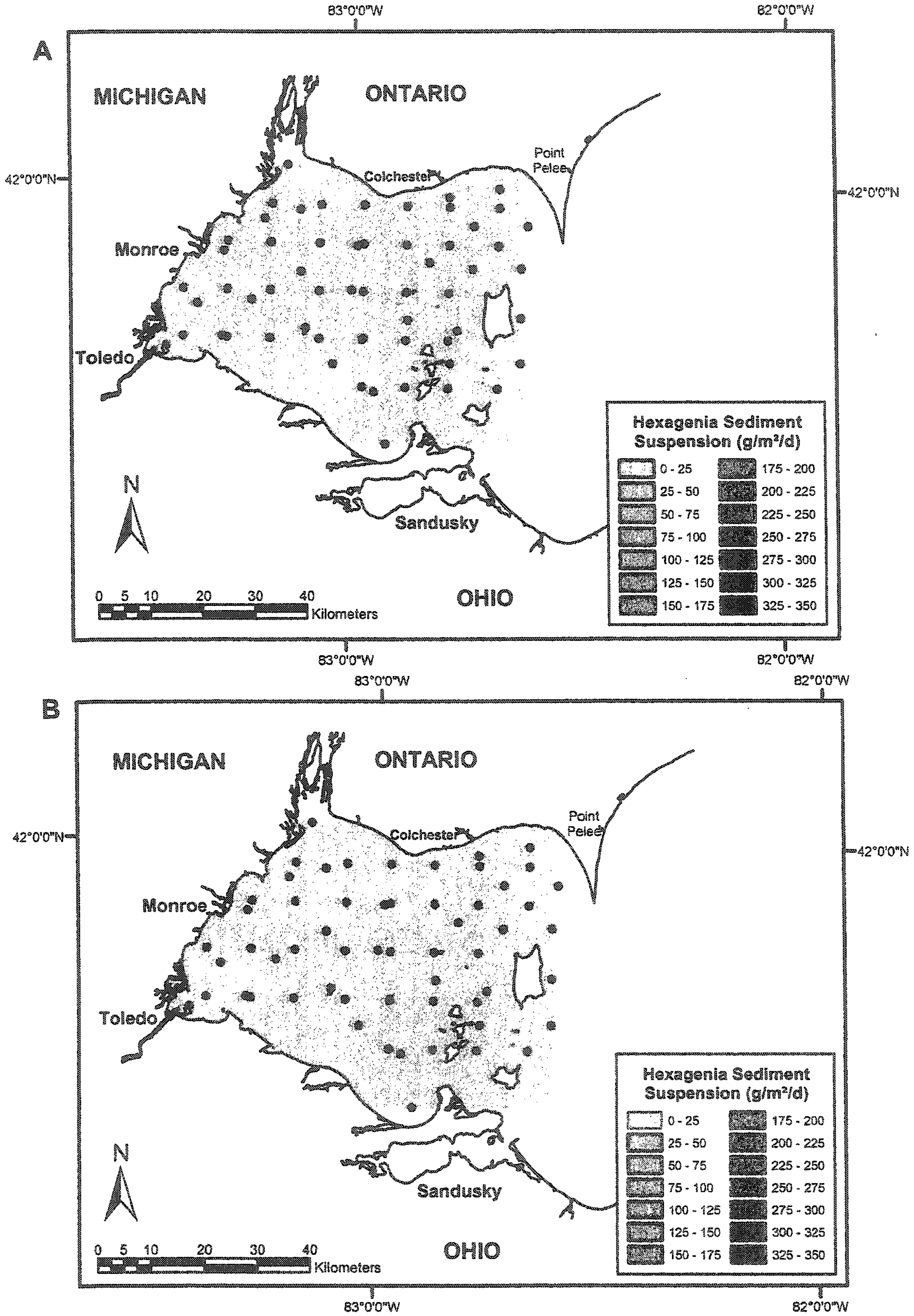

Figure 4.12: Estimated (A) minimum and (B) maximum Hexagenia larval sediment suspension in western Lake Erie for April 1998. Contours are extrapolated from Hexagenia larval densities in 1998 at sites indicated by filled circles.

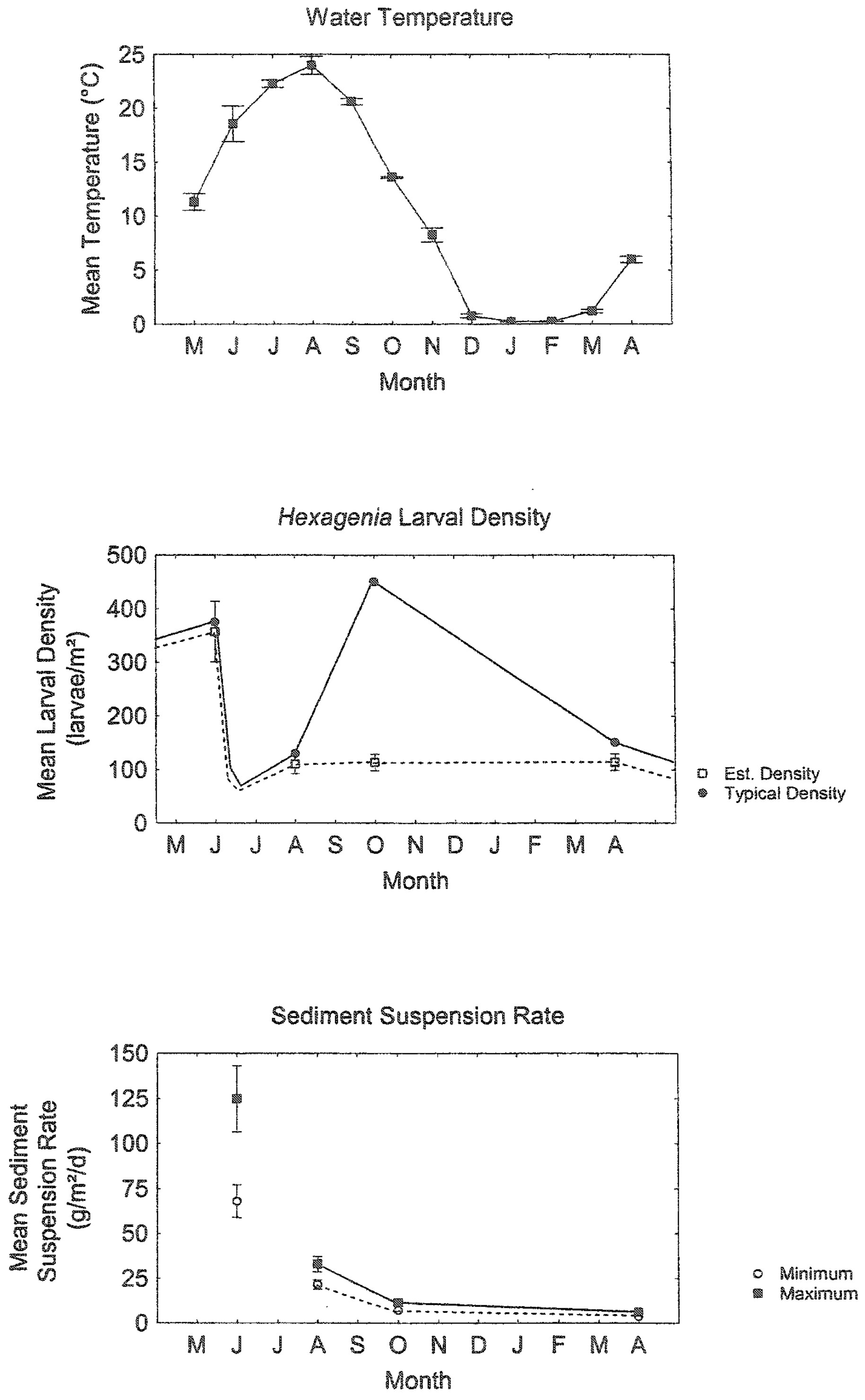

Figure 4.13: Mean basin wide monthly time course for (A) water temperature, (B) larval density and (C) *Hexagenia* sediment suspension rates from data used to estimate the sediment suspension rates in western Lake Erie. The estimated larval densities were used to estimate sediment suspension rates. Temperature data are from Chase (1998) and J. J. H. Ciborowski (unpubl.).

based on yearly averages from Chase 1998 and monthly average temperatures for October to April were based on daily temperatures from J. J. H. Ciborowski (unpubl.). Basin wide larval density ranged from a high of 358 ± 59 (early June 1997) larvae/m^2 to a low of 110 ± 18 larvae/m^2 (end of July 1997).

DISCUSSION

The model used to estimate *Hexagenia* larval-induced sediment suspension in this chapter is based on equations developed in Chapter 2 of this thesis. These equations were derived from observations of sediment suspension by *Hexagenia* larvae in laboratory experiments conducted using sediment collected from a site located in the centre of western Lake Erie (Site 357), which is an area of historically high *Hexagenia* larval density (Britt 1955a, Britt 1955b, Reynoldson and Hamilton 1993). As a result, the model assumes a uniform substrate that is suitable for *Hexagenia* larval colonization throughout the entire western basin of Lake Erie. This was done since sediment collection location did affect sediment suspension rates, but the differences were minor compared to the effects of varying larval size. This model also assumed that the size frequency distribution of the larvae on any given date did not vary among years. Between year variation in the size frequency distribution will likely not have as significant an effect on estimates of sediment suspension rate as compared to between year variation in larval density.

Estimation of the sediment suspension rate used required calculating the sediment suspension rate for each site in western Lake Erie by multiplying each size class within the size frequency distribution by the larval density at that site (Eq. 4.3). The sediment suspension rate for each size class was the multiplied by the proportion of larvae represented by each size class in the size frequency distribution. The sediment suspension rates for each size class were then summed to get the total sediment suspension rate for a specific site.

An alternative method to estimate the sediment suspension rate at each site would be to first multiply the total population density at a sampling site by the proportion of each size class represented by the size frequency distribution. This would give you the number of larvae in each size frequency distribution, which could then be used to determine the sediment suspension rate for each size class, which could then be summed to determine the total sediment suspension rate for a given site at a given temperature. This latter method would result in less accurate determination of sediment suspension rate. Equations 4.1 and 4.2 do not estimate the sediment suspension of low densities of larvae very well, because in the experiments conducted in Chapter 2 the low density treatments were represented by 1 or 2 larvae per jar. This low number of larvae in each treatment jar led to increased variability in the data and the potential lack of any synergistic effects which may occur when larval densities are higher (Hanes and Ciborowski 1992)

Areas of high and low sediment suspension due to *Hexagenia* bioturbation changed in location as a consequence of changes in population densities in the basin. Prior to the prolonged absence of larvae from the basin beginning in the early 1960s (Carr and Hiltunen 1965, Reynoldson et al. 1989), *Hexagenia* densities were highest in the centre of the basin, the Island areas (data from Wright 1955 in Schloesser et al. 2000), (Wood 1953, Wood 1973) and some locations from Colchester and to Pigeon Bay (Wood 1953, Wood 1973). These areas show the highest levels of *Hexagenia*-induced sediment suspension in western Lake Erie for the 1930 historical population data. During the period from the early 1960s to the 1990s when *Hexagenia* were absent, sediment suspension due to *Hexagania* was negligible by definition.

As *Hexagenia* populations began to recover in the early 1990s (Krieger et al. 1996, Schloesser et al. 2000) sediment suspension rates due to *Hexagenia* also began to increase. Larval densities are generally greater in the nearshore areas than the offshore areas where populations densities were formerly highest (Schloesser et al. 2000). As a result, the highest sediment suspension rates were estimated to occur in the nearshore areas also (see 1997 maps especially, Figures 4.6). Estimated sediment suspension rates are generally highest in the area near the mouth of the Maumee River and near Monroe, Michigan. In spring 1997 prior to emergence, maximum estimated sediment suspension rates in this area are as high as 350 $g/m^2/d$. This is greater than the amount of sediment suspended in one day (300 $g/m^2/d$) of a storm event, which can produce 900 g/m^2 over a 3 d period (Lick et al. 1994). The amount of sediment suspended by *Hexagenia* in the Maumee Bay/Monroe area also approaches daily sediment suspension of 584 $g/m^2/d$ from shoreline erosion (Kemp et al. 1977). Sediment suspension rates for 1993 and 1995 were estimated to be up to 14 times lower than those in 1997 since *Hexagenia* larval densities in western Lake Erie were very low in 1993 and 1995 compared to 1997.

Seasonal variation in *Hexagenia* larval sediment suspension from late spring of 1997 to early spring 1998 was estimated to be greatest in late spring just prior to emergence when larvae were largest. The late spring sediment suspension values were 4 to 5 times greater than the values estimated for the summer (post-emergence), and greater still than for the autumn and early spring the following year. Summer sediment suspension is lower because the large larvae responsible for most of the bioturbation emerged and were no longer contributing to sediment suspension, and eggs from the next generation had not yet hatched. The estimates of autumn and early spring sediment suspension rates were lower primarily due to the low water temperature, which leads to decreased larval activity and thus, decreased sediment suspension. The autumn sediment suspension rates were below 25 $g/m^2/d$ for the minimum rates and below 50 $g/m^2/d$ for the maximum rates at a water temperature of 14° C. The early spring sediment suspension rates were below 25 $g/m^2/d$ for both the minimum and maximum rates. The early spring rates are especially low since the water temperature was 10° C, which is close to the activity (Hunt 1953) and developmental (Giberson and Rosenberg 1992) threshold for *Hexagenia*. The larval densities used for the autumn 1997 and early spring 1998 calculations were from the 1998 late spring (pre-emergence) sampling period so the sediment suspension estimates for these times are a conservative estimate since the larval populations in the autumn of 1997 and early spring of 1998 were likely higher than those of the late spring 1998 (pre-emergence) sampling period. The larval densities in late spring (pre-emergence) 1998 are however, much lower than those observed in late spring 1997 (Table A2.8 and A2.11). This low density will likely not have a significant effect on sediment suspension rates since the water temperature for this time of year is at or below the developmental and activity threshold of the larvae.

Sediment suspension due to *Hexagenia* is likely of little consequence in the Maumee Bay region in terms of sediment loading since the Maumee River deposits 1.8 million metric tons of sediment into western Lake Erie annually (Kemp et al. 1977). This is equivalent to 1,502 $g/m^2/d$ of sediment deposited into western Lake Erie. This is almost five times the 350 $g/m^2/d$ of sediment suspension produced by *Hexagenia* in this portion of the basin during the spring of 1997 when larval densities were the highest recorded to date (J. J. H. Ciborowski unpubl.). However, the highest levels of suspended sediment occur in western Lake Erie during early spring (April) and are mostly due to river inputs and wave induced sediment suspension (Paul et al. 1982). This sediment suspension is more of a pulse input (Paul et al. 1982) compared the more continuous sediment suspension caused by mayfly larvae. These inputs also occur in early spring (April) and thus occur prior to the highest *Hexagenia* induced sediment suspension which occurs in early June prior to the mass emergence. The high population densities of *Hexagenia* larvae in the Maumee Bay region will lead to high levels of bioturbation, especially from their burrowing and feeding activities. Biogenic activity in the sediment can reduce the shear strength of the sediment (Rhoads and Boyer 1982) decreasing the amount of wave action or current velocity required to resuspend bottom sediment in a particular area. The Maumee Bay region is an area where some of the highest *Hexagenia* larval densities, and thus *Hexagenia* induced bioturbation, exists. It is also one of the shallowest areas of western Lake Erie (≤ 7 m deep). The decrease in sediment shear strength due to *Hexagenia* bioturbation will likely lead to increased physical sediment suspension in the shallow Maumee Bay area due to physical disturbances.

Possible Bioturbation Effects on Other Organisms

The first four contour intervals, ranging from 0 to 100 g/m²/d on the maps produced in this study represent areas where *Hexagenia*-induced sediment suspension will not likely have a significant effect on *Dreissena* filtration activity. *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 105.6 g/m²/d for a density of 2,000 mussels/m². Thus, in late spring at population densities near 1997 levels *Hexagenia* larval sediment suspension can potentially inhibit filtration by *Dreissena* in the basin. This is especially important when one considers that *Dreissena* have begun colonizing soft substrates in western Lake Erie (Berkman et al. 1998, Haultuch et al. 2000) and that most of their filtration effect occurs in the lower portions of the water column (bottom – 1 m) (Ackerman et al. 2001). In areas where large populations of *Hexagenia* occur, the sediment suspended by *Hexagenia* larvae may impede the ability of *Dreissena* mussels to colonize soft substrates by inhibiting feeding behaviour.

It may be difficult to determine if *Hexagenia* larval sediment suspension directly inhibits *Dreissena* colonization since *Hexagenia* and *Dreissena* tend to dominate in different offshore areas (Ciborowski et al. 2000), and in areas where they co-occur their densities are independent of each other (Freeman 1999, Ciborowski et al. 2000). Studies looking at reciprocal interactions between *Dreissena* and *Hexagenia* behaviour, growth and survival are required to help answer the question of what occurs in areas where *Dreissena* and *Hexagenia* co-occur. Freeman (1999) found that *Hexagenia* larvae survive better in the absence of mussels in the laboratory. In the field however, he observed higher survival of larvae at study locations where moderate levels of live *Dreissena* were present compared to locations with dead shells or a mix of live and dead shells. Freeman (1999) did not mention any effects of *Hexagenia* on *Dreissena* survival.

Studies that include a variety of *Hexagenia* larval sizes are also required to determine the effect mixed larval sizes representative of the size frequency distribution observed in western Lake Erie have on sediment suspension rate. This is important since *Hexagenia* larval have been observed sharing artificial burrows and larger larvae burrow in the sediment layers below smaller larvae (Hunt 1953). These types of experiment will permit better estimates of sediment suspension in western Lake Erie and how this sediment suspension influences other benthic invertebrates, such as *Dreissena*.

This study shows that *Hexagenia*-induced sediment suspension varies both temporally and spatially in western Lake Erie. Estimated *Hexagenia*-larval induced sediment suspension steadily increased as the basin-wide population densities increased during the years of recolonization beginning in the early 1990s. By 1997 the highest post-recovery densities and thus, the highest post-recovery *Hexagenia* sediment suspension rates were observed. The location of the highest larval densities and, thus, the highest sediment suspension rates occurred in the Maumee Bay region. This is in contrast to the historical data from 1930 where the highest larval densities and sediment suspension occurred in the middle of the basin in the island region. Over a one-year period, *Hexagenia* larval sediment suspension rates are estimated to be highest in late spring (early June) just prior to the mass emergence since larvae are largest (Manny 1991) and water temperatures are high (approx. 20° C) (Chase 1998, J. J. H. Ciborowski unpubl.). The sediment suspension rates then decrease in the summer (end of July) since the larger larvae have emerged and no longer contribute to sediment suspension. Sediment suspension rates decrease in the autumn (October) as the water temperature drops and sediment suspension remains low in early spring (April) of the following year as water temperatures remain low after the winter months.

CHAPTER 5: GENERAL CONCLUSIONS

The burrowing mayfly *Hexagenia* has once again become a dominant component of the zoobenthic community in western Lake Erie (Krieger et al. 1996, Corkum et al. 1997a, Schloesser et al. 2000) after a prolonged absence from the 1960s to early 1990s (Reynoldson et al. 1989, Krieger et al. 1996, Corkum et al. 1997a, Schloesser et al. 2000). The larval stages of this organism are common in depositional zones in both lentic and lotic systems (Keltner and McCafferty 1986, Edmunds and Waltz 1996). *Hexagenia* larvae can only survive in locations consisting of cohesive fine silt and clay substrates (Lyman 1943, Hunt 1953, Eriksen 1963a). The burrowing, feeding, and respiratory (gill beats) behaviour of *Hexagenia* larvae results in sediment suspension into the water column (Hunt 1953, Zimmerman and Wissing 1980, Keltner and McCafferty 1986). The return of *Hexagenia* to western Lake Erie may have a significant influence in western Lake Erie through its contribution to increased sediment suspension though its bioturbation activities.

Influence of Larval Size, Density and Temperature on Sediment Suspension

The research in this thesis shows that *Hexagenia* sediment suspension rates increase with increasing larval size, larval density and water temperature (Chapter 2). This is expected since larger larvae excavate larger burrows, which will displace more sediment, and a larger amount of water will be pumped through the burrows to provide the animals with oxygen. Higher densities mean that there will be more larvae burrowing and feeding, leading to a greater volume of sediment excavation per unit time and area. *Hexagenia* larval activity also increases with increasing water temperature (Zimmerman and Wissing

1978). In my experiments, this was reflected by increased bioturbation and sediment suspension. The interaction (synergy) among size, density, and temperature was by far the best predictor of sediment suspension rate for all three classes of sediment suspension rates (initial burrow construction, maximum [hungry] and minimum [fed]). This suggests that *Hexagenia* larval induced sediment suspension will be highest in the spring when larvae are largest (Manny 1991) and present in high numbers (more than 1,000 larvae/m^2 in some areas) (Chase 1998, Schloesser et al. 2000), and when water temperatures are highest (Chase 1998, J. J. H. Ciborowski unpubl.). There also appears to be a synergistic effect that occurs at higher densities since sediment suspension rates per larva appear to increase with increasing density.

Influence of Sediment Depth and Collection Location on Sediment Suspension

The depth of sediment in laboratory containers influenced larval sediment suspension rate during the initial burrow construction period. Sediment suspension rates were 18-20 % greater in the 10-cm sediment depth treatment compared to the 3.5-cm sediment depth treatment. However, sediment depth did not significantly influence the maximal (hungry larvae) sediment suspension rate. Sediment suspension rates varied with sediment collection location within western Lake Erie. Suspension rates for sediment collected from locations where larvae were absent or relatively rare were approximately twice as high as rates for sediment collected from locations supporting higher larval densities (> 200 larvae/m^2). The differences in sediment suspension rate resulting from experimental sediment depth and sediment collection location treatments are not as important as differences resulting from larval size and larval density variation. These differences, however, are less than observed between the maximal (larvae hungry) and minimal (larvae recently fed) sediment suspension rates. This decrease in sediment suspension rate after feeding is due to a high concentration of food suspended in the water column for larvae to filter feed on. This shift to filter feeding will lead to decreased burrowing activity and decreased sediment suspension. Thus, if large algal blooms were to occur due to increased eutrophication, the high amounts of suspended algal particles would decrease the amount of bioturbation by *Hexagenia* larvae since larvae potentially feed on suspended algal and detrital material (Cavaletto et al. 2003).

Among Year Variation in Western Lake Erie Sediment Suspension

Sediment suspension rates varied within western Lake Erie among years based on changes in larval density. Sediment suspension rates varied both in magnitude and spatially among years. Estimated *Hexagenia*-induced sediment suspension rates were high for 1930 when population densities were high. During the period from the early 1960s to the early 1990s when larvae were virtually absent from western Lake Erie (Carr and Hiltunen 1965, Reynoldson et al. 1989) sediment suspension due to *Hexagenia* was negligible by definition. As larvae began to recolonize western Lake Erie during the early 1990s to the present (Krieger et al. 1996, Chase 1998, Schloesser et al. 2000) *Hexagenia* sediment suspension rates increased until 1997 when basin wide populations were at their highest since recolonization began.

Seasonal (Month to Month) Variation in Sediment Suspension

Seasonal variation in *Hexagenia* sediment suspension from late spring (early June) 1997 to early spring 1998 (April) was estimated to be highest in late spring just prior to emergence when larvae are largest and water temperatures are near 20° C (Chase 1998), J. J. H. Ciborowski unpubl.). The late spring (pre-emergence) values are 4 to 5 times greater than those estimated for summer (post-emergence), and greater still than the values for the autumn and early spring of the following year. Sediment suspension rates will also change as water oxygen concentration varies throughout the year. During periods of prolonged calm weather oxygen concentrations near the sediment water interface will decrease. As a result *Hexagenia* larvae increase their gill beat frequency as oxygen concentrations decrease (Eriksen 1963b) which will lead to increased sediment suspension. This increase in sediment suspension will be further accentuated by the lack of mixing in the water column leading to more suspended sediment remaining at the sediment water interface. This will affect other benthic organisms, such as zebra mussels which show a decrease in filtration rate with increases suspended sediment (Reeders et al. 1993, Horgan and Mills 1997).

Implications for western Lake Erie

Sediment Loading

Hexagenia-induced sediment suspension in western Lake Erie is not the only source of suspended sediment and turbidity. However, compared to other sources *Hexagenia* larval sediment suspension is significant in late spring, prior to emergence. In late spring 1997 estimated maximum sediment suspension rates near the mouth of the Maumee River and near Monroe, Michigan were as high as 350 $g/m^2/d$, which is greater the daily amount of sediment suspension from a major storm event (Lick et al. 1994) and is less than that of shoreline erosion and from river inputs (Kemp et al. 1977). Thus, *Hexagenia*-induced sediment loading to western Lake Erie is a small portion of the total annual sediment load in the basin (Kemp et al. 1977). However, *Hexagenia* sediment loading is more constant compared to the pulse type inputs from rivers (Paul et al. 1982) and, thus, during late spring *Hexagenia* larval sediment suspension will likely have a greater impact on benthic organisms. *Hexagenia* sediment suspension is likely more important in northern and southern latitudes, since emergence is more prolonged in northern latitudes due to 3 to 4 overlapping cohorts (Giberson and Rosenberg 1994) and larvae can complete multiple lifecycles within one season in southern latitudes (Fremling 1970). These different emergence patterns mean that larvae are present in the sediments at a more constant density than is observed in western Lake Erie.

Bioturbation and Other Organisms

The burrowing, feeding and respiratory behaviour (bioturbation) of *Hexagenia* larvae may also indirectly influence sediment suspension by increasing the water content (McCall and Tevesz 1982) in the sediment, thus decreasing the shear strength of the substrate at the sediment water interface as has been observed with marine subsurface deposit feeders (Rhoads and Boyer 1982). This will lead to increased sediment suspension due to waves and currents. This decrease in shear strength will have the largest effect on physical sediment suspension in areas that are shallow and support high densities of *Hexagenia* larvae, such as the Maumee Bay region.

Hexagenia bioturbation will also affect egg bank dynamics, since bioturbation has been shown to move eggs both upwards and down wards depending on the bioturbation mechanism of the organism (Hairston Jr. 1996, Kearns et al. 1996). *Hexagenia* bioturbation will bury eggs deeper in the sediment (Gerlofsma 1999). Not only will *Hexagenia* eggs be buried, but also the eggs of other species. This will affect both the viability and hatching success of the buried eggs (Hairston Jr. et al. 1995, Plant et al. 2003). Thus, *Hexagenia* bioturbation will also play a role in structuring the benthic community of western Lake Erie though its influence on egg survival and hatching success. A decrease in shear strength of the bottom sediments will also lead to increased mixing of sediments and a net upward movement of eggs deposited in the bottom sediments.

Hexagenia larval sediment suspension can also affect other benthic organisms. In late spring, *Hexagenia*-induced sediment suspension can potentially inhibit filtration and feeding behaviour by *Dreissena* in the basin. This is especially important when one considers that *Dreissena* have begun to colonize soft substrates in western Lake Erie (Berkman et al. 1998, Haultuch et al. 2000) and that their filtration effects occur in the bottom meter of the water column (Ackerman et al. 2001). As a result, in areas where *Hexagenia* larval densities are high *Hexagenia* larval sediment suspension may inhibit the ability of *Dreissena* to colonize soft substrates in western Lake Erie.

Large populations of oligochaetes were present in western Lake Erie during the period when *Hexagenia* were absent (Reynoldson et al. 1989). The sediment contribution from oligochaete bioturbation at these high densities was likely not as important as *Hexagenia* bioturbation since oligochaetes are conveyor belt feeders that deposit sediment on top of the sediment in a pelletized layer (McCall and Fisher 1979). This is in contrast to *Hexagenia* larvae, which expel unconsolidated sediment into the overlying water column (Matisoff and Wang 2000).

Nutrient and Contaminant Flux

Despite the significant amount of sediment suspended by *Hexagenia* bioturbation, the amount of biologically available phosphorus entering the water column is likely inconsequential. The oxygenated sediment in larval burrows contains ferric oxyhydroxides, which cause adsorption of phosphorus (Holdren and Armstrong 1980, Wetzel 1983). This appears to occur in *Hexagenia* burrows since the concentration of total phosphorus (TP) in the water overlying sediment in experimental containers containing *Hexagenia* larvae does not significantly increase relative to controls that lack *Hexagenia* (Toot 2000). Thus, sediment bound nutrients are likely to remain bound to the suspended particles, unless the overlying water is anoxic and the ferric oxyhydroxides become reduced leading to release of adsorbed phosphorus. Thus, the possible exclusion of dreissenids by *Hexagenia*-induced sediment suspension may help in keeping western Lake Erie less eutrophic, since *Hexagenia* will generate less TP than dreissenids.

Hexagenia larval sediment suspension may increase the amount of sediment-bound contaminants resuspended and make these contaminants available to the pelagic environment. This may especially be true in the Maumee Bay region of western Lake Erie, where *Hexagenia* larval densities are highest (Chase 1998) and surficial sediments are highly enriched by metals (Cr, Cu, Ni, Pb and Zn) (Marvin et al. 2002). These enriched surface sediments are up to 3 times higher than background concentrations determined from the bottom (> 40 cm sediment depth) of sample cores (Marvin et al. 2002). However, the bioavailability of metals bound to sediment suspended by *Hexagenia rigida* are low for the bivalve *Corbicula fluminea* (Ciutat and Boudou 2003) and the assimilation of sediment-bound PAHs by dreissenids is also low (Gossiaux et al. 1998). Thus, sediment suspended by *Hexagenia* in western Lake Erie likely will not be significantly bioaccumulated in the system. Since the burial of contaminated sediment by deposition of clean particles (e.g., from shoreline erosion) is the most important part of the natural recovery of contaminated sediments (Thibodeaux and Bierman 2003), bioturbation by *Hexagenia* and activities of other organisms (e.g. zebra mussels) will play an important role in the recovery process.

Future Research

The potential decrease in sediment cohesion and shear strength due to *Hexagenia* bioturbation has important implications for sediment suspension in western Lake Erie. This is especially true for locations in the Maumee Bay region where water is shallow and the highest larval densities occur (Chase 1998). Experiments quantifying the effect of *Hexagenia* bioturbation on shear strength of western Lake Erie sediments will allow for the calculation of possible increases in sediment suspension by physical processes, such as waves, in areas where *Hexagenia* larvae are abundant.

Sediment collection location has a significant effect on *Hexagenia* larval sediment suspension rate. Even though variability in sediment suspension due to collection is low compared to other factors including larval size, density and temperature, this type of experiment will allow for verification of this finding using a larger number of sediment types than were used in the present study. Thus, experiments looking at the different sediment types in western Lake Erie are needed to better understand the effects of sediment type on the basin wide estimates of sediment flux. Results from this type of experiment will determine if inclusion of sediment type and characteristics are helpful in refining basin wide estimates of *Hexagenia*-induced sediment suspension calculated in this study. This, coupled with GIS analysis using existing sediment type data for western Lake Erie may help to determine the effects of *Hexagenia*-induced sediment suspension.

Another important avenue of investigation would be to conduct experiments using larvae of different sizes representative of the size frequency distribution observed in western Lake Erie at specific times of year. Experiments with these mixed densities would provide a better understanding of how different sized larvae interact and how this interaction influences larval sediment suspension rates. Mixed larval sizes will influence sediment suspension rates since smaller larvae burrow near the surface of the sediment and larger larvae burrow in the deeper sediments below the small larvae (Hunt 1953). Experiments using different sized larvae will likely produce lower sediment suspension rates than the experiments in this study which used uniform larval sizes. Sediment suspension rates from experiments using larval sizes representative of the size frequency distribution in Lake Erie will permit more accurate estimation of sediment suspension rates based on larval densities throughout western Lake Erie. Field studies that examine the size frequency distribution of larvae, as well as larval densities, would also provide a more accurate estimation of *Hexagenia* larval sediment suspension in western Lake Erie.

The effect of *Hexagenia* larval sediment suspension on other benthic organisms also warrants further investigation. This is especially true for dreissenids, which have become an important part of the Lake Erie ecosystem. In particular, experiments looking at potential negative effects of *Hexagenia*-induced sediment suspension on dreissenid feeding, filtration, survival and colonization ability on soft substrates, which make up much of western Lake Erie, are of importance. It has been suggested that since sediments are not a preferred food source, filtration rates of different size zebra mussels will likely be influenced by particle size distributions and their compositions in the field (Gossiaux et al. 1998). Thus, the size and type of particles that *Hexagenia* bioturbation is capable of suspending will influence feeding and filtration rates in zebra mussels. Inorganic sediments also have detrimental effects on dreissenid bioenergetic processes, such as ingestion rates, clearance rates, pseudofeces production and assimilation rates, all of which lead to a decrease in the amount of energy available for growth and reproduction in turbid environments (Madon et al. 1998). As a result, in field locations where *Hexagenia* bioturbation is high, zebra mussels will likely exhibit decreased colonization ability and growth.

However, dreissends have been shown to decrease their metabolic rate in the presence of suspended inorganic sediment, thus acclimating to chronic turbidity conditions (Summers et al. 1996) so they may be able to partially offset the effect of *Hexagenia*-induced sediment suspension. The presence of another bivalve, *Corbicula fluminea*, has been shown to decrease the plateau of *Hexagenia rigida* sediment suspension by 45% in laboratory experiments (Ciutat and Boudou 2003). Experiments with both *Hexagenia* larvae and dreissenids will also permit determination of how effective mussels are at removing *Hexagenia* suspended sediment from the water column.

Hexagenia-induced sediment suspension will significantly affect ecological processes in western Lake Erie. The ecological role of *Hexagenia* bioturbation may be as important as the role of *Hexagenia* biomass as a source of food for fish in western Lake Erie. The amount of sediment suspended by *Hexagenia* larvae will increase as densities increase and colonization of western Lake Erie continues. Sediment suspension due to larval bioturbation will influence dreissend filtration and feeding rates, possibly inhibiting colonization of soft substrates by these mussels. If dreissenids are excluded from certain locations, the phosphorus flux from the *Hexagenia* bioturbation will be less than that produced by driessenids due to the adsorption of phosphorus to the oxygenated sediment in mayfly burrows. *Hexagenia* bioturbation can also influence egg bank dynamics in western Lake Erie.

Hexagenia larval bioturbation will influence suspended sediment dynamics, nutrient dynamics and play a role in structuring the benthic community in western Lake Erie. Thus, further research to better estimate the amount of *Hexagenia*-induced sediment suspension in western Lake Erie and its interactions with other benthic organisms is required.

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APPENDIX 1: DETERMINATION OF INITIAL BURROW CONSTRUCTION, MAXIMAL AND MINIMAL TOTAL SUSPENDED SOLID ASYMPTOTES

The following figures illustrate some of the different scenarios encountered while determining the asymptotic levels of total suspended solids (TSS). These asymptotes were used to determine the sediment suspension rates for different larval size, larval density and water temperature treatment combinations in Chapter 2 and for the sediment depth and sediment collection location experiments in Chapter 3. Most of the time a distinct pattern showing TSS asymptotes for initial burrow construction, maximal (hungry) and minimal (fed) was observed over the course of the experiments (Figure A1.1). However, in some instances larvae in the jars died during the experiment, producing an increased in TSS for initial burrow construction followed by a decrease in TSS for the remainder of the experiment (Figure A1.2). In other instances no distinct pattern was observed throughout the experiment and only and estimate for initial burrow construction was calculated (Figure A1.3).

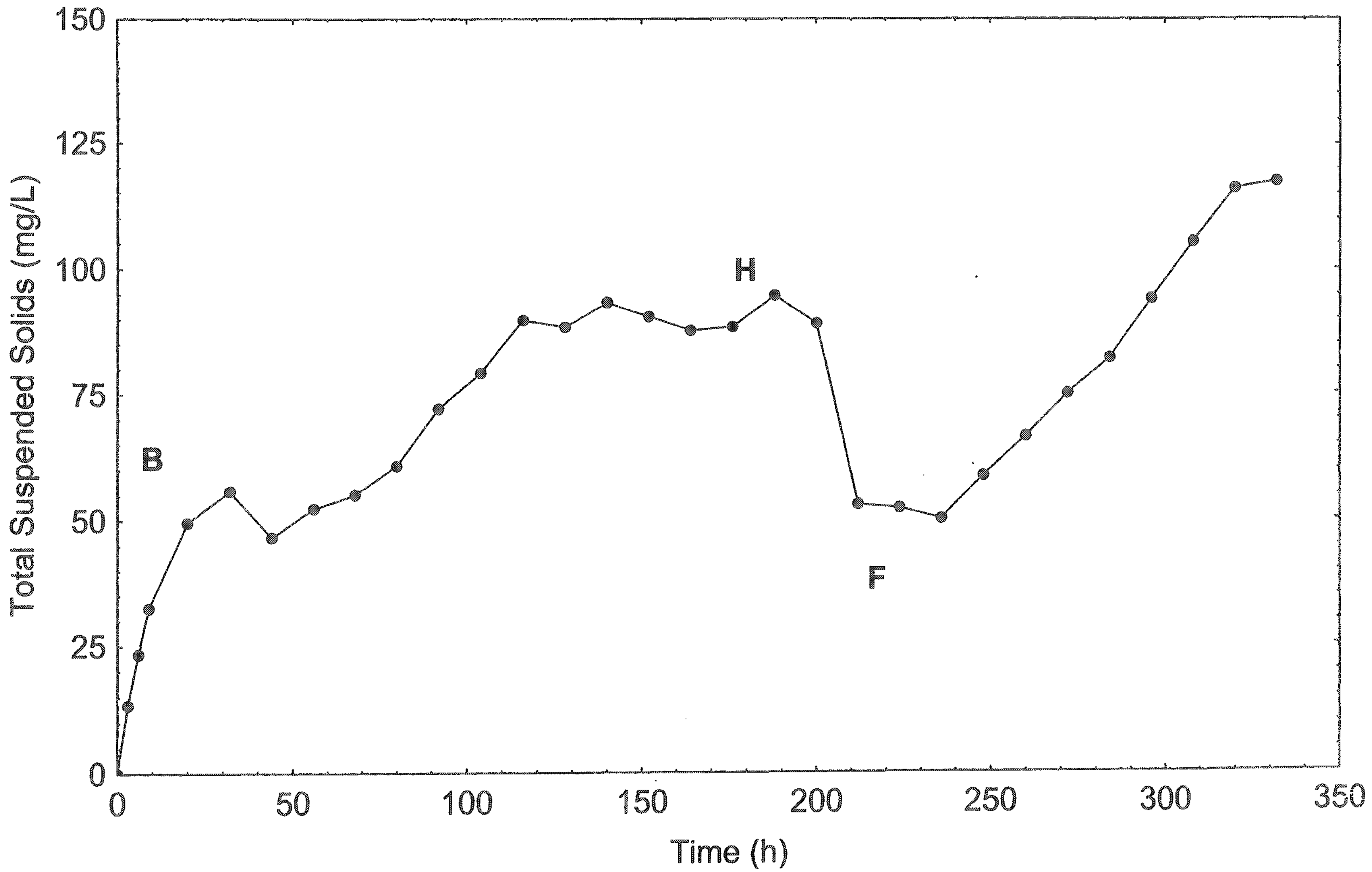

Figure A1.1: Total suspended solids asymtotes for intial burrow construction (B), maximal (hungry) (H), and minimal (fed) (F) sediment suspension for 10 mm long larvae at a density of 556 larvae/m² at 19°C (Trial #2). Food was added to experimental jars at 200 h.

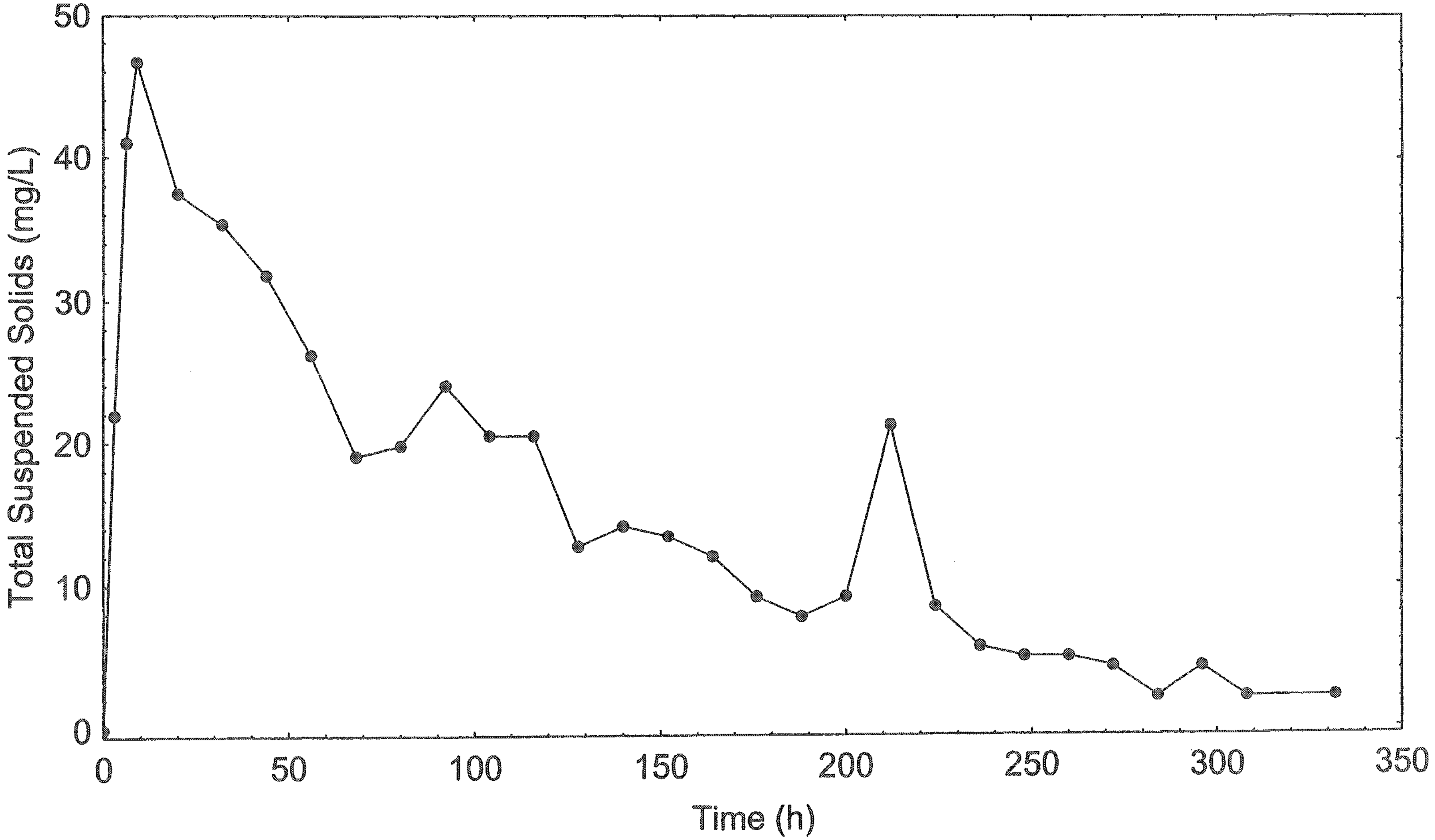

Figure A1.2: Total suspended solids (TSS) time course showing the asymptotes for a jar containing a single larva (70 larvae /m² density treatment at 19°C, Trial #2). The larva is presumed to have died during the experiement (not recovered at the end of the experiment). Note the decrease in TSS until 200 h, when food was added resulting in an increase in TSS 12 h later. TSS then began to decline again after 212 h. No estimates for maximal or minimal sediment suspension rates were calculated for experimental jars showing this type of TSS pattern.

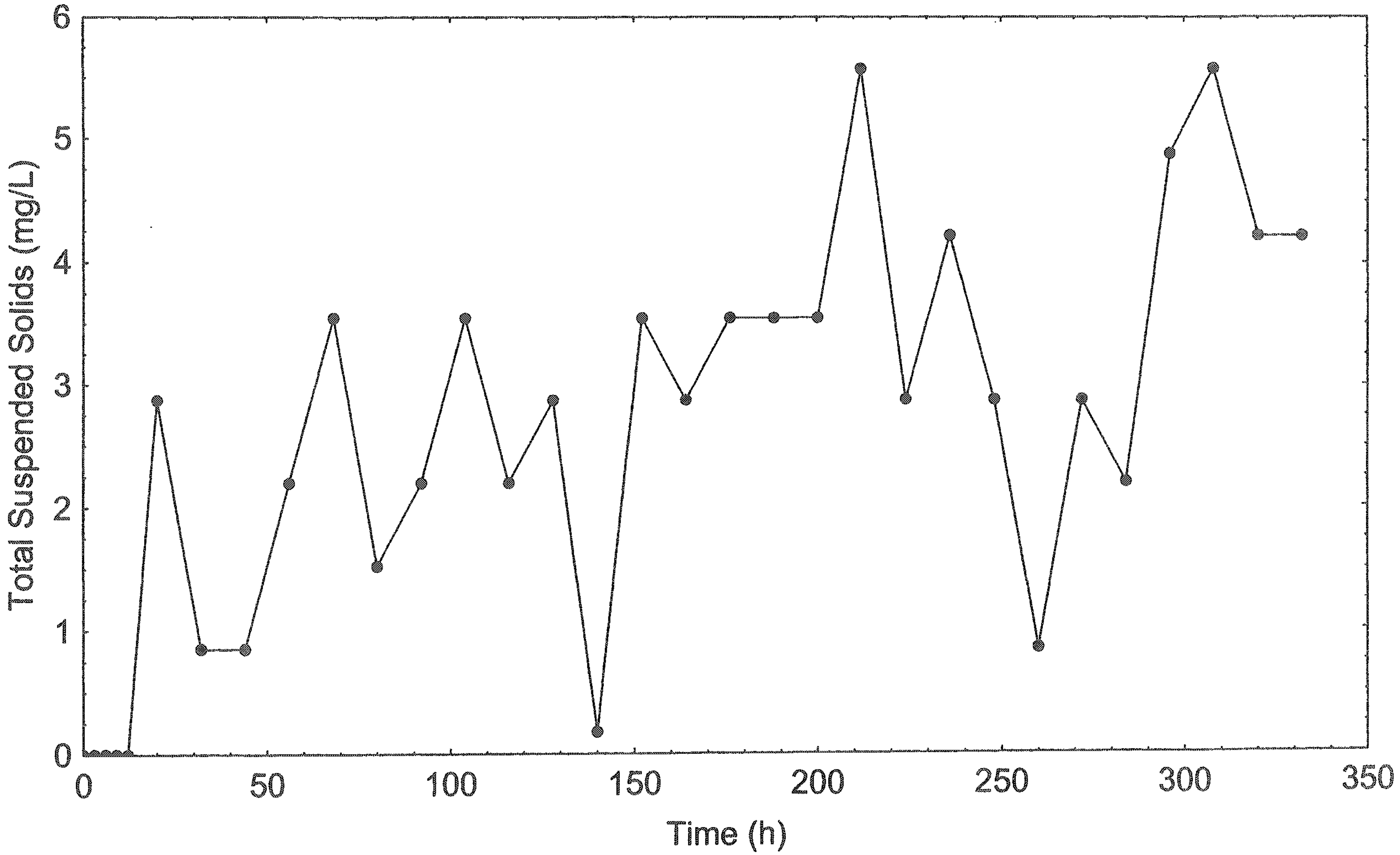

Figure A1.3: Total suspended solids (TSS) time course with no distinct asymptote for the maximal (hungry) and minimal (fed) sediment suspension. This jar contained 15 mm long larvae at a density of 139 larvae/m^2 and a temperature treatment of 10° C. Food was added to the jar at 200 h. No maximal or minimal sediment suspension rates were estimated for experimental jars showing this type of pattern.

APPENDIX 2: DATA SOURCES, LARVAL DENSITIES AND ESTIMATED SEDIMENT SUSPENSION RATES IN WESTERN LAKE ERIE USED IN GIS ANALYSIS

Table A2.1: *Hexagenia* larval density data sources used in calculations of sediment suspension rates for western Lake Erie (Chapter 4). Unpublished data from K. Kreiger and J. J. H. Ciborowski are from Heidelberg College and University of Windsor, respectively.

Year	Collection Period	No. Sites	Sampler Type	Replicates/Site	Data Source
1930	June to Sept.	67	Petersen	1 to 16	Wright 1995 (in Schloesser et al. 2000)
1951	June	184	Dredge	Unknown	Wood 1963, Wood 1973
1993	May to June	47	Ponar, Ekman	3	Chase 1998, Schloesser et al. 2000
1995	May to June	21	Ekman	4	Chase 1998, Schloesser et al. 2000
1997	May to June	58	Petersen, Petite Ponar	5	Chase 1998, Schloesser et al. 2000
1998	May to June	62	Petite Ponar	5	J.J.H. Ciborowski & K. Kreiger unpubl.
1999	May to June	39	Petite Ponar	5	J. J. H. Ciborowski unpubl.

Table A2.2: Latitude and longitude (decimal degrees), larval density, and minimum and maximum estimated sediment suspension rates for 1930 data set. Larval density data is from Wright 1955 cited in Schloesser et al. 2000. Site numbers are the identifiers used in the original data source.

Site	Latitude	Longitude	1930 Density (larvae/m²)	Min. Sed. Susp. Rate (g/m²/d)	Max. Sed. Susp. Rate (g/m²/d)
8F	41.893333	-82.786667	565	110.4	199.2
37A	41.606667	-82.605000	458	91.2	163.2
59A	41.538833	-82.697167	692	129.6	240.0
117(4R)	41.880500	-83.297167	8	4.8	4.8
126(9D)	41.969500	-83.152833	0	0.0	0.0
134(6L)	41.847167	-83.116667	462	93.6	165.6
158	41.644500	-82.850000	505	98.4	180.0
252(2M)	41.727833	-83.388833	37	12.0	16.8
254(4M)	41.755500	-83.319500	63	19.2	26.4
72	41.706667	-83.035000	328	69.6	120.0
105	41.683333	-83.241667	203	48.0	79.2
107(6M)	41.713833	-83.269500	94	26.4	38.4
109(7M)	41.733333	-83.297167	270	60.0	100.8
110	41.750000	-83.300000	162	38.4	64.8
114(8M)	41.788833	-83.355500	81	21.6	33.6
116(1R)	41.816667	-83.394500	40	12.0	19.2
116F	41.863333	-83.333333	14	4.8	7.2
118	41.891667	-83.283333	0	0.0	0.0
119(1D)	41.911167	-83.252833	162	38.4	64.8
121(2D)	41.925000	-83.252833	0	0.0	0.0
125	41.954167	-83.163833	0	0.0	0.0
127	41.951667	-83.145833	0	0.0	0.0
128(6D)	41.941667	-83.144500	13	4.8	7.2
130(4D)	41.913833	-83.136167	21	7.2	9.6
132(8L)	41.883333	-83.130500	310	67.2	115.2
200	41.887500	-83.330833	0	0.0	0.0
201	41.890000	-83.330833	0	0.0	0.0
202	41.892500	-83.331167	49	14.4	21.6
203	41.901667	-83.332167	0	0.0	0.0
204	41.903333	-83.332500	18	7.2	9.6
210(3R)	41.886167	-83.330500	0	0.0	0.0
211	41.885000	-83.322500	2	2.4	2.4
213	41.883333	-83.316667	74	21.6	31.2
214	41.885000	-83.330500	0	0.0	0.0
215	41.883333	-83.329167	32	9.6	14.4
220	42.055000	-83.130833	13	4.8	7.2
221	42.033333	-83.129167	101	26.4	40.8
221B	42.033333	-83.150000	0	0.0	0.0
222(13D)	42.008333	-83.152833	0	0.0	0.0
226	42.000000	-83.054167	0	0.0	0.0
227	41.977500	-83.041667	14	4.8	7.2
228	41.947500	-83.041667	81	21.6	33.6
229(9L)	41.916667	-83.038833	634	120.0	220.8
230	41.929167	-83.062500	189	43.2	72.0
231(7D)	41.938833	-83.088833	176	40.8	69.6
232(8D)	41.955500	-83.119500	0	0.0	0.0
235	41.680000	-83.216667	648	122.4	225.6
236(1L)	41.719500	-83.200000	94	26.4	38.4
237	41.716667	-83.233333	108	28.8	43.2
240(5D)	41.958333	-83.194500	0	0.0	0.0
250	41.700000	-83.470000	0	0.0	0.0
251(1M)	41.713833	-83.425000	2	2.4	2.4
253(3M)	41.741667	-83.355500	34	12.0	16.8
255	41.766667	-83.304167	108	28.8	43.2
256(5M)	41.772167	-83.286167	402	81.6	146.4
257	41.787500	-83.258333	182	43.2	69.6
258(2L)	41.797167	-83.230500	634	120.0	220.8
259(3L)	41.816667	-83.180500	564	108.0	199.2
260	41.833333	-83.145833	337	72.0	124.8
261	41.851667	-83.320833	344	72.0	127.2
262(5L)	41.858333	-83.183333	358	74.4	129.6
263(4L)	41.863833	-83.219500	317	67.2	117.6
264(5R)	41.872167	-83.263833	27	9.6	12.0
265	41.854167	-83.296667	0	0.0	0.0
266	41.826667	-83.308333	27	9.6	12.0
267	41.791667	-83.316667	68	19.2	28.8
268	41.773333	-83.317500	40	12.0	19.2
		Mean (± SE)	151 ± 25	32.6 ± 4.7	56.2 ± 8.6

Table A2.3: Latitude and longitude (decimal degrees), larval density, and minimum and maximum estimated sediment suspension rates for 1951 data set. Larval density, and latitude and longitude data were interpolated from maps in Wood 1963 and Wood 1973.

Site	Latitude	Longitude	1951 Density (larvae/m²)	Min. Sed. Susp. Rate (g/m²/d)	Max. Sed. Susp. Rate (g/m²/d)
1	41.700000	-83.462352	48	14.4	14.4
2	41.707692	-83.452200	48	14.4	21.6
3	41.711538	-83.442047	48	14.4	21.6
4	41.700000	-83.421743	48	14.4	14.4
5	41.700000	-83.396362	48	14.4	21.6
6	41.707692	-83.386210	48	14.4	21.6
7	41.738462	-83.376058	48	14.4	21.6
8	41.738462	-83.365905	48	14.4	21.6
9	41.746154	-83.345601	48	14.4	21.6
10	41.753846	-83.325296	48	14.4	21.6
11	41.761538	-83.299915	48	14.4	21.6
12	41.773077	-83.279611	48	14.4	21.6
13	41.788462	-83.264382	48	14.4	21.6
14	41.796154	-83.239002	48	14.4	21.6
15	41.788462	-83.233926	48	14.4	21.6
16	41.807692	-83.203469	48	14.4	21.6
17	41.792308	-83.188240	48	14.4	21.6
18	41.842308	-83.188240	48	14.4	21.6
19	41.857692	-83.152707	48	14.4	21.6
20	41.826923	-83.152707	48	14.4	21.6
21	41.815385	-83.152707	48	14.4	21.6
22	41.957692	-83.122250	48	14.4	14.4
23	41.873077	-83.122250	48	14.4	14.4
24	41.807692	-83.137479	48	14.4	21.6
25	41.823077	-83.101946	48	14.4	21.6
26	41.807692	-83.101946	48	14.4	21.6
27	41.803846	-83.091794	48	14.4	21.6
28	41.938462	-83.091794	48	14.4	21.6
29	41.953846	-83.071489	48	14.4	21.6
30	41.830769	-83.056261	48	14.4	21.6
31	41.823077	-83.051184	48	14.4	21.6
32	41.788462	-83.071489	48	14.4	21.6
33	41.907692	-83.056261	48	14.4	21.6
34	41.892308	-83.051184	48	14.4	21.6
35	41.873077	-83.041032	48	14.4	21.6
36	41.865385	-83.025804	48	14.4	21.6
37	41.853846	-83.025804	48	14.4	21.6
38	41.823077	-83.041032	48	14.4	21.6
39	41.773077	-83.025804	48	14.4	21.6
40	41.957692	-83.025804	48	14.4	14.4
41	41.907692	-83.020728	48	14.4	21.6
42	41.842308	-83.010575	48	14.4	21.6
42A	41.826923	-83.005499	48	14.4	21.6
43	41.819231	-83.000423	48	14.4	21.6
44	41.842308	-82.990271	48	14.4	21.6
45	41.830769	-82.990271	48	14.4	21.6
46	41.819231	-82.985195	48	14.4	21.6
47	41.876923	-82.990271	48	14.4	21.6
48	41.953846	-82.980118	198	45.6	76.8
49	41.888462	-82.975042	198	45.6	76.8
50	41.796154	-82.975042	198	45.6	76.8
51	41.784615	-82.969966	198	45.6	76.8
52	41.753846	-82.985195	198	45.6	76.8
53	41.907692	-82.954738	198	45.6	76.8
54	41.892308	-82.954738	198	45.6	76.8
55	41.884615	-82.949662	198	45.6	76.8
56	41.869231	-82.959814	198	45.6	76.8
57	41.803846	-82.954738	198	45.6	76.8
58	41.792308	-82.949662	198	45.6	76.8
59	41.773077	-82.949662	198	45.6	76.8
60	41.761538	-82.939509	198	45.6	76.8
61	41.742308	-82.929357	198	45.6	76.8
62	41.723077	-82.944585	198	45.6	76.8
63	41.750000	-82.914129	398	81.6	144.0
64	41.738462	-82.903976	398	81.6	144.0
65	41.738462	-82.914129	398	81.6	144.0
66	41.726923	-82.909052	398	81.6	144.0
67	41.726923	-82.888748	398	81.6	144.0
68	41.707692	-82.909052	398	81.6	144.0

Table A2.3: (continued)

Site	Latitude	Longitude	1951 Density (larvae/m²)	Min. Sed. Susp. Rate (g/m²/d)	Max. Sed. Susp. Rate (g/m²/d)
69	41.707692	-82.873519	398	81.6	144.0
70	41.688462	-82.863367	398	81.6	144.0
71	41.673077	-82.832910	398	81.6	144.0
72	41.819231	-82.924281	198	45.6	76.8
73	41.923077	-82.929357	198	45.6	76.8
74	41.938462	-82.929357	198	45.6	76.8
75	41.950000	-82.929357	198	45.6	76.8
76	41.961538	-82.914129	398	81.6	144.0
77	41.961538	-82.893824	398	81.6	144.0
78	41.950000	-82.888748	398	81.6	144.0
79	41.938462	-82.878596	398	81.6	144.0
80	41.911538	-82.878596	398	81.6	144.0
81	41.903846	-82.858291	398	81.6	144.0
82	41.957692	-82.863367	398	81.6	144.0
83	41.953846	-82.853215	398	81.6	144.0
84	41.926923	-82.843063	398	81.6	144.0
85	41.876923	-82.843063	398	81.6	144.0
86	41.846154	-82.822758	398	81.6	144.0
87	41.811538	-82.807530	398	81.6	144.0
88	41.780769	-82.782149	398	81.6	144.0
89	41.776923	-82.771997	398	81.6	144.0
90	41.746154	-82.787225	398	81.6	144.0
91	41.657692	-82.792301	398	81.6	144.0
92	41.646154	-82.777073	500	98.4	177.6
93	41.626923	-82.761844	500	98.4	177.6
94	41.957692	-82.807530	500	98.4	177.6
95	41.961538	-82.797377	500	98.4	177.6
96	41.953846	-82.787225	500	98.4	177.6
97	41.942308	-82.797377	398	81.6	144.0
98	41.911538	-82.792301	398	81.6	144.0
99	41.880769	-82.792301	398	81.6	144.0
100	41.842308	-82.792301	398	81.6	144.0
101	41.819231	-82.782149	398	81.6	144.0
102	41.680769	-82.777073	398	81.6	144.0
103	41.673077	-82.771997	398	81.6	144.0
104	41.703846	-82.792301	398	81.6	144.0
105	41.711538	-82.787225	398	81.6	144.0
106	41.723077	-82.756768	398	81.6	144.0
107	41.734615	-82.746616	398	81.6	144.0
108	41.746154	-82.741540	198	45.6	76.8
109	41.957692	-82.761844	500	98.4	177.6
110	41.957692	-82.741540	500	98.4	177.6
111	41.957692	-82.716159	500	98.4	177.6
112	41.953846	-82.706007	500	98.4	177.6
113	41.957692	-82.695854	500	98.4	177.6
114	41.957692	-82.670474	500	98.4	177.6
115	41.930769	-82.711083	398	81.6	144.0
116	41.919231	-82.716159	398	81.6	144.0
117	41.907692	-82.711083	398	81.6	144.0
118	41.919231	-82.680626	398	81.6	144.0
119	41.892308	-82.726311	398	81.6	144.0
120	41.873077	-82.726311	398	81.6	144.0
121	41.842308	-82.726311	398	81.6	144.0
122	41.819231	-82.746616	398	81.6	144.0
123	41.811538	-82.741540	198	45.6	76.8
124	41.757692	-82.731387	198	45.6	76.8
125	41.765385	-82.726311	198	45.6	76.8
126	41.780769	-82.706007	198	45.6	76.8
127	41.776923	-82.726311	198	45.6	76.8
128	41.792308	-82.716159	198	45.6	76.8
129	41.807692	-82.706007	48	14.4	21.6
130	41.834615	-82.700931	48	14.4	21.6
131	41.876923	-82.690778	198	45.6	76.8
132	41.680769	-82.731387	398	81.6	144.0
133	41.711538	-82.695854	198	45.6	76.8
134	41.692308	-82.680626	198	45.6	76.8
135	41.676923	-82.680626	198	45.6	76.8
136	41.673077	-82.670474	198	45.6	76.8
137	41.696154	-82.751692	398	81.6	144.0
138	41.557692	-82.736464	398	81.6	144.0
139	41.561538	-82.706007	398	81.6	144.0

Table A2.3: (continued)

Site	Latitude	Longitude	1951 Density (larvae/m²)	Min. Sed. Susp. Rate (g/m²/d)	Max. Sed. Susp. Rate (g/m²/d)
140	41.576923	-82.690778	198	45.6	76.8
141	41.561538	-82.685702	198	45.6	76.8
142	41.538462	-82.675550	48	14.4	21.6
143	41.603846	-82.680626	198	45.6	76.8
144	41.615385	-82.670474	48	14.4	21.6
145	41.642308	-82.645093	48	14.4	21.6
146	41.650000	-82.665398	198	45.6	76.8
147	41.669231	-82.634941	198	45.6	76.8
148	41.703846	-82.645093	500	98.4	177.6
149	41.738462	-82.599408	398	81.6	144.0
150	41.796154	-82.609560	48	14.4	21.6
151	41.819231	-82.589255	48	14.4	21.6
152	41.838462	-82.629865	48	14.4	21.6
153	41.953846	-82.624788	500	98.4	177.6
154	41.957692	-82.579103	500	98.4	177.6
155	41.919231	-82.579103	198	45.6	76.8
156	41.884615	-82.574027	48	14.4	21.6
157	41.846154	-82.579103	48	14.4	21.6
158	41.873077	-82.528342	48	14.4	21.6
159	41.842308	-82.543570	48	14.4	21.6
160	41.823077	-82.563875	48	14.4	21.6
161	41.803846	-82.563875	48	14.4	21.6
162	41.807692	-82.528342	198	45.6	76.8
163	41.773077	-82.579103	198	45.6	76.8
164	41.769231	-82.513113	198	45.6	76.8
165	41.738462	-82.563875	500	98.4	177.6
166	41.703846	-82.568951	500	98.4	177.6
167	41.669231	-82.584179	198	45.6	76.8
168	41.669231	-82.533418	48	14.4	21.6
169	41.588462	-82.584179	48	14.4	21.6
170	41.573077	-82.553723	48	14.4	21.6
171	41.507692	-82.574027	48	14.4	21.6
172	41.488462	-82.518190	48	14.4	21.6
173	41.476923	-82.487733	48	14.4	21.6
174	41.569231	-82.497885	48	14.4	21.6
175	41.546154	-82.467428	48	14.4	21.6
176	41.503846	-82.436971	48	14.4	21.6
177	41.530769	-82.411591	48	14.4	21.6
178	41.669231	-82.487733	48	14.4	21.6
179	41.669231	-82.436971	48	14.4	21.6
180	41.734615	-82.472504	198	45.6	76.8
181	41.719231	-82.436971	198	45.6	76.8
182	41.703846	-82.386210	48	14.4	21.6
183	41.669231	-82.391286	48	14.4	21.6
		Mean (± S.E.)	216 ± 12	46.9 ± 2.3	80.7 ± 4.3

Table A2.4: Latitude and longitude (decimal degrees), larval density, and minimum and maximum estimated sediment suspension rates for 1993 data set. Larval density data is from Chase 1998. Site numbers are the identifiers used in the original data source

Site	Latitude	Longitude	1993 Density (larvae/m^2)	Min. Sed. Susp. Rate (g/m^2/d)	Max. Sed. Susp. Rate (g/m^2/d)
0.5	41.548667	-82.916667	13	4.8	7.2
0.6	41.600000	-83.041667	0	0.0	0.0
0.6	41.650000	-83.150000	19	7.2	9.6
0.7	41.750000	-83.104167	0	0.0	0.0
0.7	41.733333	-82.970833	0	0.0	0.0
0.8	41.640333	-82.944500	0	0.0	0.0
0.8	41.687500	-83.040333	6	2.4	4.8
1D	41.911167	-83.252833	13	4.8	7.2
2D	41.925000	-83.252833	13	4.8	7.2
3D	41.938833	-83.202833	32	9.6	14.4
4D	41.913833	-83.136167	26	9.6	12.0
5D	41.958333	-83.194500	0	0.0	0.0
6D	41.941667	-83.144500	6	2.4	4.8
7D	41.944333	-83.088833	26	9.6	12.0
8D	41.955500	-83.119500	6	2.4	4.8
9D	41.969500	-83.152833	19	7.2	9.6
10D	41.988833	-83.163833	0	0.0	0.0
11D	41.988833	-83.125000	38	12.0	16.8
12D	41.972167	-83.091667	13	4.8	7.2
13D	42.008333	-83.152833	0	0.0	0.0
14D	42.008333	-83.100000	26	9.6	12.0
15D	42.033333	-83.152833	6	2.4	4.8
16D	42.025000	-83.069500	0	0.0	0.0
1L	41.719500	-83.200000	0	0.0	0.0
2L	41.792167	-83.230500	0	0.0	0.0
3L	41.816667	-83.180500	0	0.0	0.0
4L	41.863833	-83.219500	0	0.0	0.0
5L	41.864167	-83.183333	6	2.4	4.8
6L	41.842167	-83.116667	6	2.4	4.8
7L	41.816667	-83.000000	0	0.0	0.0
8L	41.883333	-83.130500	0	0.0	0.0
9L	41.916667	-83.038833	6	2.4	4.8
10L	41.894333	-82.986167	6	2.4	4.8
1M	41.713833	-83.425000	13	4.8	7.2
2M	41.727833	-83.388333	0	0.0	0.0
3M	41.741667	-83.355500	0	0.0	0.0
4M	41.755500	-83.319500	0	0.0	0.0
5M	41.772167	-83.286167	26	9.6	12.0
6M	41.713833	-83.269500	26	9.6	12.0
7M	41.733333	-83.297167	26	9.6	12.0
8M	41.788833	-83.355500	26	9.6	12.0
1R	41.816667	-83.394500	26	9.6	12.0
2R	41.844500	-83.352833	0	0.0	0.0
3R	41.886167	-83.330500	0	0.0	0.0
4R	41.880500	-83.297167	0	0.0	0.0
5R	41.872167	-83.263833	0	0.0	0.0
6R	41.902833	-83.300000	19	7.2	9.6
		Mean (± SE)	9 ± 2	3.5 ± 0.6	4.9 ± 0.8

Table A2.5: Latitude and longitude (decimal degrees), larval density, and minimum and maximum estimated sediment suspension rates for 1995 data set. Larval density data is from Chase 1998. Site numbers are the identifiers used in the orginal data source.

Site	Latitude	Longitude	1995 Density (larvae/m²)	Min. Sed. Susp. Rate (g/m²/d)	Max. Sed. Susp. Rate (g/m²/d)
0.5	41.548667	-82.916667	0	0.0	0.0
0.7	41.750000	-83.104167	5	2.4	2.4
0.7	41.733333	-82.970833	0	0.0	0.0
0.8	41.640333	-82.944500	0	0.0	0.0
0.8	41.687500	-83.040333	29	9.6	14.4
3D	41.938833	-83.202833	183	43.2	72.0
8D	41.955500	-83.119500	38	12.0	16.8
15D	42.033333	-83.152833	0	0.0	0.0
2L	41.797167	-83.230500	87	24.0	36.0
6L	41.847167	-83.116667	34	12.0	16.8
7L	41.816667	-83.000000	5	2.4	2.4
10L	41.894333	-82.986167	14	4.8	7.2
1M	41.713833	-83.425000	58	16.8	26.4
7M	41.733333	-83.297167	115	28.8	45.6
8M	41.788833	-83.355500	96	26.4	40.8
4R	41.430500	-83.297167	10	4.8	4.8
5B	41.691667	-82.766667	43	14.4	19.2
6B	41.866667	-82.816667	0	0.0	0.0
1K	41.750000	-82.750000	29	9.6	14.4
2K	41.766667	-82.866667	0	0.0	0.0
1T	41.696833	-83.468833	0	0.0	0.0
		Mean (± SE)	35 ± 11	10.1 ± 2.6	15.2 ± 4.2

Table A2.6: Latitude and longitude (decimal degrees), larval density, and minimum and maximum estimated sediment suspension rates for 1997 data set. Larval density data is from Chase 1998 and Schloesser et al. 2000. Site numbers are the identifiers used in the orginal data sources.

Site	Latitude	Longitude	1997 Density (larvae/m²)	Min. Sed. Susp. Rate (g/m²/d)	Max. Sed. Susp. Rate (g/m²/d)
ER01	41.967500	-83.183000	27	9.6	12.0
ER02	41.967167	-83.067667	240	52.8	91.2
ER03	41.967500	-82.967167	578	110.4	204.0
ER04	41.967333	-82.867000	676	127.2	235.2
ER05	41.967333	-82.765833	71	19.2	31.2
ER06	41.967333	-82.651333	18	7.2	9.6
ER07	41.900167	-83.283000	862	156.0	292.8
ER08	41.899500	-83.183500	498	98.4	177.6
ER09	41.900000	-83.068500	240	52.8	91.2
ER10	41.900000	-82.967667	213	48.0	81.6
ER11	41.900000	-82.866667	107	28.8	43.2
ER12	41.900333	-82.767167	0	0.0	0.0
ER13	41.899667	-82.651667	44	14.4	19.2
ER14	41.817167	-83.383500	1378	230.4	453.6
ER15	41.817000	-83.282833	782	144.0	268.8
ER16	41.817167	-83.183167	382	79.2	139.2
ER17	41.817000	-83.068833	284	62.4	105.6
ER18	41.817167	-82.967333	551	108.0	194.4
ER19	41.816667	-82.867167	89	24.0	36.0
ER20	41.817167	-82.766500	36	12.0	16.8
ER21	41.733667	-83.383167	116	28.8	48.0
ER22	41.733500	-83.283333	1440	237.6	472.8
ER23	41.733667	-83.183167	1013	177.6	340.8
ER24	41.733500	-83.068333	0	0.0	0.0
ER25	41.734000	-82.968667	0	0.0	0.0
ER26	41.734000	-82.867000	196	45.6	74.4
ER27	41.733667	-82.766667	196	45.6	74.4
ER34	41.935000	-82.584500	18	7.2	9.6
ER35	42.000833	-82.651333	9	4.8	4.8
ER36	41.984833	-82.766833	169	40.8	67.2
ER37	41.861500	-82.599167	18	7.2	9.6
ER38	41.775167	-82.599333	18	7.2	9.6
ER39	41.695500	-82.599333	329	69.6	120.0
ER40	41.934167	-82.759500	18	7.2	9.6
ER41	41.852167	-82.706000	0	0.0	0.0
4R	41.880500	-83.297167	418	84.0	151.2
1T	41.696833	-83.468833	144	36.0	57.6
2T	41.742500	-83.447667	202	48.0	76.8
3T	41.736833	-83.462667	24	9.6	12.0
5B	41.691667	-82.766667	624	117.6	218.4
6B	41.866667	-82.816667	154	38.4	60.0
3D	41.938833	-82.202833	302	64.8	112.8
8D	41.955500	-83.119500	1680	271.2	544.8
15D	42.033333	-83.152833	10	4.8	4.8
1K	41.750000	-82.750000	216	50.4	81.6
2K	41.766667	-82.866667	0	0.0	0.0
2L	41.797167	-83.230500	283	62.4	105.6
6L	41.847167	-83.116667	149	36.0	60.0
7L	41.816667	-83.000000	619	117.6	216.0
10L	41.894500	-82.986167	216	50.4	81.6
1M	41.713833	-83.425000	499	98.4	177.6
7M	41.733333	-83.297167	2064	321.6	660.0
8M	41.768833	-83.355500	1109	192.0	369.6
1P	41.548667	-82.916667	384	79.2	139.2
4P	41.750000	-83.104167	10	4.8	4.8
5P	41.733333	-82.970833	0	0.0	0.0
6P	41.640333	-82.944500	250	55.2	93.6
7P	41.687500	-83.040333	763	139.2	261.6
		Mean (± SE)	357 ± 59	68.0 ± 9.6	124.7 ± 19.3

Table A2.7: Latitude and longitude (decimal degrees), larval density, and minimum and maximum estimated sediment suspension rates for 1999 data set. Larval density data is from Ciborowski unpublished data. Site numbers are the identifiers used in the orginal data source.

Site	Latitude	Longitude	1999 Density (larvae/m²)	Min. Sed. Susp. Rate (g/m²/d)	Max. Sed. Susp. Rate (g/m²/d)
ER01	41.964347	-83.187333	0	0.0	0.0
ER02	41.964350	-83.071330	622	117.6	216.0
ER03	41.965355	-82.971327	738	136.8	254.4
ER04	41.964358	-82.871323	720	134.4	249.6
ER05	41.964362	-82.770320	196	45.6	74.4
ER06	41.964367	-82.655315	89	24.0	36.0
ER07	41.897338	-83.287332	604	115.2	211.2
ER08	41.897342	-83.188328	951	168.0	321.6
ER09	41.897347	-83.073325	258	57.6	96.0
ER10	41.897350	-82.972322	222	50.4	84.0
ER11	41.897353	-82.871318	551	108.0	194.4
ER12	41.897358	-82.771315	71	19.2	31.2
ER13	41.897362	-82.656312	80	21.6	33.6
ER14	41.814330	-83.388330	853	153.6	290.4
ER15	41.814333	-83.287327	391	81.6	141.6
ER16	41.814337	-83.187323	240	52.8	91.2
ER17	41.814342	-83.073320	62	19.2	26.4
ER18	41.814345	-82.971317	240	52.8	91.2
ER19	41.814348	-82.871313	98	26.4	40.8
ER20	41.814353	-82.771310	631	120.0	220.8
ER21	41.731325	-83.387323	462	93.6	165.6
ER22	41.731328	-83.287320	347	72.0	127.2
ER23	41.731332	-83.187317	436	88.8	156.0
ER24	41.731337	-83.072313	116	28.8	48.0
ER25	41.731340	-82.972310	36	12.0	16.8
ER26	41.731343	-82.871307	53	16.8	24.0
ER27	41.731348	-82.771303	44	14.4	19.2
ER30	41.648335	-82.972305	178	43.2	69.6
ER31	41.648338	-82.871302	231	52.8	88.8
ER32	41.648343	-82.771298	551	108.0	194.4
ER33	41.648347	-82.656295	160	38.4	62.4
ER34	41.932367	-82.589312	9	4.8	4.8
ER35	41.997368	-82.655318	9	4.8	4.8
ER36	41.981363	-82.771320	213	48.0	81.6
ER37	41.858362	-82.603307	27	9.6	12.0
ER38	41.772357	-82.603302	0	0.0	0.0
ER39	41.693352	-82.603295	62	19.2	26.4
ER40	41.931362	-82.713315	71	19.2	31.2
ER41	41.856357	-82.714310	204	48.0	79.2
		Mean (± SE)	278 ± 42	57.1 ± 7.5	100.4 ± 14.3

Table A2.8: Latitude and longitude (decimal degrees), larval density, and minimum and maximum estimated sediment suspension rates for late spring 1997 larval densities. Larval density data is from Chase 1998 and Schloesser et al. 2000. Site numbers are the identifiers used in the original data sources.

Site	Latitude	Longitude	Density (larvae/m²)	Min. Sed. Susp. Rate (g/m²/d)	Max. Sed. Susp. Rate (g/m²/d)
ER01	41.967500	-83.183000	27	9.6	12.0
ER02	41.967167	-83.067667	240	52.8	91.2
ER03	41.967500	-82.967167	578	110.4	204.0
ER04	41.967333	-82.867000	676	127.2	235.2
ER05	41.967333	-82.765833	71	19.2	31.2
ER06	41.967333	-82.651333	18	7.2	9.6
ER07	41.900167	-83.283000	862	156.0	292.8
ER08	41.899500	-83.183500	498	98.4	177.6
ER09	41.900000	-83.068500	240	52.8	91.2
ER10	41.900000	-82.967667	213	48.0	81.6
ER11	41.900000	-82.866667	107	28.8	43.2
ER12	41.900333	-82.767167	0	0.0	0.0
ER13	41.899667	-82.651667	44	14.4	19.2
ER14	41.817167	-83.383500	1378	230.4	453.6
ER15	41.817000	-83.282833	782	144.0	268.8
ER16	41.817167	-83.183167	382	79.2	139.2
ER17	41.817000	-83.068833	284	62.4	105.6
ER18	41.817167	-82.967333	551	108.0	194.4
ER19	41.816667	-82.867167	89	24.0	36.0
ER20	41.817167	-82.766500	36	12.0	16.8
ER21	41.733667	-83.383167	116	28.8	48.0
ER22	41.733500	-83.283333	1440	237.6	472.8
ER23	41.733667	-83.183167	1013	177.6	340.8
ER24	41.733500	-83.068333	0	0.0	0.0
ER25	41.734000	-82.968667	0	0.0	0.0
ER26	41.734000	-82.867000	196	45.6	74.4
ER27	41.733667	-82.766667	196	45.6	74.4
ER34	41.935000	-82.584500	18	7.2	9.6
ER35	42.000833	-82.651333	9	4.8	4.8
ER36	41.984833	-82.766833	169	40.8	67.2
ER37	41.861500	-82.599167	18	7.2	9.6
ER38	41.775167	-82.599333	18	7.2	9.6
ER39	41.695500	-82.599333	329	69.6	120.0
ER40	41.934167	-82.759500	18	7.2	9.6
ER41	41.852167	-82.706000	0	0.0	0.0
4R	41.880500	-83.297167	418	84.0	151.2
1T	41.696833	-83.468833	144	36.0	57.6
2T	41.742500	-83.447667	202	48.0	76.8
3T	41.736833	-83.462667	24	9.6	12.0
5B	41.691667	-82.766667	624	117.6	218.4
6B	41.866667	-82.816667	154	38.4	60.0
3D	41.938833	-82.202833	302	64.8	112.8
8D	41.955500	-83.119500	1680	271.2	544.8
15D	42.033333	-83.152833	10	4.8	4.8
1K	41.750000	-82.750000	216	50.4	81.6
2K	41.766667	-82.866667	0	0.0	0.0
2L	41.797167	-83.230500	283	62.4	105.6
6L	41.847167	-83.116667	149	36.0	60.0
7L	41.816667	-83.000000	619	117.6	216.0
10L	41.894500	-82.986167	216	50.4	81.6
1M	41.713833	-83.425000	499	98.4	177.6
7M	41.733333	-83.297167	2064	321.6	660.0
8M	41.788833	-83.355500	1109	192.0	369.6
1P	41.548667	-82.916667	384	79.2	139.2
4P	41.750000	-83.104167	10	4.8	4.8
5P	41.733333	-82.970833	0	0.0	0.0
6P	41.640333	-82.944500	250	55.2	93.6
7P	41.687500	-83.040333	763	139.2	261.6
N = 58		Mean (±SE)	358 ± 59	68.0 ± 9.6	124.7 ± 19.3

Table A2.9: Latitude and longitude (decimal degrees), larval density, and minimum and maximum estimated sediment suspension rates for summer 1997 larval densities. Larval density data is modified to reflect loss of larvae during the mass emergence period and subsequent survival from Chase 1998 and Schloesser et al. 2000. Site numbers are the identifiers used in the original data sources.

Site	Latitude	Longitude	1997 Density (after 60d)	Min. Sed. Susp. Rate ($g/m^2/d$)	Max. Sed. Susp. Rate ($g/m^2/d$)
ER01	41.967500	-83.183000	8	4.8	4.8
ER02	41.967167	-83.067667	74	19.2	26.4
ER03	41.967500	-82.967167	178	36.0	52.8
ER04	41.967333	-82.867000	208	38.4	60.0
ER05	41.967333	-82.765833	22	7.2	9.6
ER06	41.967333	-82.651333	6	2.4	4.8
ER07	41.900167	-83.283000	265	48.0	74.4
ER08	41.899500	-83.183500	153	31.2	48.0
ER09	41.900000	-83.068500	74	19.2	26.4
ER10	41.900000	-82.967667	65	16.8	24.0
ER11	41.900000	-82.866667	33	9.6	14.4
ER12	41.900333	-82.767167	0	0.0	0.0
ER13	41.899667	-82.651667	14	4.8	7.2
ER14	41.817167	-83.383500	424	67.2	108.0
ER15	41.817000	-83.282833	240	43.2	69.6
ER16	41.817167	-83.183167	117	26.4	38.4
ER17	41.817000	-83.068833	87	21.6	31.2
ER18	41.817167	-82.967333	169	33.6	50.4
ER19	41.816667	-82.867167	27	9.6	12.0
ER20	41.817167	-82.766500	11	4.8	7.2
ER21	41.733667	-83.383167	36	12.0	14.4
ER22	41.733500	-83.283333	443	69.6	112.8
ER23	41.733667	-83.183167	311	52.8	84.0
ER24	41.733500	-83.068333	0	0.0	0.0
ER25	41.734000	-82.968667	0	0.0	0.0
ER26	41.734000	-82.867000	60	16.8	21.6
ER27	41.733667	-82.766667	60	16.8	21.6
ER34	41.935000	-82.584500	6	2.4	4.8
ER35	42.000833	-82.651333	3	2.4	2.4
ER36	41.984833	-82.766833	52	14.4	19.2
ER37	41.861500	-82.599167	6	2.4	4.8
ER38	41.775167	-82.599333	6	2.4	4.8
ER39	41.695500	-82.599333	101	24.0	33.6
ER40	41.934167	-82.759500	6	2.4	4.8
ER41	41.852167	-82.706000	0	0.0	0.0
4R	41.880500	-83.297167	128	26.4	40.8
1T	41.696833	-83.468833	44	12.0	16.8
2T	41.742500	-83.447667	62	16.8	24.0
3T	41.736833	-83.462667	7	2.4	4.8
5B	41.691667	-82.766667	192	36.0	57.6
6B	41.866667	-82.816667	47	14.4	19.2
3D	41.938833	-82.202833	93	21.6	31.2
8D	41.955500	-83.119500	516	76.8	127.2
15D	42.033333	-83.152833	3	2.4	2.4
1K	41.750000	-82.750000	66	16.8	24.0
2K	41.766667	-82.866667	0	0.0	0.0
2L	41.797167	-83.230500	87	21.6	31.2
6L	41.847167	-83.116667	46	12.0	19.2
7L	41.816667	-83.000000	190	36.0	57.6
10L	41.894500	-82.986167	66	16.8	24.0
1M	41.713833	-83.425000	153	31.2	48.0
7M	41.733333	-83.297167	634	88.8	151.2
8M	41.788833	-83.355500	341	57.6	91.2
1P	41.548667	-82.916667	118	26.4	38.4
4P	41.750000	-83.104167	3	2.4	2.4
5P	41.733333	-82.970833	0	0.0	0.0
6P	41.640333	-82.944500	77	19.2	26.4
7P	41.687500	-83.040333	235	43.2	67.2
N = 58		Mean (± SE)	110 ± 18	21.4 ± 2.8	32.8 ± 4.5

Table A2.10: Latitude and longitude (decimal degrees), larval density, and minimum and maximum estimated sediment suspension rates for fall 1997 larval densities. Larval density data is from the 1998 spring sampling from J. J. H. Ciborowski unpublished and K. Kreiger unpublished. Site numbers are the identifiers used in the original data sources.

Site	Latitude	Longitude	Density (larvae/m²)	Min. Sed. Susp. Rate (g/m²/d)	Max. Sed. Susp. Rate (g/m²/d)
ER01	41.964347	-83.187333	0	0.0	0.0
ER02	41.964350	-83.071330	53	4.8	7.2
ER03	41.965355	-82.971327	142	9.6	14.4
ER04	41.964358	-82.871323	249	14.4	21.6
ER05	41.964362	-82.770320	151	9.6	16.8
ER06	41.964367	-82.655315	18	2.4	4.8
ER07	41.897338	-83.287332	71	7.2	9.6
ER08	41.897342	-83.188328	258	14.4	24.0
ER09	41.897347	-83.073325	89	7.2	12.0
ER10	41.897350	-82.972322	116	7.2	12.0
ER11	41.897353	-82.871318	116	7.2	12.0
ER12	41.897358	-82.771315	36	4.8	4.8
ER13	41.897362	-82.656312	27	2.4	4.8
ER14	41.814330	-83.388330	107	7.2	12.0
ER15	41.814333	-83.287327	444	19.2	33.6
ER16	41.814337	-83.187323	98	7.2	12.0
ER17	41.814342	-83.073320	89	7.2	12.0
ER18	41.814345	-82.971317	151	9.6	16.8
ER19	41.814348	-82.871313	18	2.4	4.8
ER20	41.814353	-82.771310	0	0.0	0.0
ER21	41.731325	-83.387323	0	0.0	0.0
ER22	41.731328	-83.287320	284	14.4	24.0
ER23	41.731332	-83.187317	204	12.0	19.2
ER24	41.731337	-83.072313	0	0.0	0.0
ER25	41.731340	-82.972310	0	0.0	0.0
ER26	41.731343	-82.871307	36	4.8	4.8
ER27	41.731348	-82.771303	160	9.6	16.8
ER30	41.648335	-82.972305	80	7.2	9.6
ER31	41.648338	-82.871302	107	7.2	12.0
ER32	41.648343	-82.771298	196	12.0	19.2
ER33	41.648347	-82.656295	9	2.4	2.4
ER34	41.932367	-82.589312	27	2.4	4.8
ER35	41.997368	-82.655318	27	2.4	4.8
ER36	41.981363	-82.771320	142	9.6	14.4
ER37	41.858362	-82.603307	0	0.0	0.0
ER38	41.772357	-82.603302	27	2.4	4.8
ER39	41.693352	-82.603295	18	2.4	4.8
ER40	41.931362	-82.713315	0	0.0	0.0
ER41	41.856357	-82.714310	9	2.4	2.4
4R	41.880500	-83.297167	5	2.4	2.4
1T	41.696833	-83.468833	5	2.4	2.4
2T	41.742500	-83.447667	38	4.8	7.2
3T	41.736833	-83.462667	10	2.4	2.4
5B	41.691667	-82.766667	240	14.4	21.6
6B	41.866667	-82.816667	72	7.2	9.6
3D	41.938833	-82.202833	298	14.4	26.4
8D	41.955500	-83.119500	250	14.4	21.6
15D	42.033333	-83.152833	5	2.4	2.4
1K	41.750000	-82.750000	302	14.4	26.4
2K	41.766667	-82.866667	14	2.4	2.4
2L	41.797167	-83.230500	259	14.4	24.0
6L	41.847167	-83.116667	34	4.8	4.8
7L	41.816667	-83.000000	110	7.2	12.0
10L	41.894500	-82.986167	38	4.8	7.2
1M	41.713833	-83.425000	494	21.6	36.0
7M	41.733333	-83.297167	518	21.6	38.4
8M	41.788833	-83.355500	394	19.2	31.2
1P	41.548667	-82.916667	115	7.2	12.0
4P	41.750000	-83.104167	5	2.4	2.4
5P	41.733333	-82.970833	0	0.0	0.0
6P	41.640333	-82.944500	86	7.2	9.6
7P	41.687500	-83.040333	173	9.6	16.8
N = 62		Mean (± SE)	113 ± 16	7.0 ± 0.7	11.3 ± 1.2

Table A2.11: Latitude and longitude (decimal degrees), larval density, and minimum and maximum estimated sediment suspension rates for early spring 1998 larval densities. Larval density data is from the 1998 spring sampling from J. J. H. Ciborowski unpublished and K. Kreiger unpublished. Site numbers are the identifiers used in the original data sources.

Site	Latitude	Longitude	Density (larvae/m^2)	Min. Sed. Susp. Rate (g/m^2/d)	Max. Sed. Susp. Rate (g/m^2/d)
ER01	41.964347	-83.187333	0	0.0	0.0
ER02	41.964350	-83.071330	53	2.4	4.8
ER03	41.965355	-82.971327	142	4.8	7.2
ER04	41.964358	-82.871323	249	7.2	12.0
ER05	41.964362	-82.770320	151	4.8	9.6
ER06	41.964367	-82.655315	18	2.4	2.4
ER07	41.897338	-83.287332	71	2.4	4.8
ER08	41.897342	-83.188328	258	7.2	12.0
ER09	41.897347	-83.073325	89	4.8	7.2
ER10	41.897350	-82.972322	116	4.8	7.2
ER11	41.897353	-82.871318	116	4.8	7.2
ER12	41.897358	-82.771315	36	2.4	2.4
ER13	41.897362	-82.656312	27	2.4	2.4
ER14	41.814330	-83.388330	107	4.8	7.2
ER15	41.814333	-83.287327	444	9.6	16.8
ER16	41.814337	-83.187323	98	4.8	7.2
ER17	41.814342	-83.073320	89	4.8	7.2
ER18	41.814345	-82.971317	151	4.8	9.6
ER19	41.814348	-82.871313	18	2.4	2.4
ER20	41.814353	-82.771310	0	0.0	0.0
ER21	41.731325	-83.387323	0	0.0	0.0
ER22	41.731328	-83.287320	284	7.2	14.4
ER23	41.731332	-83.187317	204	7.2	9.6
ER24	41.731337	-83.072313	0	0.0	0.0
ER25	41.731340	-82.972310	0	0.0	0.0
ER26	41.731343	-82.871307	36	2.4	2.4
ER27	41.731348	-82.771303	160	4.8	9.6
ER30	41.648335	-82.972305	80	2.4	4.8
ER31	41.648338	-82.871302	107	4.8	7.2
ER32	41.648343	-82.771298	196	7.2	9.6
ER33	41.648347	-82.656295	9	0.0	2.4
ER34	41.932367	-82.589312	27	2.4	2.4
ER35	41.997368	-82.655318	27	2.4	2.4
ER36	41.981363	-82.771320	142	4.8	7.2
ER37	41.858362	-82.603307	0	0.0	0.0
ER38	41.772357	-82.603302	27	2.4	2.4
ER39	41.693352	-82.603295	18	2.4	2.4
ER40	41.931362	-82.713315	0	0.0	0.0
ER41	41.856357	-82.714310	9	0.0	2.4
4R	41.880500	-83.297167	5	0.0	0.0
1T	41.696833	-83.468833	5	0.0	0.0
2T	41.742500	-83.447667	38	2.4	2.4
3T	41.736833	-83.462667	10	0.0	2.4
5B	41.691667	-82.766667	240	7.2	12.0
6B	41.866667	-82.816667	72	2.4	4.8
3D	41.938833	-82.202833	298	7.2	14.4
8D	41.955500	-83.119500	250	7.2	12.0
15D	42.033333	-83.152833	5	0.0	0.0
1K	41.750000	-82.750000	302	7.2	14.4
2K	41.766667	-82.866667	14	2.4	2.4
2L	41.797167	-83.230500	259	7.2	12.0
6L	41.847167	-83.116667	34	2.4	2.4
7L	41.816667	-83.000000	110	4.8	7.2
10L	41.894500	-82.986167	38	2.4	2.4
1M	41.713833	-83.425000	494	9.6	19.2
7M	41.733333	-83.297167	518	9.6	19.2
8M	41.788833	-83.355500	394	9.6	16.8
1P	41.548667	-82.916667	115	4.8	7.2
4P	41.750000	-83.104167	5	0.0	0.0
5P	41.733333	-82.970833	0	0.0	0.0
6P	41.640333	-82.944500	86	4.8	7.2
7P	41.687500	-83.040333	173	4.8	9.6
N = 62		Mean (± SE)	113 ± 16	3.7 ± 0.4	6.1 ± 0.7

APPENDIX 3: SEDIMENT SUSPENSION RATES FOR ALL LARVAL SIZE, LARVAL DENSITY AND WATER TEMPERATURE TREATMENTS FROM CHAPTER 2

Table A3.1: Initial burrow construction, maximum and minimum *Hexagenia* larval sediment suspension rates for each treatment used over the three trials of the larval size, larval density and water temperature experiment (Chapter 2). '--' represents treatments where no distinct total suspended solid asymptotes were observed for the respective sediment suspension rates.

Initial Burrow Construction Rate = Burrow Rate, Maximum (Hungry) Rate = Maximum Rate, Minimum (Fed) Rate = Minimum Rate

Trial No.	Water Temp. (°C)	Density (larvae/m²)	Length (mm)	Burrow Rate (g/m²/h)	Maximum Rate (g/m²/h)	Minimum Rate (g/m²/h)
1	10	70	12.5	0.1	0.0	0.1
1	10	139	12.5	0.1	0.0	0.0
1	10	278	12.5	0.0	0.0	0.0
1	10	556	12.5	0.1	-0.1	0.0
1	10	1111	12.5	0.1	0.0	0.1
1	10	70	17	0.3	0.1	0.2
1	10	278	17	0.0	0.0	0.0
1	10	1111	17	1.0	0.5	0.3
1	10	70	20.5	1.0	0.1	0.1
1	10	139	20.5	0.2	0.1	0.2
1	10	278	20.5	0.5	0.4	0.3
1	10	556	20.5	0.6	0.3	0.3
1	10	1111	20.5	1.2	0.7	0.5
1	10	70	23.5	0.2	0.1	0.0
1	10	278	23.5	0.2	0.1	0.0
1	10	556	23.5	0.7	0.0	-0.1
1	10	1111	23.5	0.9	0.8	0.4
1	10	139	27.5	0.2	0.2	0.3
1	10	278	27.5	0.2	0.0	0.1
1	10	556	27.5	1.0	0.5	0.4
1	15	70	12.5	0.4	0.3	0.4
1	15	139	12.5	0.5	0.2	0.1
1	15	278	12.5	0.6	0.8	0.3
1	15	556	12.5	0.3	0.5	0.4
1	15	1111	12.5	1.5	2.5	1.5
1	15	70	17	1.0	1.0	1.0
1	15	278	17	0.4	0.5	0.4
1	15	1111	17	1.4	1.9	1.0
1	15	70	20.5	1.4	1.5	1.8
1	15	139	20.5	0.9	0.3	0.2
1	15	278	20.5	1.2	1.4	1.2
1	15	556	20.5	1.3	1.2	0.9
1	15	1111	20.5	1.3	1.8	0.9
1	15	70	23.5	0.2	0.2	0.2
1	15	278	23.5	0.7	1.1	1.0

Table A3.1: Initial burrow construction, maximum and minimum *Hexagenia* larval sediment suspension rates for each treatment used over the three trials of the larval size, larval density and water temperature experiment (Chapter 2). '--' represents treatments where no distinct total suspended solid asymptotes were observed for the respective sediment suspension rates.

Initial Burrow Construction Rate = Burrow Rate, Maximum (Hungry) Rate = Maximum Rate, Minimum (Fed) Rate = Minimum Rate

Trial No.	Water Temp. (°C)	Density (larvae/m^2)	Length (mm)	Burrow Rate ($g/m^2/h$)	Maximum Rate ($g/m^2/h$)	Minimum Rate ($g/m^2/h$)
1	15	556	23.5	1.1	0.9	0.6
1	15	1111	23.5	4.5	2.8	1.5
1	15	139	27.5	0.7	0.2	0.2
1	15	278	27.5	1.3	0.5	0.2
1	19	70	12.5	0.6	0.3	0.2
1	19	139	12.5	0.1	0.1	0.1
1	19	278	12.5	0.4	0.4	0.2
1	19	556	12.5	1.2	4.0	2.1
1	19	1111	12.5	1.6	2.9	1.7
1	19	70	17	0.0	0.0	0.0
1	19	278	17	4.0	4.5	2.9
1	19	1111	17	2.0	4.7	2.5
1	19	70	20.5	0.4	0.6	0.5
1	19	139	20.5	0.5	0.7	0.5
1	19	278	20.5	2.1	2.4	2.0
1	19	556	20.5	1.3	1.7	1.2
1	19	1111	20.5	2.9	4.1	2.0
1	19	70	23.5	0.4	0.8	0.6
1	19	278	23.5	1.9	4.0	2.7
1	19	556	23.5	1.9	1.5	1.7
1	19	1111	23.5	25.5	21.4	12.3
1	19	139	27.5	0.6	0.4	0.3
1	19	278	27.5	1.0	1.2	1.0
1	22	70	12.5	0.2	0.4	0.3
1	22	139	12.5	0.2	0.2	0.1
1	22	278	12.5	0.3	2.5	1.8
1	22	556	12.5	0.4	1.2	0.3
1	22	1111	12.5	8.2	13.1	4.2
1	22	70	17	0.0	0.0	0.0
1	22	278	17	0.5	1.2	0.9
1	22	1111	17	8.3	13.7	7.4
1	22	70	20.5	0.2	0.4	0.1
1	22	139	20.5	1.0	1.9	1.7
1	22	278	20.5	1.6	4.4	2.9
1	22	556	20.5	3.7	13.4	8.5

Table A3.1: Initial burrow construction, maximum and minimum *Hexagenia* larval sediment suspension rates for each treatment used over the three trials of the larval size, larval density and water temperature experiment (Chapter 2). '--' represents treatments where no distinct total suspended solid asymptotes were observed for the respective sediment suspension rates.

Initial Burrow Construction Rate = Burrow Rate, Maximum (Hungry) Rate = Maximum Rate, Minimum (Fed) Rate = Minimum Rate

Trial No.	Water Temp. (°C)	Density (larvae/m²)	Length (mm)	Burrow Rate (g/m²/h)	Maximum Rate (g/m²/h)	Minimum Rate (g/m²/h)
1	22	1111	20.5	13.4	17.8	9.3
1	22	70	23.5	0.1	0.3	0.1
1	22	278	23.5	1.3	2.7	2.2
1	22	556	23.5	2.3	4.9	3.2
1	22	1111	23.5	9.2	10.0	5.9
1	22	139	27.5	1.1	2.3	1.9
1	22	278	27.5	3.8	4.5	4.0
1	25	70	12.5	0.1	0.0	0.0
1	25	139	12.5	0.2	0.5	0.3
1	25	278	12.5	0.4	1.3	0.8
1	25	556	12.5	2.1	6.3	2.8
1	25	1111	12.5	0.8	3.4	0.8
1	25	70	17	0.2	0.1	0.1
1	25	278	17	0.9	5.1	3.1
1	25	1111	17	8.4	41.4	16.2
1	25	70	20.5	0.2	0.5	0.5
1	25	139	20.5	1.3	3.0	2.9
1	25	278	20.5	1.9	3.2	2.2
1	25	556	20.5	4.0	8.0	4.5
1	25	1111	20.5	17.1	34.3	19.6
1	25	70	23.5	0.2	0.5	0.2
1	25	278	23.5	1.7	2.4	1.4
1	25	556	23.5	1.2	3.2	2.4
1	25	1111	23.5	17.7	19.6	13.8
1	25	139	27.5	0.8	2.1	1.8
1	25	278	27.5	0.5	1.1	0.9
1	25	556	27.5	6.1	8.1	5.4
2	10	70	12.5	0.2	0.3	0.3
2	10	139	12.5	0.2	0.3	0.3
2	10	278	12.5	0.2	0.1	--
2	10	556	12.5	0.2	0.3	0.1
2	10	1111	12.5	1.0	0.9	0.4
2	10	70	17	0.0	0.0	0.0
2	10	278	17	0.1	0.1	0.1
2	10	1111	17	0.9	0.5	0.2

Table A3.1: Initial burrow construction, maximum and minimum *Hexagenia* larval sediment suspension rates for each treatment used over the three trials of the larval size, larval density and water temperature experiment (Chapter 2). '--' represents treatments where no distinct total suspended solid asymptotes were observed for the respective sediment suspension rates.

Initial Burrow Construction Rate = Burrow Rate, Maximum (Hungry) Rate = Maximum Rate, Minimum (Fed) Rate = Minimum Rate

Trial No.	Water Temp. (°C)	Density (larvae/m^2)	Length (mm)	Burrow Rate (g/m^2/h)	Maximum Rate (g/m^2/h)	Minimum Rate (g/m^2/h)
2	10	70	20.5	0.4	0.3	0.2
2	10	139	20.5	0.1	0.1	0.0
2	10	278	20.5	0.3	0.2	0.1
2	10	556	20.5	0.8	0.7	0.3
2	10	1111	20.5	1.4	1.0	0.3
2	10	70	23.5	0.1	0.1	0.0
2	10	278	23.5	0.4	0.2	0.1
2	10	556	23.5	2.1	2.4	1.4
2	10	1111	23.5	2.8	1.2	0.4
2	10	70	27.5	0.0	0.0	0.0
2	10	139	27.5	0.3	0.2	0.2
2	10	278	27.5	0.5	0.2	0.1
2	10	556	27.5	1.9	0.6	0.2
2	15	70	12.5	0.1	0.1	0.0
2	15	139	12.5	0.3	0.4	0.4
2	15	278	12.5	0.1	0.1	0.0
2	15	556	12.5	0.1	0.1	0.0
2	15	1111	12.5	1.3	2.6	0.7
2	15	70	17	0.2	0.1	-0.1
2	15	278	17	0.2	0.6	0.5
2	15	1111	17	0.9	1.2	0.4
2	15	70	23.5	0.1	0.1	0.1
2	15	139	20.5	0.8	1.2	0.7
2	15	278	20.5	0.6	0.9	0.2
2	15	556	20.5	1.2	0.6	0.4
2	15	1111	20.5	2.8	2.4	0.8
2	15	70	20.5	0.2	0.1	0.1
2	15	278	23.5	0.5	0.7	0.3
2	15	556	23.5	2.1	2.1	0.6
2	15	1111	23.5	3.3	1.5	0.5
2	15	70	27.5	0.1	0.0	0.0
2	15	139	27.5	0.4	0.4	0.2
2	15	278	27.5	0.9	0.6	0.1
2	15	556	27.5	2.3	1.6	0.9
2	19	70	12.5	0.1	0.2	0.1

Table A3.1: Initial burrow construction, maximum and minimum *Hexagenia* larval sediment suspension rates for each treatment used over the three trials of the larval size, larval density and water temperature experiment (Chapter 2). '--' represents treatments where no distinct total suspended solid asymptotes were observed for the respective sediment suspension rates.

Initial Burrow Construction Rate = Burrow Rate, Maximum (Hungry) Rate = Maximum Rate, Minimum (Fed) Rate = Minimum Rate

Trial No.	Water Temp. (°C)	Density (larvae/m^2)	Length (mm)	Burrow Rate (g/m^2/h)	Maximum Rate (g/m^2/h)	Minimum Rate (g/m^2/h)
2	19	139	12.5	0.1	0.1	0.1
2	19	278	12.5	0.4	0.8	0.5
2	19	556	12.5	0.5	0.8	0.4
2	19	1111	12.5	0.8	1.6	0.6
2	19	70	17	0.1	0.1	0.1
2	19	278	17	0.3	0.2	0.2
2	19	1111	17	2.6	4.9	2.4
2	19	70	20.5	0.2	0.4	0.2
2	19	139	20.5	0.4	0.7	0.4
2	19	278	20.5	1.0	1.7	1.2
2	19	556	20.5	0.8	0.5	0.4
2	19	1111	20.5	3.6	4.3	2.2
2	19	70	23.5	0.3	0.5	0.4
2	19	278	23.5	1.3	1.8	0.8
2	19	556	23.5	2.2	1.9	0.9
2	19	1111	23.5	7.5	9.1	3.6
2	19	70	27.5	1.1	--	--
2	19	139	27.5	0.9	1.5	1.2
2	19	278	27.5	2.0	0.9	0.6
2	19	556	27.5	2.3	2.0	--
2	22	70	12.5	0.0	--	--
2	22	139	12.5	0.2	0.3	0.3
2	22	278	12.5	0.3	0.3	0.2
2	22	556	12.5	0.3	0.4	0.1
2	22	1111	12.5	1.7	2.2	0.9
2	22	70	17	0.4	0.7	0.6
2	22	278	17	0.6	0.5	0.4
2	22	1111	17	5.2	5.9	2.3
2	22	70	20.5	0.2	0.2	0.2
2	22	139	20.5	0.2	0.3	0.4
2	22	278	20.5	0.8	0.8	0.5
2	22	556	20.5	2.2	2.9	2.0
2	22	1111	20.5	3.7	3.8	2.1
2	22	70	23.5	3.7	13.2	6.6
2	22	278	23.5	0.4	0.3	0.2

Table A3.1: Initial burrow construction, maximum and minimum *Hexagenia* larval sediment suspension rates for each treatment used over the three trials of the larval size, larval density and water temperature experiment (Chapter 2). '--' represents treatments where no distinct total suspended solid asymptotes were observed for the respective sediment suspension rates.

Initial Burrow Construction Rate = Burrow Rate, Maximum (Hungry) Rate = Maximum Rate, Minimum (Fed) Rate = Minimum Rate

Trial No.	Water Temp. (°C)	Density (larvae/m²)	Length (mm)	Burrow Rate (g/m²/h)	Maximum Rate (g/m²/h)	Minimum Rate (g/m²/h)
2	22	556	23.5	4.6	4.5	2.8
2	22	1111	23.5	7.9	6.1	4.9
2	22	70	27.5	0.2	0.5	0.5
2	22	139	27.5	0.6	0.7	0.7
2	22	278	27.5	0.5	0.6	0.4
2	22	556	27.5	1.9	1.4	0.9
2	25	70	12.5	0.1	0.1	0.1
2	25	139	12.5	0.1	0.1	0.1
2	25	278	12.5	0.6	0.5	0.4
2	25	556	12.5	0.6	0.7	0.4
2	25	1111	12.5	0.5	1.0	0.4
2	25	70	17	0.3	0.6	0.4
2	25	278	17	0.6	0.8	0.5
2	25	1111	17	4.4	4.9	2.0
2	25	70	20.5	0.5	0.5	0.2
2	25	139	20.5	0.5	--	--
2	25	278	20.5	2.3	4.4	3.0
2	25	556	20.5	1.5	2.6	2.1
2	25	1111	20.5	3.8	5.9	3.5
2	25	70	23.5	0.1	0.3	--
2	25	278	23.5	2.3	5.0	3.4
2	25	556	23.5	4.3	8.3	4.5
2	25	1111	23.5	8.8	10.4	20.6
2	25	70	27.5	0.1	0.3	0.3
2	25	139	27.5	0.2	0.2	0.1
2	25	278	27.5	1.8	5.2	2.9
2	25	556	27.5	1.7	2.5	1.9
3	10	70	12.5	0.0	0.0	0.0
3	10	139	12.5	0.0	0.0	0.0
3	10	278	12.5	0.0	0.0	0.0
3	10	556	12.5	0.2	0.4	0.1
3	10	70	17	0.0	0.0	0.0
3	10	139	17	0.0	0.0	0.0
3	10	278	17	0.1	0.0	0.0
3	10	556	17	1.2	0.6	0.0

Table A3.1: Initial burrow construction, maximum and minimum *Hexagenia* larval sediment suspension rates for each treatment used over the three trials of the larval size, larval density and water temperature experiment (Chapter 2). '--' represents treatments where no distinct total suspended solid asymptotes were observed for the respective sediment suspension rates.

Initial Burrow Construction Rate = Burrow Rate, Maximum (Hungry) Rate = Maximum Rate, Minimum (Fed) Rate = Minimum Rate

Trial No.	Water Temp. (°C)	Density (larvae/m²)	Length (mm)	Burrow Rate (g/m²/h)	Maximum Rate (g/m²/h)	Minimum Rate (g/m²/h)
3	10	1111	17	1.1	1.9	0.4
3	10	70	20.5	0.1	0.1	0.0
3	10	139	20.5	0.2	0.5	0.2
3	10	278	20.5	0.2	0.8	0.5
3	10	556	20.5	1.3	2.9	1.0
3	10	1111	20.5	1.7	2.2	0.7
3	10	70	23.5	0.1	0.6	0.3
3	10	139	23.5	0.0	0.1	0.1
3	10	278	23.5	0.3	0.5	0.0
3	10	556	23.5	0.9	1.1	0.3
3	10	1111	23.5	1.6	1.0	0.4
3	10	70	27.5	0.1	0.1	0.0
3	10	556	27.5	1.4	0.8	0.4
3	15	70	12.5	0.0	0.0	0.0
3	15	139	12.5	0.0	0.1	0.0
3	15	278	12.5	0.1	0.1	0.1
3	15	556	12.5	1.1	9.1	3.5
3	15	70	17	0.1	0.3	0.2
3	15	139	17	2.2	8.7	7.1
3	15	278	17	0.8	2.5	1.3
3	15	556	17	1.1	2.7	1.2
3	15	1111	17	1.3	3.1	1.1
3	15	70	20.5	0.1	0.2	0.2
3	15	139	20.5	0.2	0.1	0.1
3	15	278	20.5	0.6	0.9	0.5
3	15	556	20.5	1.3	1.4	0.7
3	15	1111	20.5	3.1	2.7	0.9
3	15	70	23.5	0.0	0.1	0.0
3	15	139	23.5	0.1	0.1	0.1
3	15	278	23.5	0.1	0.6	0.4
3	15	556	23.5	1.1	2.4	1.1
3	15	1111	23.5	1.1	1.7	1.0
3	15	70	27.5	0.2	--	--
3	19	70	12.5	0.0	0.0	0.0
3	19	139	12.5	0.0	0.0	0.0

Table A3.1: Initial burrow construction, maximum and minimum *Hexagenia* larval sediment suspension rates for each treatment used over the three trials of the larval size, larval density and water temperature experiment (Chapter 2). '--' represents treatments where no distinct total suspended solid asymptotes were observed for the respective sediment suspension rates.

Initial Burrow Construction Rate = Burrow Rate, Maximum (Hungry) Rate = Maximum Rate, Minimum (Fed) Rate = Minimum Rate

Trial No.	Water Temp. (°C)	Density (larvae/m^2)	Length (mm)	Burrow Rate ($g/m^2/h$)	Maximum Rate ($g/m^2/h$)	Minimum Rate ($g/m^2/h$)
3	19	278	12.5	0.0	0.0	0.0
3	19	556	12.5	0.1	0.5	0.2
3	19	70	17	0.2	0.2	0.2
3	19	139	17	0.1	0.0	0.0
3	19	278	17	--	--	--
3	19	556	17	0.6	2.5	1.2
3	19	1111	17	3.0	4.4	1.5
3	19	70	20.5	0.0	--	--
3	19	139	20.5	0.1	0.2	0.2
3	19	278	20.5	0.2	0.6	0.3
3	19	556	20.5	2.0	7.0	3.6
3	19	1111	20.5	3.4	6.4	2.1
3	19	70	23.5	0.2	0.9	0.5
3	19	139	23.5	0.2	0.2	0.2
3	19	278	23.5	0.7	0.5	0.4
3	19	556	23.5	1.2	1.8	0.6
3	19	1111	23.5	4.5	5.0	2.9
3	19	70	27.5	0.1	0.2	0.1
3	22	70	12.5	0.0	0.1	0.0
3	22	139	12.5	0.2	0.4	0.3
3	22	278	12.5	0.1	0.2	0.1
3	22	556	12.5	2.4	46.5	19.0
3	22	70	17	0.2	0.2	--
3	22	139	17	0.0	0.1	0.0
3	22	278	17	0.5	0.7	0.5
3	22	556	17	8.6	42.4	21.0
3	22	1111	17	4.8	8.9	4.3
3	22	70	20.5	0.2	--	--
3	22	139	20.5	0.1	0.3	0.3
3	22	278	20.5	0.9	1.5	0.9
3	22	556	20.5	4.4	7.6	4.9
3	22	1111	20.5	2.5	3.6	1.7
3	22	70	23.5	0.1	0.6	0.5
3	22	139	23.5	0.1	0.6	0.4
3	22	278	23.5	0.9	2.9	2.4

Table A3.1: Initial burrow construction, maximum and minimum *Hexagenia* larval sediment suspension rates for each treatment used over the three trials of the larval size, larval density and water temperature experiment (Chapter 2). '--' represents treatments where no distinct total suspended solid asymptotes were observed for the respective sediment suspension rates.

Initial Burrow Construction Rate = Burrow Rate, Maximum (Hungry) Rate = Maximum Rate, Minimum (Fed) Rate = Minimum Rate

Trial No.	Water Temp. (°C)	Density (larvae/m²)	Length (mm)	Burrow Rate (g/m²/h)	Maximum Rate (g/m²/h)	Minimum Rate (g/m²/h)
3	22	556	23.5	1.0	0.9	0.7
3	22	1111	23.5	--	--	--
3	22	70	27.5	0.1	0.3	0.3
3	22	556	27.5	4.0	4.6	2.3
3	25	70	12.5	0.0	--	--
3	25	139	12.5	0.0	0.0	0.0
3	25	278	12.5	0.1	0.3	0.1
3	25	556	12.5	0.1	0.1	0.0
3	25	1111	12.5	0.6	0.6	0.2
3	25	70	17	0.1	--	--
3	25	278	17	0.9	0.9	0.6
3	25	1111	17	1.6	1.4	0.6
3	25	70	20.5	0.1	--	--
3	25	139	20.5	0.2	0.4	0.3
3	25	278	20.5	0.6	0.6	0.4
3	25	556	20.5	1.0	4.7	3.0
3	25	1111	20.5	5.4	7.9	3.9
3	25	70	23.5	0.4	--	--
3	25	139	23.5	0.8	0.1	0.1
3	25	278	23.5	0.5	0.5	0.4
3	25	556	23.5	2.0	4.0	2.7
3	25	1111	23.5	3.7	--	--
3	25	70	27.5	0.6	3.5	3.0
3	25	556	27.5	4.3	5.0	3.5