Do Tube-dwelling Midges Inhibit the Establishment of Burrowing Mayflies?

Wes Plant, Jan J.H. Ciborowski, and Lynda D. Corkum[*]

Department of Biological Sciences
University of Windsor
Windsor, Ontario N9B 3P4

ABSTRACT. *There are some locations in Lake Erie where, despite the presence of suitable habitat, mayfly* (Hexagenia) *nymphal density is low or absent, and midge (Chironomidae) larval density is high. We conducted laboratory experiments to determine if biotic interactions account for this spatial distribution. In the first experiment, we measured the effect of* Hexagenia *(0, 256, 512, 768, 1,024 nymphs m^{-2}) and* Chironomus *(5,120, 2,560, 1,280, 640, 0 larvae m^{-2}) density on survivorship and increase in body length of newly-hatched and large* Hexagenia *nymphs. Results did not suggest competition for space. Since the outcome of competition may be influenced by order of establishment, we tested temporal overlap by adding* Chironomus *larvae to containers with* Hexagenia *nymphs at different stages in their development and vice versa (experiment 2). Newly-hatched mayflies showed the smallest increase in body length after being exposed to midges after 0 and 10 days, but exhibited no significant difference from the control after 20, 40, and 60 days of exposure to midges. In experiment 3, we tested if* Hexagenia *or* Chironomus *larvae ate mayfly eggs.* Chironomus *larvae significantly reduced the number of* Hexagenia *eggs at densities examined and we speculate that the reduction occurred because of egg consumption. In contrast, the number of eggs remaining in the presence of a* Hexagenia *nymph did not differ significantly from the control. We confirmed that midges were present in Lake Erie sediments when* Hexagenia *oviposit. These findings suggest that tube-dwelling* Chironomus *larvae may contribute to the inability of* Hexagenia *to become established in certain locations in western Lake Erie.*

INDEX WORDS: *Competition, temporal overlap, predation,* Chironomus, Hexagenia, *Lake Erie.*

INTRODUCTION

Lake Erie has undergone major changes during the last century due to cultural eutrophication, sediment contamination, and establishment of invasive species, resulting in substantial impacts on aquatic communities (Makarewicz and Bertram 1991, Tyson and Knight 2001). *Hexagenia* mayflies were formerly a prominent component of the benthic fauna of Lake Erie (Reynoldson and Hamilton 1993), and their near extirpation from the western basin that began in the mid-1950s was attributed to anoxia in bottom waters (Britt 1955). There was a shift in the benthic community from *Hexagenia* and *Oecetis* (caddisfly) in the 1930s to one dominated by chironomids and oligochaetes in the 1960s (Shelford and Boesel 1942, Carr and Hiltunen 1965). *Hexagenia* nymphs were rarely reported from open waters of western Lake Erie from 1965

to 1992 (Schloesser *et al.* 2000), but monitoring of mayflies since the early 1990s showed that nymphs increased from near to off-shore areas, recovering to former mean density levels (350 nymphs m^{-2}) at many locations in the basin (Krieger *et al.* 1996, Corkum *et al.* 1997a, Schloesser *et al.* 2000). The recovery of *Hexagenia* is attributed to effects of phosphorus abatement programs on water quality and the ability of zebra mussels, *Dreissena polymorpha*, to remove suspended sediments and plankton from the water column (Corkum *et al.* 1997a).

Recent observations indicate that high densities of both *Hexagenia* and *Chironomus* larvae do not co-occur in western Lake Erie. For example, field surveys of benthic invertebrates in western Lake Erie show that when density of larval chironomids is high (> 550 larvae/m^2), the density of *Hexagenia* nymphs is low and *vice versa* (Fig. 1). Additionally, there are areas in western Lake Erie (Pigeon Bay and south of Middle Sister and East Sister islands),
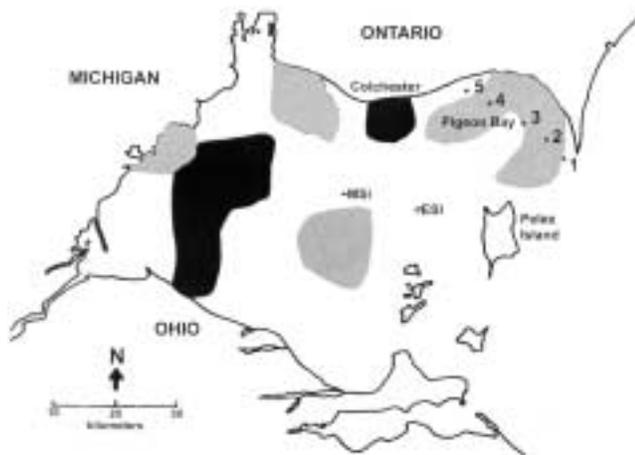
FIG. 1.   Delineated areas of Hexagenia *nymphs (black) where density is > 550 nymphs per m² and chironomid larvae (gray) where density is > 550 larvae per m². Data were collected in spring 1998 by J.J.H. Ciborowski. Five replicate Ponar grabs were taken at each of five sites in Pigeon Bay. MSI, Middle Sister Island; ESI, East Sister Island.*

where *Hexagenia* nymphal density is low or absent when *Chironomus* larvae are present (Ciborowski, unpublished data). Gerlofsma (1999) demonstrated that, although substrate type is suitable for burrowing mayflies in these locations, the reduction or absence of *Hexagenia* was not attributed to anoxia, contaminated sediments, or lack of oviposition events. These findings led us to think that biotic interactions may account for the differences in spatial distribution between taxa.

Because *Hexagenia* and *Chironomus* larvae occupy similar clay/mud substrate types and exhibit overlapping burrowing depths (Charbonneau and Hare 1998, Matisoff and Wang 2000), these taxa may compete for space. Competition also may be influenced by temporal overlap during key times in development. Specifically, the success of a given taxon could decline if it colonized a habitat at increasingly later times than an earlier colonizing competitor (Alford 1989). Although competition for food between *Chironomus* and *Hexagenia* is unlikely because diets of these taxa differ (Kajak and Warda 1968, Coffman and Ferrington 1996), areas of western Lake Erie where *Hexagenia* failed to recover, but where *Chironomus* prevail, could result from predation rather than competitive events.

We conducted a series of experiments to determine if biological processes could potentially account for the spatial distribution of *Hexagenia*

relative to *Chironomus* in the western basin of Lake Erie. Each experiment separately tested the following three hypotheses: competitive interactions, temporal overlap, predation events. We also collected samples to confirm the relative abundance of *Hexagenia* and chironomids in an area where *Hexagenia* is presumed to oviposit.

METHODS

Experimental Animals

Newly-hatched nymphs were obtained by collecting *Hexagenia* female imagos at Colchester Harbour (northwestern shore of Lake Erie), Ontario, Canada (41°59′N, 82°56′W) after sunset throughout June 2001. Female imagos were placed into 2-L polyethylene bags containing aerated, dechlorinated water into which they oviposited. Since both *H. limbata* and *H. rigida* occur at the study site and the taxonomic distinction of female adults is not possible (Edmunds *et al.* 1976), eggs from 30 females were thoroughly mixed to ensure that all treatments were comparable. Eggs were kept at 20°C for 6 d, at 14°C for 6 d, and then stored at 8°C, a temperature that induces dormancy, until required (Friesen 1981). To obtain day-old nymphs, several hundred eggs were placed into Petri dishes at room temperature and monitored daily for hatching.

Large *Hexagenia* nymphs were collected from Lake St. Clair at Walpole Island, near Wallaceburg, Ontario, Canada (42°38′N, 82°28′W). Nymphs were obtained by wading and sampling nearshore using dip nets. Nymphs were transported to the laboratory in coolers containing aerated river water and 2-cm lengths (0.5 cm inner diameter) of plastic tubing into which individual nymphs "burrowed." Nymphs were held in 40-L tanks containing Lake Erie sediment for 2 weeks before experiments began.

Larvae of *Chironomus riparius*, a non-biting midge, were reared from egg masses (obtained from the Canada Centre for Inland Waters) in 38-L glass covered tanks with silica sand for burrowing. At room temperature, the life cycle is usually completed in about 4 weeks. Study organisms were fed based on initial densities per container and given a mixture of 10 g Tetramin® fish food, 7 g baker's yeast, and 7 g alfalfa pellets dissolved in 500 mL distilled water (Hanes and Ciborowski 1992).

Competitive Interactions (Experiment 1)

The experiment was conducted in 2-L glass containers with aerated dechlorinated water at 16 h L: 8

TABLE 1. *Summary of experimental treatments with numbers of* **Hexagenia** *nymphs and* **Chironomus** *larvae in 2-L glass containers (surface area: 156.25 cm²) and equivalent field densities, number per m² (in parentheses), used to determine survivorship and growth of* **Hexagenia** *and survivorship of* **Chironomus.**

	Treatment						
Taxa	1	2	3	4	5	6	7
Hexagenia	0	4	8	12	16	8	0
	(0)	(256)	(512)	(768)	(1,024)	(512)	(0)
Chironomus	80	40	20	10	0	0	20
	(5,120)	(2,560)	(1,280)	(640)	(0)	(0)	(1,280)

h D and 23°C to represent summer field conditions. Five cm of natural clay/mud sediment from western Lake Erie (collected offshore from Colchester) were placed into each container to provide sufficient volume for burrowing (Hanes and Ciborowski 1992). Before adding Lake Erie sediment to containers, we froze it to kill any macroinvertebrates and later washed the thawed sediment through a 125 μm sieve to remove dead organisms. Three mL of food were added to each container 1 week before an experiment began. Food was added twice weekly. Newly-hatched *Hexagenia* nymphs and *Chironomus* were fed 7 mL/organism; large *Hexagenia* nymphs were fed 14 mL/organism.

We examined survivorship and increase in body length of *Hexagenia* nymphs and *Chironomus riparius* larvae reared together using seven combinations of densities with five replicates per treatment (Table 1). Laboratory densities were selected to represent the range of densities for these taxa found in western Lake Erie. Controls with a single taxon were examined to determine density dependent effects on survivorship and growth. We studied the effects of *Chironomus* larvae (mean ± SE: 9.6 ± 1.5 mm in body length, BL) on large *Hexagenia* nymphs (20.0 ± 3.1 mm BL excluding cerci) for 60 d, 28 September to 27 November (Trial 1) and on day-old *Hexagenia* nymphs (1.0 ± 0.1 mm BL excluding cerci) for 90 d, 19 July to 15 October (Trial 2). The effects of large *Hexagenia* nymphs on second instar larval *Chironomus* were determined for 30 d (31 October to 30 November) (Trial 3).

Temporal Overlap (Experiment 2)

Since the outcome of competition may be influenced by the order of establishment, we tested ef-

fects of *Chironomus riparius* larvae on growth and survivorship of *Hexagenia* nymphs by introducing midges at different times during mayfly development. We set up 2-L glass containers with washed and sieved Lake Erie sediment (7 cases (6 treatments + one control) × 2 sizes of *Hexagenia* × 5 replicates). Containers with either 8 newly-hatched or 8 large *Hexagenia* nymphs (512 m⁻²) were inoculated with 20 larval *Chironomus* (1,280 m⁻²) throughout the 61 d experiment (Table 2). A minimum of 8 mayfly nymphs per container was used to avoid Allee effects, i.e., increased mortality at low density (Hanes and Ciborowski 1992). The experiment was conducted with day-old *Hexagenia* nymphs (18 July to 18 September) and large *Hexagenia* nymphs (10 August to 10 October). We also examined effects of adding *Hexagenia* nymphs at different times in the development of *Chironomus* larvae on midge survivorship. Containers with 20 *Chironomus* larvae were inoculated with eight large *Hexagenia* nymphs on day 0, 5, 10, 15, 20, 30 (five

TABLE 2. *Containers with Hexagenia nymphs were inoculated with 20 Chironomus larvae at different days during mayfly development (n = 5 replicates). Small and large Hexagenia were tested separately. The experiment ended on day 61.*

Day of *Chironomus* Inoculation	Time (d) exposed to *Chironomus*
Control	Control
0	61
10	51
20	41
30	31
40	21
60	1

replicates each). This experiment (conducted from 19 November to 20 December) ended on day 31 to account for the shorter life span of *Chironomus*.

Predation (Experiment 3)

To determine if midges or mayflies ate *Hexagenia* eggs, we added 10 (2,923 m^{-2}), 30 (8,769 m^{-2}), or 50 (14,615 m^{-2}) *Hexagenia* eggs to sediment cores for 48 h with 1 *Chironomus* larva, 1 *Hexagenia* nymph, or neither organism present. *Hexagenia* egg densities were within observed field densities. A survey of sediments (11 July 2000) from Colchester Harbour 4 km lakeward into the western basin of Lake Erie showed that *Hexagenia* eggs densities were 14,890 ($\pm$ 2,510) m^{-2} (Corkum unpublished).

In the laboratory, we placed 45 cores (3 densities $\times$ 3 treatments $\times$ 5 replicates) in large opaque plastic containers to block out light, mimicking field conditions. Cores were 25.5 cm long (inner diameter 6.5 cm) and filled with 4 cm of natural western Lake Erie sediment that was previously frozen and sieved (125 μm mesh) to eliminate organisms. The water in the sediment cores was aerated using capillary tubing for 1 week. We turned off the air to add the eggs and larvae to the cores using a wide-mouth pipette and checked the pipettes afterwards using a microscope to ensure that all individuals were added. *Chironomus* larvae were obtained from cultures grown in the laboratory from egg masses collected from females that emerged from the western basin of Lake Erie. *Hexagenia* nymphs were collected from Lake St. Clair near Walpole Island (previously described). After 48 h, sediment was washed through a 90 μm sieve and a dye, lignin pink, was added to stain the *Hexagenia* eggs to facilitate recovery. Eggs were recovered by sorting through the sediment using a dissection microscope.

To confirm the relative abundance of mayflies and midges in the clay/mud sediment of Lake Erie in areas where *Hexagenia* oviposit but where mayfly density is low, we took five petite Ponar samples (225 cm^2 jaw opening) at each of five stations along a transect in Pigeon Bay, 25 July 2001 (Fig. 1). Samples were taken after the mating swarm of mayflies and before most eggs would have hatched. Ponar samples were washed through a 250 μm sieve bucket in the field and preserved. Samples were sorted for mayflies and midges in the laboratory.

Data for the three experiments were analysed using a one-way ANOVA with planned comparison tests. Survivorship and increase in length were analysed for *Hexagenia* nymphs; survivorship was analysed for *Chironomus* in experiments 1 and 2.

RESULTS

Competitive Interactions

There were significant differences (P < 0.025) in mean survivorship of newly-hatched mayflies when they were exposed to larval *Chironomus*. The 4 *Hexagenia* – 40 *Chironomus* treatment with the greatest number of organisms had the highest mayfly survivorship (95 $\pm$ 5.0%). In contrast, the control (8 *Hexagenia* – 0 *Chironomus*) with the fewest number of organisms had the lowest mayfly survivorship (50 $\pm$ 13.1%). Of the planned comparisons, two were significant (4 *Hexagenia* – 40 *Chironomus* vs. others, P < 0.025; and, 16 *Hexagenia* – 0 *Chironomus* vs. 8 *Hexagenia* – 0 *Chironomus*, P < 0.025). There were no significant differences in mean increase of newly-hatched *Hexagenia* body lengths among any of the treatments and no planned comparisons were significant.

Larval *Chironomus* had no effect on survivorship (55 $\pm$ 11.6% to 67 $\pm$ 10.2%) of large *Hexagenia* nymphs (P > 0.05). Similarly, larval *Chironomus* had no significant effect on increase in body length of large *Hexagenia* nymphs among treatments.

Survivorship of *Chironomus* larvae in the 30-day competitive interaction experiment was not significantly different in the presence of large *Hexagenia* nymphs (P > 0.05). Overall, *Chironomus* survivorship was high, ranging from 90 $\pm$ 3.5% to 96 $\pm$ 2.9%.

Temporal Overlap

Chironomus larvae significantly inhibited the growth of newly-hatched *Hexagenia* (P < 0.005) when *Chironomus* larvae were added to cultures of mayflies early in their life cycle (Fig. 2). Newly-hatched mayflies showed the smallest increase in body length after being exposed to *Chironomus* after 0 and 10 days, but exhibited no significant difference from the control after 20, 40, and 60 days of exposure to midges. Survivorship of newly-hatched *Hexagenia* nymphs was not affected by exposure to *Chironomus* larvae. Neither change in body length nor survivorship of large *Hexagenia* differed when *Chironomus* larvae were added to mayfly cultures on different days.

Addition of large *Hexagenia* nymphs (effects of day-old nymphs on midges were not examined) had
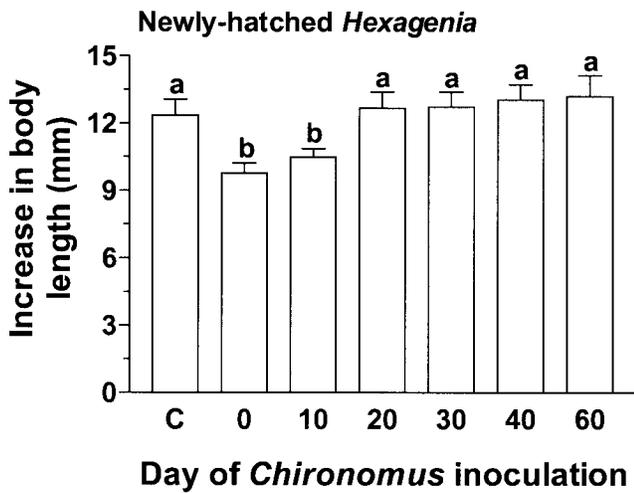
Newly-hatched *Hexagenia*

FIG. 2. *Treatments showing effect of* **Chironomus** *on increase in body length of newly-hatched* **Hexagenia** *nymphs. C = control (8* **Hexagenia** *nymphs and no* **Chironomus** *larvae added). There were no significant differences among treatments labeled "a." Treatments labeled "b" showed significantly reduced body length.*

no effect on survivorship of *Chironomus* larvae, regardless of when mayflies were added to the midge cultures (P > 0.05).

Predation

In all cases, the mean number of *Hexagenia* eggs remaining in cores was significantly reduced in the presence of *Chironomus* (10 eggs/core, $F_{2, 13}$ = 7.189, P = 0.01; 30 eggs/core, $F_{2, 14}$ = 24.21, P < 0.001; and, 50 eggs/ core, $F_{2, 14}$ = 19.872, P < 0.001). In contrast, the number of eggs in the presence of a *Hexagenia* nymph was not significantly different from controls (Fig. 3).

Our field collections at sites in Pigeon Bay of western Lake Erie revealed relatively low *Hexagenia* densities and higher chironomid densities (Fig. 4). At three sites, mean density of chironomids (midges) was significantly greater than mayflies (site 2, t = 4.743, P < 0.005; site 4, t = 3.737, P < 0.025; site 5, t = 4.566, P < 0.005). There were no significant differences in densities of midges and mayflies at the remaining two sites. The maximum mean (±SE) density of mayflies was 169 (59) nymphs m^{-2} (site 3), well below the historical mean density of 350 nymphs m^{-2}. Maximum density of chironomids was 852 (148) larvae m^{-2} (site 5).
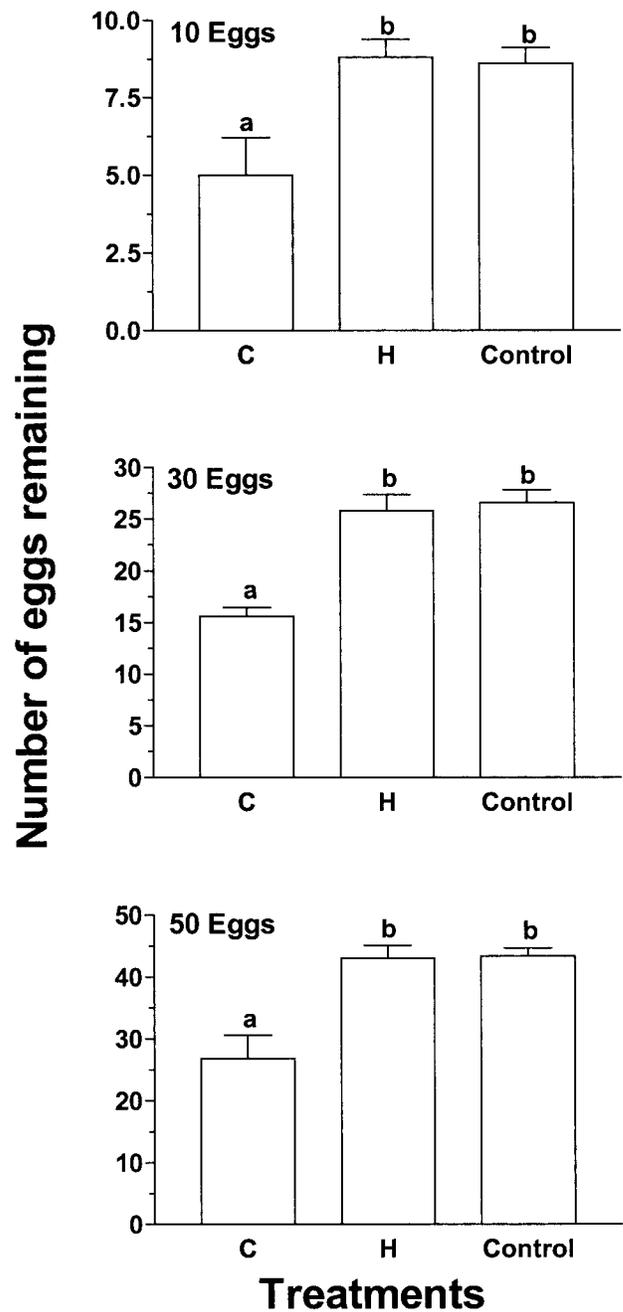

FIG. 3. *Number of* **Hexagenia** *eggs remaining in cores after 48-h trials at three egg densities with one* **Chironomus** *(C) larva, one* **Hexagenia** *(H) nymph, and no fauna (Control). There were five replicates per treatment. In each case, there were significantly fewer* **Hexagenia** *eggs in the treatment with one* **Chironomus** *(a) than the other two treatments (b).*
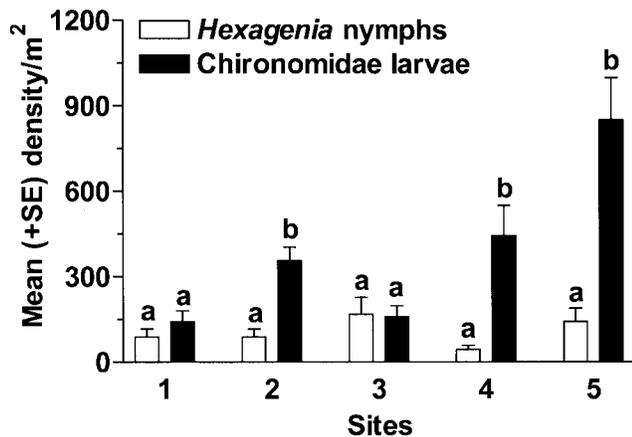
FIG. 4. *Mean (+SE) density per m² of Chironomidae and* **Hexagenia** *spp. at five sites in Pigeon Bay of western Lake Erie. There was no significant difference between mean density of taxa (labeled "a") at sites 1 and 3. Significant differences between mean density of taxa (labeled "a" and "b") were recorded at the remaining three sites.*

DISCUSSION

Although we anticipated competition for space between *Chironomus* larvae and *Hexagenia* nymphs, neither survivorship nor increases in body length differed between treatment and control for small or large *Hexagenia* nymphs when added simultaneously with *Chironomus*. In fact, treatments with the highest ratio of *Chironomus* larvae to *Hexagenia* nymphs resulted in the highest survivorship of small mayflies. In other experiments, the effect of large *Hexagenia* nymphs had no effect on the survivorship of *Chironomus* larvae. Although *Chironomus* and *Hexagenia* have overlapping mean burrowing depths between 4.5 and 5.5 cm, *Hexagenia* are known to exceed all other taxa in the depth and lengths of burrows constructed (Charbonneau *et al.* 1997). This suggests that mayflies may be able to avoid midges in Lake Erie by burrowing deeper in the sediment.

The lack of competitive interactions between *Hexagenia* and *Chironomus* in the present study also may be explained by the amount of time spent in burrows. Charbonneau *et al.* (1997) confirmed that *Hexagenia limbata* are not required to leave the sediment to construct new burrows; rather, nymphs create new burrows below existing ones. In contrast, some chironomid larvae are known to expose up to 75% of their body as they sometimes "flick

out" of their burrows to feed (Walshe 1947, Dillon 1985, Hershey 1987). The mucous tubes constructed by chironomids, which protect the midges from predators (Dillon 1985), may create a barrier between organisms of the same feeding guild.

Our results from the temporal overlap experiment showed that newly-hatched mayfly nymphs exposed to *Chironomus* larvae on days 0 and 10 exhibited a diminished increase in body length relative to the control, suggesting that biotic interactions have important life history implications for *Hexagenia.* The outcome of interactions may result in increased maintenance costs related to burrow construction, resulting in less time available to feed (Cuker 1983). Also, *Hexagenia* nymphs whose early growth is reduced in the presence of *Chironomus* larvae would be expected to emerge later. Later emerging adults would be less fecund, less likely to find a mate and more susceptible to predation.

Arrival of species in new habitats is often a function of their breeding activities and migration patterns. However, differences in life history events between taxa also reflect the response of a species to environmental variables or seasonal changes. Seasonal effects are distinct from temporal overlap, whose outcome depends on arrival times or activity of interacting taxa (Lawler and Morin 1993). In Lake Erie, peak *Chironomus* emergence occurs in late April or May (Hilsenhoff 1966, Plant personal observation), whereas mass *Hexagenia* mating swarms are present from mid-June to early July (Corkum *et al.* 1997b), beginning when water temperatures reach 20°C (Corkum, personal observation). Early *Chironomus* instars are metabolically active in spring when lake temperatures are about 12°C, a temperature at which no mayfly growth occurs (Corkum and Hanes 1992). Thus, *Chironomus* larvae have an advantage over mayflies as they colonize new habitats (Soster and McCall 1990). Even if organisms do not interact directly, the presence of other organisms burrowing in the sediment affects the suitability of the mud for other colonizers (Wilson 1991).

Large numbers of *Hexagenia* eggs are oviposited in western Lake Erie during mayfly swarms in mid June to early July. *Hexagenia* eggs settle in the mud and hatch in about 2 weeks at about 20°C (Hunt 1953, Corkum *et al.* 1997b). Our present field study confirmed that chironomid larvae are present in western Lake Erie in July, indicating a potential for interaction between larval midges and mayfly eggs. In the laboratory, we found that *Chironomus* larvae significantly reduced numbers of *Hexagenia* eggs at

all three egg densities examined, and we speculate that this reduction occurred because of active egg consumption.

Although *Hexagenia* nymphs did not consume *Hexagenia* eggs, nymphal burrowing activity may affect the viability and hatching of mayfly eggs. Gerlosfma (1999) showed that the burrowing activity of *Hexagenia* nymphs buried eggs deeper into the substrate. Egg burial could delay or prevent hatching of mayfly nymphs especially in deep sediments where anoxic conditions prevail (Fremling 1967). This scenario has been documented in other animals (copepods, Lutz *et al.* 1992, halibut, Helvik and Walther 1993, lake herring, Brooke and Colby 1980).

Soster and McCall (1990) showed that maximum density of *Chironomus plumosus* larvae occurred in western Lake Erie in late October (4,673 ± 2,850 individuals.m^{-2}), but larvae were also abundant from mid-July (2,109 ± 499 individuals.m^{-2}) to early August (5,695 ± 1,103 individuals.m^{-2}), a time that corresponds to the maximum abundance of *Hexagenia* eggs on the bottom sediments. Schloesser and Nalepa (2001) suggested that recruitment of *Hexagenia* depends on the success of emergence, mating, egg deposition, and hatching. Additionally, *Hexagenia* eggs will not survive in areas of high predator density. Predation by *Chironomus* larvae on *Hexagenia* eggs at times when both midge larval density and mayfly egg density are high could account for the lower densities of *Hexagenia* nymphs in specific locations of the western basin of Lake Erie.

Chironomids are not the only invertebrates to consume eggs or embryos. Other dipterans feed on egg masses of frogs (Vonesh 2000). Copepodites of the cyclopoid *Acanthocyclops robustus* enter the brood pouches of daphniids, where they feed on eggs (Gliwicz and Lampert 1994). Caddisfly larvae that eat egg masses of the spotted salamander (*Ambystoma maculatum*) and bullhead fish (*Cottus gobio*) often grow more quickly than those fed a diet of other food items (Fox 1978, Stout *et al.* 1992). If *Chironomus* larval growth is greater when fed a diet of *Hexagenia* eggs than other food items, the outcome may result in larger, more fecund midges.

REFERENCES

Alford, R.A. 1989. Competition between larval *Rana palustris* and *Bufo americanus* is not affected by variation in reproductive phenology. *Copeia* 1989:993–1000.

Britt, N.W. 1955. Stratification in Western Lake Erie in summer 1953: effects on the *Hexagenia* (Ephemeroptera) population. *Ecology* 36:239–244.

Brooke, L.T., and Colby, P.J. 1980. Development and survival of embryos of lake herring at different constant oxygen concentrations and temperatures. *Progress. Fish-Cult.* 42:3–9.

Carr, J.F., and Hiltunen, J.K. 1965. Changes in the bottom fauna of western Lake Erie from 1930–1961. *Limnol. Oceanogr.* 10:551–569.

Charbonneau, P., and Hare, L. 1998. Burrowing behavior and biogenic structures of mud-dwelling insects. *J. North Am. Benthol. Soc.* 17:239–249.

_____, Hare, L., and Carignan, R. 1997. Use of X-ray images and a contrasting agent to study the behavior of animals in soft sediments. *Limnol. Oceanogr.* 42: 1823–1828.

Coffman, W.P., and Ferrington, Jr., L.C. 1996. Chironomidae. In *An introduction to the aquatic insects of North America.* 3rd Edition, eds. R.W. Merritt and K.W. Cummins, pp. 635–754. Dubuque, Iowa: Kendall/Hunt Publishing Company.

Corkum, L.D., and Hanes, E.C. 1992. Effects of temperature and photoperiod on larval size and survivorship of a burrowing mayfly (Ephemeroptera, Ephemeridae). *Can. J. Zool.* 70:256–263.

_____, Ciborowski, J.J.H., and Lazar, R. 1997a. The distribution and contaminant burdens of adults of the burrowing mayfly, *Hexagenia*, in Lake Erie. *J. Great Lakes Res.* 23:383–390.

_____, Ciborowski, J.J.H., and Poulin R.G. 1997b. Effects of emergence date and maternal size on egg development and sizes of eggs and first-instar nymphs of a semelparous aquatic insect. *Oecologia* 111:69–75.

Cuker, B.E. 1983. Competition and coexistence among the grazing snail *Lymnaea*, Chironomidae, and microcrustacea in an arctic epilithic lacustrine community. *Ecology* 64:10–15.

Dillon, P.M. 1985. Chironomid size and case presence influence capture success achieved by dragonfly larvae. *Freshwat. Invertebrate Biol.* 4:22–29.

Edmunds, Jr., G.F., Jensen, S.L., and Berner, L. 1976. *The mayflies of North and Central America*. Minneapolis: University of Minnesota Press.

Fox, P.J. 1978. Caddis larvae (Trichoptera) as predators of fish eggs. *Freshwat. Biol.* 8:343–345.

Fremling, C.R. 1967. Methods for mass-rearing of *Hexa-*

genia mayflies (Ephemeroptera: Ephemeridae). *Trans. Am. Fish. Soc.* 96:407–410.

Friesen, M.K. 1981 *Hexagenia rigida* McDunnough. In *Manual for the culture of selected freshwater invertebrates*, ed. S.G. Lawrence, pp. 127–142. Ottawa: Can Spec. Publ. Fish. Aquat. Sci. 54.

Gerlofsma, J. 1999. The effects of anoxia and temperature on the development and survivorship on *Hexagenia* (Ephemeroptera: Ephemeridae) embryos, and implications for western Lake Erie populations. M.Sc. thesis, University of Windsor, Windsor, ON.

Gliwicz, Z.M., and Lampert, W. 1994. Clutch-size variability in *Daphnia*: body-size related effects of egg predation by cyclopoid copepods. *Limnol. Oceanogr.* 39: 479–85.

Hanes, E.C., and Ciborowski, J.J.H. 1992. Effects of density and food on size variation and mortality of larval *Hexagenia rigida* (Ephemeroptera: Ephemeridae). *Can. J. Zool.* 70:1824–1832.

Helvik, J.V., and Walther, B.T. 1993. Environmental parameters affecting induction of hatching in halibut (*Hippoglossus hippoglosses*) embryos. *Mar. Biol.* 116:39–45.

Hershey, A.E. 1987. Tubes and foraging behavior in larval Chironomidae: implications for predator avoidance. *Oecologia* 73:236–241.

Hilsenhoff, W.L. 1966. The biology of *Chironomus plumosus* (Diptera: Chironomidae) in Lake Winnebago, Wisconsin. *Ann. Ent. Soc. Am.* 59:465–473.

Hunt, B.P. 1953. The life history and economic importance of a burrowing mayfly, *Hexagenia limbata*, in southern Michigan Lakes. Michigan Dept. Conservation, Inst. Fisheries Res. Bull. No. 4.

Kajak, X., and Warda, J. 1968. Feeding of benthic non-predatory Chironomidae in lakes. *Ann. Zool. Fenn.* 5:57–64.

Krieger, K.A., Schloesser, D.W., Manny, B.A., Trisler, C.E., Heady, S.E., Ciborowski, J.J.H., Muth, K.M. 1996. Recovery of burrowing mayflies (Ephemeroptera: Ephemeridae: *Hexagenia*) in western Lake Erie. *J. Great Lakes Res.* 22:254–263.

Lawler, S.P., and Morin, P.J. 1993. Temporal overlap, competition, and priority effects in larval anurans. *Ecology* 74:174–182.

Lutz, R.V., Marcus, N.H., and Chanton, J.P. 1992. Effects of low oxygen concentrations on the hatching and viability of eggs of marine calanoid copepods. *Mar. Biol.* 14:241–247.

Makarewicz, J.C., and Bertram, P. 1991. Evidence for the restoration of the Lake Erie ecosystem: water quality, oxygen levels, and pelagic function appear to be improving. *BioScience* 41:216–223.

Matisoff, G., and Wang, X. 2000. Particle mixing by freshwater infaunal bioirrigators: midges (Chironomidae: Diptera) and mayflies (Ephemeridae: Ephemeroptera). *J. Great Lakes Res.* 26:174–182.

Reynoldson, T.B., and Hamilton, A.L. 1993. Historic changes in populations of burrowing mayflies (*Hexagenia limbata*) from Lake Erie based on sediment tusk profiles. *J. Great Lakes Res.* 19:250–257.

Schloesser, D.W., and Nalepa, T.F. 2001. Changing abundance of *Hexagenia* mayfly nymphs in western Lake Erie of the Laurentian Great Lakes: impediments to assessment of lake recovery? *Int. Rev. Hydrobiol.* 86:87–103.

_____, Krieger, K.A., Ciborowski, J.J.H., and Corkum L.D. 2000. Recolonization and possible recovery of burrowing mayflies (Ephemeroptera: Ephemeridae: *Hexagenia* spp.) in Lake Erie of the Laurentian Great Lakes. *J. Aquat. Ecosys. Stress & Recovery* 8:125–141.

Shelford, V.E., and Boesel, M.W. 1942. Bottom animal communities of the island area of western Lake Erie in the summer of 1937. *Ohio J. Sci.* 42:179–190.

Soster, F.M., and McCall, P.L. 1990. Benthos response to disturbance in western Lake Erie: field experiments. *Can. J. Fish. Aquat. Sci.* 47:1970–1985.

Stout, B.M., Stout, K.K., and Stihler, C.W. 1992. Predation by the caddisfly *Banksiola dossuaria* on egg masses of the spotted salamander *Ambystoma maculatum. Am. Midl. Nat.* 127:368–372.

Tyson, J.T., and Knight, R.L. 2001. Response of yellow perch to changes in the benthic invertebrate community of Western Lake Erie. *Trans. Am. Fish. Soc.* 130:766–82.

Vonesh, J.R. 2000. Dipteran predation on the arboreal eggs of four *Hyperolius* frog species in western Uganda. *Copeia* 2000:560–566.

Walshe, B.M. 1947. Feeding mechanisms of *Chironomus* larvae. *Nature* 160:474.

Wilson, W.H. 1991. Competition and predation in marine soft-sediment communities. *Annu. Rev. Ecol. Syst.* 21:221–241.