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Spatial-temporal patterns of recolonizing adult mayflies in Lake Erie after a major disturbance

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ABSTRACT

This 12-year study of *Hexagenia* male imagos documents the recovery of two species of burrowing mayflies, *Hexagenia limbata* and *Hexagenia rigida* in western Lake Erie after a 30-year absence due to hypoxia, resulting from cultural eutrophication. Annual adult mayfly collections were made at night during the peak emergence period at four sites along the north shore of the western basin of Lake Erie, 1997 to 2008. *H. rigida*, the dominant species in upstream riverine waterbodies, was the early colonizer, representing about 90% of all male imagos sampled in 1997. In 2000, when the two species were co-dominant, both inland aerial dispersal (5.5 km) and lakeward (0.25 to 4 km) oviposition patterns confirmed species co-existence. Twice weekly collections throughout the extended emergence period at one site confirmed that *H. rigida* was the dominant species in 1997, *H. limbata* and *H. rigida* were co-dominant in 2000, and *H. limbata* was dominant in 2002. Once *H. limbata* became the dominant species (>90%) in 2000 to 2002 (depending on the site), it remained so. Both species followed a similar inland dispersal pattern, decreasing in density with increasing distance from shore; most mayflies were present within 1 km from shore. There was no significant difference in mean egg density of the two species among the sites extending lakeward in 2000 when the two species were equally abundant. The transition from the dominance of *H. rigida* to *H. limbata* may have resulted from several factors, including differential competition and growth between species or predation effects.

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Introduction

A disturbance is an event that damages or kills residents, creating opportunities for others to establish (Sousa, 1984; Connell, 1997). At one extreme, disturbances decrease diversity by eliminating species (Pickett et al., 1989), yet moderate disturbances may enhance local diversity by decreasing the abundance of a dominant species, enabling competitors to persist (Connell, 1978). Recolonization rates by species after disturbance are a function, in part, of the magnitude and type of disturbance. For example, seeds stored in serotinous cones are released following forest fires, insuring rapid recolonization of species (Wellington, 1989); whereas movement of hot lava that resulted from the Mount St. Helens eruption eliminated propagules so that succession arose from species colonizing the area from offsite (del Moral and Wood, 1993). The 1993 flood in the Mississippi River Basin, resulted in increased nutrient loads (concentrations were 5–10 times higher than previously reported) being transported downstream into the Gulf of Mexico. This nutrient disturbance resulted in significant increases in phytoplankton blooms that subsequently decomposed, doubling the size of the dead zone (the aerial extent of hypoxia) in the Gulf for many years (Sparks et al., 1998). During low Mississippi River flows, the area of hypoxia in the Gulf of Mexico shrinks, but it rises again with in-

creased flows (Rabalais et al., 2007). Tropical storms and hurricanes also disrupt stratification, resulting in immediate increases in oxygen levels in bottom waters (Rabalais et al., 2007), facilitating perhaps the temporary recovery of some species with short life spans.

Other well-known disturbance events that resulted from a change in trophic condition occurred in western Lake Erie of the Laurentian Great Lakes of North America. *Hexagenia* nymphs are detritivores that burrow as deep as 10 cm into the bottom sediments (Charbonneau et al., 1997). Using palaeo-ecological data from 1-m sediment cores in which tusks (sclerotized extensions of mandibles used in tunneling) of *Hexagenia* nymphs had been preserved, Reynoldson and Hamilton (1993) documented the history of the nymphs over time. These researchers identified two disturbance periods in Lake Erie since 1740. One disturbance occurred in the late 1880s when the Black Swamp at the western end of Lake Erie was drained, increasing nutrient loadings into the basin; and, the second disturbance occurred in the 1950s, a time of cultural eutrophication. The decline in nymphal tusks in sediment cores (and corresponding decline of mayflies from the lake) corresponded with these increased nutrient events.

The shallow (mean depth: 7.6 m) western basin of Lake Erie is separated from the deeper Central Basin by a chain of islands from the tip of Point Pelee on the north shore in Canada across the lake to the American shoreline (Fig. 1). Waters of the western basin are typically well-mixed ensuring normoxic conditions. However, the basin occasionally stratifies, leading to hypoxia near the lake bottom

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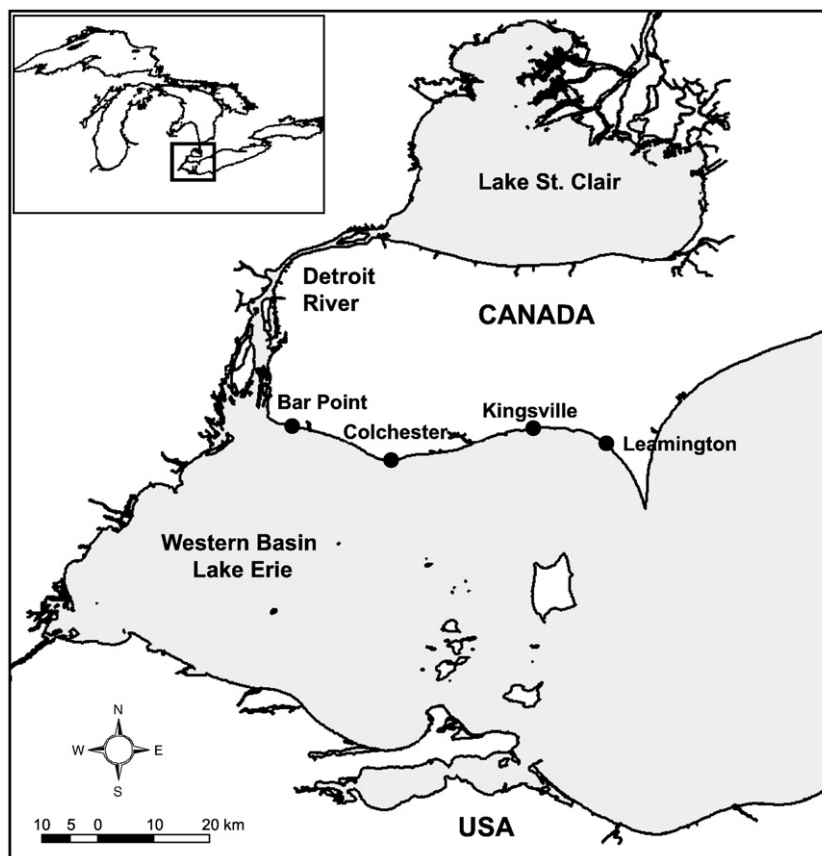


Fig. 1. Western basin of Lake Erie and upstream waterbodies (Detroit River and Lake St. Clair), indicating the four sites (Bar Point; Colchester; Kingsville, and Leamington) sampled for adult male *Hexagenia limbata* and *H. rigida*.

(Bridgeman et al., 2006). In the 1950s, a combination of accelerated eutrophication and calm days, which prevented mixing of waters, induced hypoxia at the sediment–water interface (Britt, 1955). With a few exceptions, this hypoxia resulted in the near extirpation of burrowing *Hexagenia* mayfly nymphs and any fertilized eggs buried within the sediment from 1961 to 1991 (Winter et al. 1996). However, small populations of *Hexagenia* nymphs were reported in isolated pockets (the species of which were unknown) near the islands of western Lake Erie in the late 1950s and in 1962–1965 (Britt et al., 1968; Britt et al., 1973; Edsall et al., 1999).

The recolonization of habitats after a major disturbance depends on the magnitude and persistence of the disturbance, the life history of the organisms, fecundity and propensity of species to disperse, distance of source population to colony, and barriers to migration (Niemi et al., 1990). Recolonization by burrowing mayflies in the western basin of Lake Erie was delayed until the late 1980s (Krieger et al., 1996) when upgrading of sewage treatment plants and related clean-up activities reduced nutrient loads and corresponding algal biomass, resulting in increased oxygen levels at the sediment–water interface (Makarewicz et al., 1999). External phosphorus loadings to Lake Erie were reduced to levels below 11 kt per year, a target level established by the Great Lakes Water Quality Agreement (Dolan, 1993). The establishment of filter feeding zebra, *Dreissena polymorpha* (Pallas), and quagga, *Dreissena rostriformis bugensis* (Andrusov) mussels in the late 1980s (Hebert et al., 1989; May and Marsden, 1992) in Lake Erie also enhanced transparency in the shallow western basin and shoreline areas of central and eastern basins (Holland, 1993; Leach, 1993; Ackerman et al., 2001), facilitating the presence of oxygen at sediment surfaces where mayfly nymphs burrow (Gerlofsma, 1999).

By 1996, *Hexagenia* nymphs had recolonized most of the western basin from nearshore Lake Erie locations and source populations in the Detroit River and Lake St. Clair (Krieger et al., 1996; Corkum et al., 1997). Basin-wide densities of *Hexagenia* nymphs gradually increased to historical levels. In 1997 mean (standard error, SE) *Hexagenia* nymphal density was $392 (\pm 66)/m^2$ with maximum densities of about $2000/m^2$ (Schloesser et al., 2000). In the early 1990s, adult nighttime swarms of *Hexagenia* attracted to shoreline lights were being reported (Krieger et al. 1996).

Because species identification of *Hexagenia* nymphs and adult females is uncertain, historical comparisons of *Hexagenia limbata* (Serville) and *Hexagenia rigida* McDunnough are dependent on sexually mature adult (i.e. imago) males (Burks, 1953) or eggs (Koss, 1968). However, McCafferty (1975) used the shape of the developing penis lobes to distinguish late instars of male nymphs of *H. limbata* (hooked) and *H. rigida* (straight). Earlier (Edsall et al. 1999 and references within) and more recent nymphal surveys (e.g., Schloesser et al. 2000) refer only to the genus, *Hexagenia*. However, Chandler (1963) reported that *H. limbata* occurred in 75% of samples, whereas *H. rigida* occurred in 25% of samples prior to 1947.

In this study, I present spatial and temporal recolonization patterns of male imagos of two mayfly species (*H. limbata* and *H. rigida*) at sites where they had previously been absent for more than 30 years. The aquatic burrowing nymphal stage of both species depends on oviposition by aerial female imagos at sites with clay-mud sediment. Ephemeroptera (mayflies) spend most of their lives (1 to 2 years in Lake Erie) as aquatic nymphs, and then emerge as adult winged forms. Mayflies have two adult stages, the subimago (dun) and the sexually mature form, the imago (spinner); both stages are short-lived, lasting 1 to 2 days (Edmunds et al., 1976).

I compared *Hexagenia* species of male imagos during peak emergence (maximum densities) at four locations (Bar Point, Colchester, Kingsville, and Leamington) on the north shore of western Lake Erie from 1997 to 2008. In 1997, 2000 and 2002 when there was a species shift in male imagos, I compared species presence throughout the extended emergence period at Colchester Harbour (a site with maximum mayfly density). In 2000, the year in which both species were equally dominant at Colchester Harbour, I monitored adult (subimago and imago) males of *H. limbata* and *H. rigida* and females (species combined) to compare inland dispersal patterns. Lake sediment samples also were analysed in 2000 to compare the spatial distribution of eggs of both species.

Methods

Monitoring of male imagos

From 1997 to 2008, I collected adult burrowing mayflies during peak emergence, which is typically the third week of June (Corkum et al., 2006) at four locations (Bar Point, Colchester Harbour, Kingsville, and Leamington) from the western to eastern extent along the north shore of western Lake Erie (a distance of about 80 km) to detect changes in abundance, if any, of two closely related species that recolonized western Lake Erie after their near extirpation (Fig. 1). The Colchester Harbour location was sampled continuously from 1997 to 2008; Kingsville was not sampled in 1998 or 1999; Bar Point was not sampled in 1998; and Leamington was not sampled in 1999. At each of the four sites, five replicate hoops (91-cm diameter) were each placed upon a white sheet on the ground within the sphere of a high intensity mercury vapour street light to determine density of swarming adult mayflies from sunset (21:30 h EDT) until 23:00 h. Hoops were positioned within sight of the water's edge (within a distance of ca. 10–30 m). Although all adult *Hexagenia* were collected, only male imagos were considered in the analysis. Male imagos were identified using genitalia (*H. limbata*, “penis lobes hook shaped at apexes;” *H. rigida*: “penis lobes, elongate, almost straight”) and presence (*H. limbata*) or absence (*H. rigida*) of a conspicuous dark band along the outer margin of the hind wing (Burks, 1953). The proportion of *H. limbata* male imagos was plotted for each of four sites annually, 1997 to 2008 using Prism Version 4 (GraphPad Software Inc., 2003). All graphs were used with this software.

I assumed that the number of mayflies on the ground represented aerial adult *Hexagenia*, which were attracted to street lights. This protocol may have underestimated aerial density. For example, Kriska et al. (1998) reported that white, matt-finished cloth, which reflects light diffusely, underestimates the number of some mayfly species, e.g., *Rhithrogena semicolorata* (Curtis), and *Epeorus sylvicola* (Pictet); whereas shiny black plastic sheets, with a high degree of polarization, serve as an attractant.

In 1997, 2000, and 2002, I sampled throughout the emergence period at Colchester Harbour (once to twice each week; 5 replicates each date) to determine if *Hexagenia* abundance at peak emergence (the time of sampling throughout the monitoring program) reflected overall species patterns of emergence and to detect species differences, if any, in temporal emergence patterns. Specimens collected were adult *Hexagenia* that landed within each of the 5 plastic hoops placed upon a white sheet on the ground, but only male imagos were analysed. The mean (SE) density of male imagos was plotted on a log scale for each species throughout the emergence period in all 3 years.

Inland dispersal

To compare inland dispersal patterns of *Hexagenia* adults, subimagos and imagos of males (*H. limbata* and *H. rigida*) and females (species combined) were monitored at sunset for 90 min (21:30 to 23:00 h) during peak emergence on 19, 21 and 23 June 2000 (the year

in which the two species were co-dominant) at seven sites extending from Colchester Harbour, ON, (41°59N, 82°55W), on the north-central shoreline of western Lake Erie, inland for 5.5 km. The seven sites, each located under a street light, were 0.1 km, 0.25 km, 0.4 km, 0.7 km, 2 km, 3.3 km and 5.5 km from shore along a road north from Colchester Harbour to the town of Harrow (3.3 km) and beyond. Mean (\pm SE) density of specimens was plotted at all sites.

Three hoops (each set on white sheets placed on the ground) were monitored by trained volunteers. Our nighttime collections were made to avoid mating swarms that occur from 20:00 to 20:30 h, but to capture dispersing adults that are attracted to lights. Swarming mayfly adults around street lights in Lake Erie communities were a common feature historically (Langlois, 1951). Air temperature, wind speed and wind direction were noted at Colchester Harbour at 21:30 h on each sampling date (19 June: 21.5 °C, 6.9 km/h, ESE; 21 June: 23 °C, 1.2 km/h, WSW/SW; 23 June: 23 °C, 9.2 km/h, ESE/SE).

Lakeward deposition of eggs

Hexagenia egg collections were obtained from sediment samples in western Lake Erie offshore from Colchester Harbour, 18 days after the peak emergence, prior to anticipated egg hatching. Hatching typically is 3 weeks after egg deposition at summer temperatures (Corkum et al., 1997). On 11 July 2000, SCUBA divers collected sediment using plastic core samplers at five locations (250 m, 500 m, 1 km, 2 km and 4 km) offshore from Colchester Harbour. Five core samples (i.d., 65 mm; total length, 27.5 cm) were each pushed half way down into the sediment. The cores were topped up with lake water, capped at both ends and secured in a holder for transport to the surface where they were retrieved by assistants on the boat. Labeled cores were placed on ice in coolers, transported to the lab and stored at 4 °C until processed a day later. To recover eggs from the core, the top 2 mm of sediment from the core were sieved through a 90 μ m mesh sieve, suitable to retain *Hexagenia* eggs that are typically 300 μ m \times 200 μ m (Hunt, 1953). Eggs and associated sediment were preserved with 80% ethanol. Each sample was stained with lignin pink dye to facilitate the subsequent sorting of eggs from sediment. Once sorted, all *Hexagenia* eggs were placed on glass slides, stained with CMC-9AF mounting media, identified using Koss (1968) and counted. Data were analysed (1-way ANOVA) and graphed.

Results

Monitoring of male imagos

In 1997, *H. rigida* was the dominant *Hexagenia* species at all four sampling sites, from west (Bar Point) to east (Leamington), along the north shore of western Lake Erie, representing ca. 90% of all male imago specimens collected at these sites (Fig. 2). From 1998 to 2000 (Leamington) and from 1998 to 2001 (Colchester Harbour), both species of *Hexagenia* were commonly collected, although *H. limbata* was more abundant than *H. rigida* during this interval (Fig. 2). By 2000, *H. limbata* represented over 95% of the *Hexagenia* species captured at Bar Point and Kingsville. This level of dominance represented by *H. limbata* occurred at Leamington and Colchester Harbour in 2001 and 2002, respectively (Fig. 2). Once *H. limbata* became the dominant species (i.e., >90%) at all four north shore sites (2000 to 2002), it has remained so during the following years. Variability in the numbers of male imagos captured at sites was high among the years, yet patterns between species were consistent among sites (Fig. 2).

The mayfly emergence period is an extended one for both *H. limbata* and *H. rigida* as indicated by the patterns of adults collected at Colchester Harbour throughout the summer in 1997, 2000, and 2002 (Fig. 3). In all cases, the species patterns at peak emergence were consistent throughout the extended emergence period. Although each adult (subimago and imago) stage lives only for about a day, the time

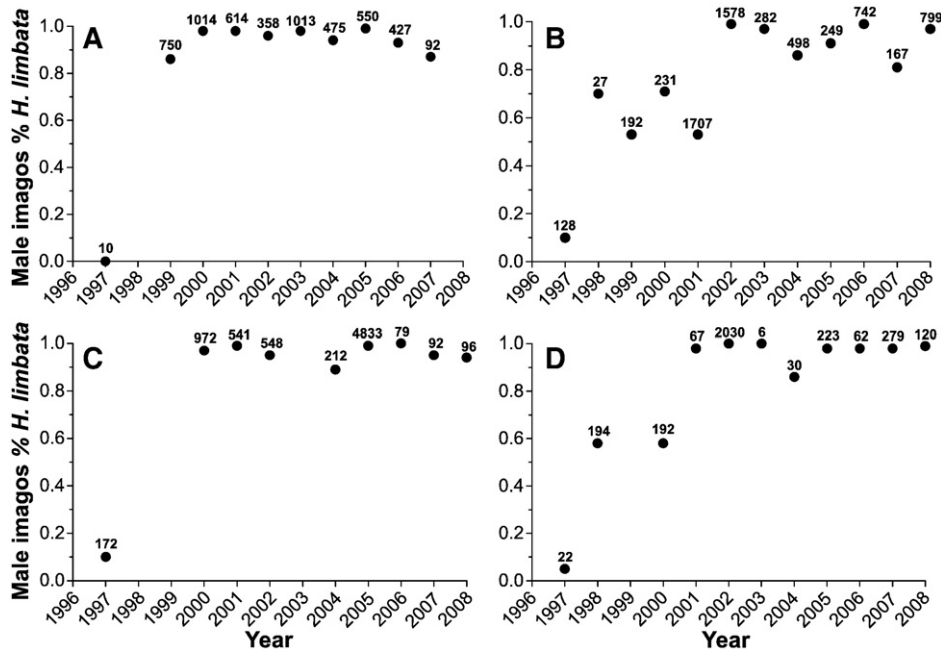


Fig. 2. The percentage of *H. limbata* male imagos (adults) at nighttime sample collections from 1997 to 2008 at Bar Point (A), Colchester Harbour (B), Kingsville (C) and Leamington (D). The number above each sampling period represents the total number of male imagos caught during peak emergence. For example, at Kingsville (C) in 1997, 10% of the 172 adult mayflies caught were *H. limbata* and 90% were *H. rigida*.

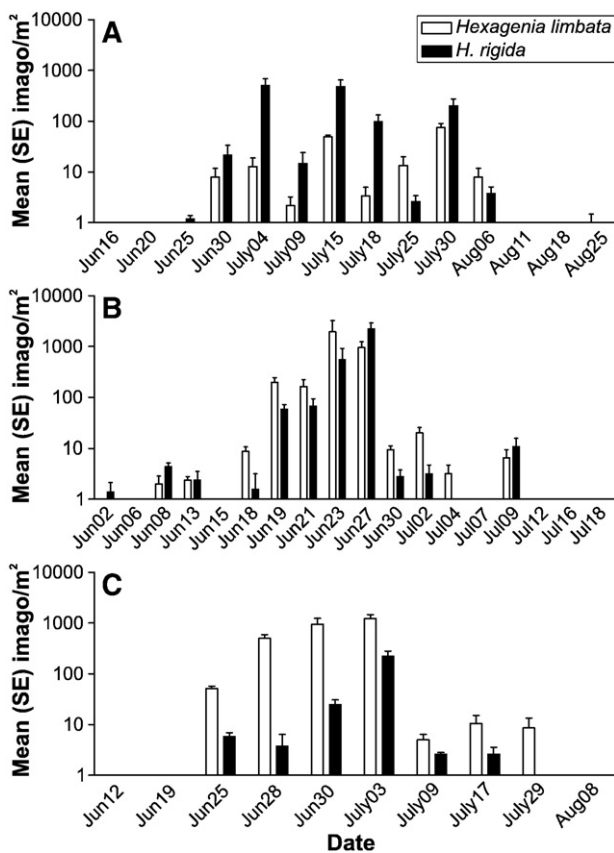


Fig. 3. Mean (standard error) density (plotted on a log scale) of male imagos per m² of *H. limbata* (open bars) and *H. rigida* (black bars) collected throughout the emergent period in 1997 (A), 2000 (B), and 2002 (C). The range of calendar dates on the X-axis differs for each year.

over which emergence occurs ranged from 5 to 10 weeks for both species. The date at which adults first appeared varied (June 2 to June 25) each year and abundance was a function of temperature and wind conditions (Corkum et al., 2006). These summertime collections confirmed that *H. rigida* was the dominant species in 1997, *H. limbata* and *H. rigida* were co-dominant in 2000, and *H. limbata* was the dominant species in 2002 (Fig. 3). Data from 2000, a year in which both species were common, showed that emergence patterns for the two species were somewhat offset with the peak emergence of *H. limbata* (June 23) preceding *H. rigida* (June 27). A body size comparison of male imagos (June 27) showed that mean (SE) body length (excluding cerci) was significantly different (2-tailed $t_{327} = 3.45$, $P = 0.0006$) between *H. limbata* ($18.28 \text{ mm} \pm 0.126$) and *H. rigida* ($17.64 \text{ mm} \pm 0.135$).

Inland dispersal

In 2000, the inland dispersal patterns for subimago and imago males (both species) and females (species combined) were similar, but the nearshore density of females was ten-fold higher than males (Fig. 4). Overall, the density of male imago *H. limbata* (mean \pm SE: 1689 ± 900) retrieved was three-fold higher than *H. rigida* (514 ± 334). Most specimens were captured within the first 1 km from shore and numbers declined abruptly beyond 1 km; only a few specimens were collected 5.5 km inland (Fig. 4). Although there was overlap of female subimagos and imagos near shore, more female imagos than subimagos were present at inland sites, ranging from 2 km to 5.5 km from shore.

Lakeward deposition of eggs

Mean (SE) density of *Hexagenia* eggs retrieved from sediment cores collected offshore from Colchester Harbour ranged from 25.6 (± 9.30) per 33.2 cm² at 0.5 km from shore to 66.8 (± 18.6) per 33.2 cm² at 2 km from shore in 2000 (Fig. 5). However, results from a 1-way ANOVA test showed that there was no significant difference in mean egg density collected from sites, ranging from 0.25 km to 4 km

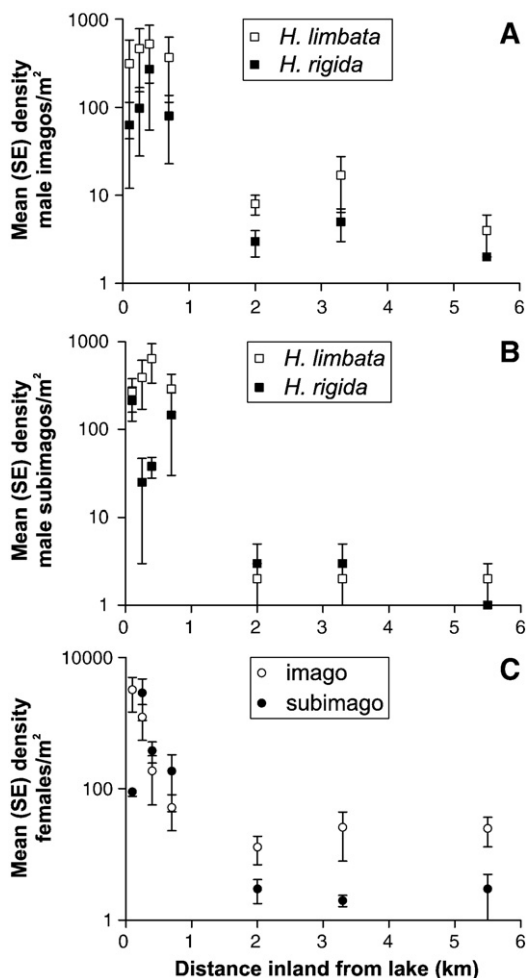


Fig. 4. The mean (SE) density of imago males (A; both species), subimago males (B; both species), and females (C; species combined) were plotted on a log scale (up to 1000 for males and 10,000 for females) at increasing distance inland from the lake. Values were calculated from samples collected on 19, 21 and 23 June 2000.

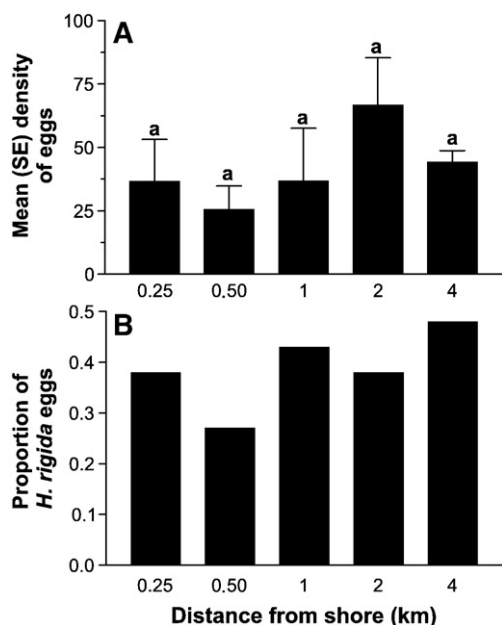


Fig. 5. A: Mean (SE) of *Hexagenia* egg density ($n = 5$) obtained from lake sediment samples at 5 sites from shore, 11 July 2000. The letter “a” indicates that there is no difference among mean egg density among sites ($F_{4,19} = 0.97, P = 0.44$). B: The proportion of *H. rigida* eggs present at each of the five sites.

from shore ($F_{4,19} = 0.97, P = 0.44$). Eggs of both species were retrieved from all samples (5 replicates/site \times 5 sites). The proportion of *H. rigida* eggs ranged from 0.27 (0.5 km from shore) to 0.48 (4 km from shore). These values compare to the proportion of adult *H. rigida* at Colchester Harbour in 1999 (0.47) and 2000 (0.30).

Discussion

Monitoring of male imagos

Recovery endpoints (Niemi et al., 1990) of the *Hexagenia* population can be based on two measures: 1. the relative abundance of the two species determined by adults; and, 2. the recovery of nymphal density compared to conditions before disturbance. Evidence of recolonization of *Hexagenia* (species not indicated) was the reported aerial mayfly swarm on 15 July 1992 in the open waters of Lake Erie (Krieger et al., 1996) and the presence in the following year of nymphs retrieved from bottom sediments (Schloesser and Nalepa, 2001). By summer 1994 (Corkum et al., 1997) and 1996 (Dobrin and Corkum, 1999), adult *H. rigida* emergence was observed at shoreline and open water locations within the western basin. Results of the present study confirm that adult *H. limbata* and *H. rigida* were present beginning in 1997 at all four sites along the northern shoreline of western Lake Erie. The relative proportion of male imagos in the two species matched the historic 3:1 ratio of *H. limbata* to *H. rigida* (Chandler, 1940) by 1998 (Colchester), 1999 (Bar Point), 2000 (Kingsville) and 2001 (Leamington), recognizing the discontinuous sampling record at Bar Point and Kingsville. Recovery of *Hexagenia* nymphal density levels of up to 350 per m^2 in the western basin of Lake Erie were equivalent to historic nymphal records in 1942–1944 reported by Chandler (1963). Schloesser et al. (2000) reported that in 1997 nymphs were present at 88% of all sites previously reported historically; however, nymphs were found at fewer offshore sites than nearshore sites.

Colonization sources

Because of the limited movement of mayfly nymphs in the bottom sediments in which they dwell during their aquatic phase, aerial adults were responsible for recolonizing Lake Erie in the 1990s and beyond. It is likely that mayflies either flew or were wind-blown to the north shore of Lake Erie from the Detroit River and upstream Lake St. Clair or from U.S. tributaries in the south (Fig. 1). The Detroit River is the major tributary entering Lake Erie, contributing 90% of inflowing water (Carter and Hites, 1992). On the basis of annual *Hexagenia* production in Lake St. Clair, this lake is reported to have among the best habitat for burrowing nymphs in North America, owing to suitable substrate, high flushing rate (5 to 7 days) and well-mixed, shallow (mean depth: 3 m) waters that ensure sediment aeration and abundant detrital food for nymphs (Edsall et al., 2001). Thus, Lake St. Clair is more riverine than lacustrine with physical conditions that may favour one species (i.e., *H. rigida*) over another.

Both *Hexagenia* species are found in the Detroit River and Lake St. Clair and persisted in these waterbodies over the time when mayflies were absent from Lake Erie (Thornley, 1985; Kovats et al., 1996; Corkum et al. 1997). *H. rigida* remained the dominant species in the Detroit–St. Clair system with the ratio of *H. rigida* to *H. limbata* male imagos of 1.8:1 (Corkum et al., 1997). Although both species co-occur in Lake St. Clair, the relative abundance of the two species is unknown.

Using forewing to body length relationships of imagos, it was determined that small lentic and large riverine mayflies are more likely to disperse than other mayflies (Corkum, 1987). Given both the higher density of *H. rigida* than *H. limbata* in the Detroit River, it is not surprising that *H. rigida* would be the earlier colonizer in Lake Erie. However, one might argue that since *H. limbata* was present (albeit in low numbers) in 1997 that the changes in relative abundance between species over time could be attributed to superior growth of

H. limbata compared with *H. rigida*, differential predation or other factors.

The presence of low numbers of *Hexagenia* adults at distances up to 5.5 km inland from the Colchester shore, suggests the possibility for long-distant flight for both species. In July 1999, Masteller and Obert (2000) reported clouds of *Hexagenia* adults over the southeastern shoreline of Lake Erie near the town of Erie, Pennsylvania. These swarms or clouds of mayflies (confirmed to be *Hexagenia* from local collections) were tracked by Doppler radar; the swarm was estimated to be 3–6 km wide, 16–24 km long and an estimated 125–250 m in height (Masteller and Obert, 2000; E. Masteller, personal communication). The dominant species in the 1999 swarm was *H. rigida*, demonstrating the early colonizing habits of this species in both eastern (Masteller and Obert, 2000) and western (this study) regions of Lake Erie.

Inland dispersal

In 2000, record *Hexagenia* mating swarms were observed along the Canadian shoreline of Lake Erie (Corkum et al., 2006; this study) and these swarms can be attributed in part to onshore winds. Specifically, onshore winds (from ESE and WSW, see Methods) from 19 to 23 June 2000 likely contributed to the abundance of adult *Hexagenia* at Colchester Harbour (near shore) and at sites northward up to 5.5 km inland. Moreover, rain on June 14 (11.8 mm) and 20 (18.2 mm) 2000 (Environment Canada, Climate Data recorded in Kingsville) may have delayed transformation from subimago to imagos, resulting in the excessive numbers of mayflies near shore during this time.

Ten-fold more females than males were collected near shore (Fig. 4). High densities of males engage in mating swarms before sunset (Corkum, personal observation) to attract female imagos. Perhaps many male imagos die after swarming, reducing their numbers at lights after sunset. After mating, females appear to gather for oviposition flight after sunset, presumably to avoid predation. Subimagos tend to rest near shore before molting into imagos, whereas female imagos engage in oviposition flight, evidenced by their large numbers near shore.

The present study showed that male imagos of *H. limbata* and *H. rigida* exhibited similar inland dispersal patterns perhaps due to wind assisted flight (up to 9.2 km/h). These flight distances are consistent with Kovats et al. (1996), who showed that while most *Hexagenia* (species were not distinguished) adults from the Detroit River and Lake St. Clair dispersed < 1.5 km, some adults were collected 5 km from shore. Kovats et al. (1996) also showed that average dispersal distance corresponded more closely with body size than wing loading i.e., body mass/wing area. Wing loading of *Hexagenia* is low (0.054) compared to other insects (Kovats et al., 1996), but body size is large. Given the relationship between body length and dispersal (Kovats et al., 1996), the larger body size of *H. limbata* compared with *H. rigida* (Giberson and Rosenberg, 1994; this study) may account for the larger accumulated presence of *H. limbata* in the lake over time. Thus, when wind is not a factor, *H. limbata* should disperse farther than *H. rigida*. Both Giberson and Rosenberg (1994) and Corkum et al. (1997) showed that *Hexagenia* female body size is larger than males, suggesting that adult females are able to disperse farther than males. This dispersal advantage to female imagos is an obvious aid during oviposition. Because female body size is related to fecundity (Giberson and Rosenberg, 1994), one would expect more propagules to be repeatedly added to the lake by *H. limbata* compared with *H. rigida*.

Lakeward deposition of eggs

Fertilized eggs of *Hexagenia* retrieved from sediment cores in 2000 confirmed the co-dominance of *H. limbata* and *H. rigida* adults collected at the shoreline sites. Since most adults were collected within 1 km inland, one might have expected the highest egg density (esti-

mated from sediment core samples) to be within the same distance lakeward, but this was not the case. Egg density did not differ among samples taken from sediments collected in the lake at distances ranging from 0.25 km to 4 km from shore. A combination of factors, including dispersal of female imagos, sinking rate of eggs, and hydrological factors (horizontal and vertical velocities within the water column), was likely responsible for a more even distribution of eggs lakeward.

Summary

The recolonization by both *Hexagenia* species into the western basin of Lake Erie has been in response to the recovery of oxygenated conditions (Makarewicz and Bertram, 1991; Gerlofsma, 1999). This study documents the recolonization trends of two species of *Hexagenia* over time and space. Clearly, *H. rigida* was the early colonizer. However, since 2000, *H. limbata* has represented over 90% of the adult population. Few differences were noted between species with respect to time of emergence, inland dispersal or spatial differences in the deposition of eggs. Only the size difference between adults (*H. limbata* was larger than *H. rigida*) may account for a dispersal advantage and an increase in fecundity that would favour *H. limbata*. I can only speculate that *H. limbata* may exhibit an advantage over *H. rigida* in terms of growth, competition or resistance to predators. Experiments are underway to examine these factors.

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References

- Ackerman, J.D., Loewen, M.R., Hamblin, P.F., 2001. Benthic–pelagic coupling over a zebra mussel bed in the western basin of Lake Erie. *Limnol Oceanogr* 46, 892–904.
- Bridgeman, T.B., Schloesser, D.W., Krause, A.E., 2006. Recruitment of *Hexagenia* mayfly nymphs in western Lake Erie linked to environmental variability. *Ecol Appl* 16, 601–811.
- Britt, N.W., 1955. Stratification in western Lake Erie in summer of 1953: effects on the *Hexagenia* (Ephemeroptera) population recovery. *Ecology* 36, 239–244.
- Britt, N.W., Skoch, E.J., Smith, K.R., 1968. Record low dissolved oxygen in the island area of Lake Erie. *J Ohio J Sci* 68, 175–179.
- Britt, N.W., Addis, J.T., Engel, R., 1973. Limnological studies of the island area of western Lake Erie. *Bull Ohio Biol Surv* 43, 1–89.
- Burks, B.D., 1953. The mayflies or Ephemeroptera of Illinois. *Bull Ill Nat Hist Surv* 26, 1–216.
- Carter, D.S., Hites, R.A., 1992. Fate and transport of Detroit River derived pollutants throughout Lake Erie. *Environ Sci Technol* 26, 1333–1341.
- Chandler, D.C., 1940. Limnological studies of western Lake Erie. 1. Plankton and certain physical–chemical data of the Bass Island region, from September, 1938 to November, 1939. *Ohio J Sci* 40, 291–336.
- Chandler, D.C., 1963. Burrowing mayfly nymphs in western Lake Erie previous to 1947. *Proceedings of the Sixth Conference Great Lakes Research*. Abstract, p. 247.
- Charbonneau, P., Hare, L., Carignan, R., 1997. Use of x-rays images and a contrasting agent to study the behavior of animals in soft sediments. *Limnol Oceanogr* 42, 1823–1828.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1309.
- Connell, J.H., 1997. Disturbance and recovery of coral assemblages. *Coral Reefs* 16 (Suppl), S101–S113.
- Corkum, L.D., 1987. Patterns of mayfly (Ephemeroptera) wing length: adaptation to dispersal? *Can Entomol* 119, 783–790.
- Corkum, L.D., Ciborowski, J.J.H., Poulin, R., 1997. 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.
- Corkum, L.D., Ciborowski, J.J.H., Dolan, D.M., 2006. Timing of *Hexagenia* (Ephemeroptera) mayfly swarms. *Can J Zool* 84, 1616–1622.
- del Moral, R., Wood, D.M., 1993. Early primary succession on the volcano Mount St. Helens. *J Veg Sci* 4, 223–234.
- Dobrin, M., Corkum, L.D., 1999. Can fluctuating asymmetry in adult burrowing mayflies (*Hexagenia rigida*, Ephemeroptera) be used as a measure of contaminant stress? *J Great Lakes Res* 25, 339–346.

- Dolan, D.M., 1993. Point source loadings of phosphorus to Lake Erie: 1986–1990. *J Great Lakes Res* 19, 212–223.
- Edmunds Jr., G.F., Jensen, S.L., Berner, L., 1976. *The Mayflies of North and Central America*. University of Minnesota Press, Minneapolis.
- Edsall, T.A., Madenjian, C.P., Manny, B.A., 1999. Burrowing mayflies in Lake Erie—a review. In: Munawar, M., Edsall, T., Munawar, I.F. (Eds.), *State of Lake Erie (SOLE)—Past, Present and Future*. Backhuys Publ., The Netherlands, pp. 219–231.
- Edsall, T.A., Haas, R.C., Adams, J.V., 2001. Annual production of burrowing mayfly nymphs (*Hexagenia* spp.) in U.S. waters of Lake St. Clair. *J Great Lakes Res* 27, 449–456.
- Gerlofsma J., 1999. The effects of anoxia and temperature on the development and survivorship of *Hexagenia* (Ephemeroptera: Ephemeridae) embryos, and implications for western Lake Erie populations. M.Sc. Thesis. Department of Biological Sciences. University of Windsor. Windsor, ON, Canada. 149 pp.
- Giberson, D.J., Rosenberg, D.M., 1994. Life-histories of burrowing mayflies (*Hexagenia limbata* and *H. rigida*, Ephemeroptera, Ephemeridae) in a northern Canadian reservoir. *Freshw Biol* 32, 501–518.
- GraphPad Software Inc., 2003. GraphPad Prism Version 4. Graph Pad Software Inc., San Diego, CA.
- Hebert, P.D.N., Muncaster, B.W., Mackie, G.L., 1989. Ecological and genetic studies on *Dreissena polymorpha* (Pallas): a new mollusc in the Great Lakes. *Can J Fish Aquat Sci* 46, 1587–1591.
- Holland, R.E., 1993. Changes in planktonic diatoms and water transparency in Hatchery Bay, Bass Island area, western Lake Erie since the establishment of the zebra mussel. *J Great Lakes Res* 19, 617–624.
- Hunt, B.P., 1953. The life history and economic importance of a burrowing mayfly, *Hexagenia limbata*, in southern Michigan lakes. Michigan Department of Conservation. *Inst Fish Res Bull* 4, 1–151.
- Koss, R.W., 1968. Morphology and taxonomic use of Ephemeroptera eggs. *Ann Entomol Soc Am* 61, 696–721.
- Kovats, Z.E., Ciborowski, J.J.H., Corkum, L.D., 1996. Inland dispersal by adult aquatic insects. *Freshw Biol* 36, 265–276.
- 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.
- Kriska, G., Horváth, G., Andrikovics, S., 1998. Why do mayflies lay their eggs en masse on dry asphalt roads? Water-imitating polarized light reflected from asphalt attracts Ephemeroptera. *J Exp Biol* 201, 2273–2286.
- Langlois, T.H., 1951. The mayfly crop in 1951. *Ohio Cons Bull* 15, 15–32.
- Leach, J.H., 1993. Impacts of the zebra mussel (*Dreissena polymorpha*) on water quality and fish spawning reefs in western Lake Erie. In: Nalepa, T.F., Schloesser, D.W. (Eds.), *Zebra Mussels: Biology, Impacts, and Control*. Lewis Publishers/CRC Press, Boca Raton, Florida, pp. 381–397.
- Makarewicz, J.C., Bertram, P., 1991. Evidence for the restoration of the Lake Erie ecosystem. *BioScience* 41, 216–223.
- Makarewicz, J.C., Lewis, T.W., Bertram, P., 1999. Phytoplankton composition and biomass in the offshore waters of Lake Erie: pre and post-*Dreissena* introduction (1983–1993). *J Great Lakes Res* 25, 135–148.
- Masteller, E.C., Obert, E.C., 2000. Excitement along the shores of Lake Erie—*Hexagenia*—echoes from the past. *Great Lakes Res Rev* 5, 25–36.
- May, B., Marsden, J.E., 1992. Genetic identification and implications of a second invasive species of dreissenid mussel in the Great Lakes. *Can J Fish Aquat Sci* 49, 1501–1506.
- McCafferty, W.P., 1975. The burrowing mayflies of the United States (Ephemeroptera: Ephemeridae). *Trans Am Entomol Soc* 101, 447–504.
- Niemi, G.J., DeVore, P., Detenbeck, N., Taylor, D., Lima, A., Pastor, J., Yount, J.D., Naiman, R.J., 1990. Overview of case studies on recovery of aquatic systems from disturbance. *Environ Manage* 14, 571–587.
- Pickett, S.T.A., Kolasa, J., Armesto, J.J., Collins, S.L., 1989. The ecological concept of disturbance and its expression at various hierarchical levels. *Oikos* 54, 129–136.
- Rabalais, N.N., Turner, R.E., Sen Gupta, B.K., Boesch, D.F., Chapman, P., Murrell, M.C., 2007. Hypoxia in the northern Gulf of Mexico: does the science support the plan to reduce, mitigate and control hypoxia? *Estuar Coasts* 30, 753–772.
- Reynoldson, T.B., 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., 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.
- Schloesser, D.W., Krieger, K.A., Ciborowski, J.J.H., 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 Ecosyst Stress Recovery* 8, 125–141.
- Sousa, W.P., 1984. The role of disturbance in natural communities. *Annu Rev Ecol Syst* 16, 353–391.
- Sparks, R.E., Nelson, J.C., Yin, Y., 1998. Naturalization of the flood regime in regulated rivers. *BioScience* 48, 706–720.
- Thornley, S., 1985. Macrozoobenthos of the Detroit and St. Clair rivers with comparison to neighboring waters. *J Great Lakes Res* 11, 290–296.
- Wellington, A.B., 1989. Seedling regeneration and population dynamics of eucalypts. In: Nobel, J.C., Bradstock, R.A. (Eds.), *Mediterranean Landscapes in Australia*. CSIRO, East Melbourne, pp. 155–167.
- Winter, A., Ciborowski, J.J.H., Reynoldson, T.B., 1996. Effects of chronic hypoxia and reduced temperature on survival and growth of burrowing mayflies, *Hexagenia limbata* (Ephemeroptera: Ephemeridae). *Can J Fish Aquat Sci* 53, 1565–1571.