Journal of Great Lakes Research 36 (2010) 338–344

Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

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

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A R T I C L E I N F O

Article history:
Received 28 July 2009
Accepted 4 January 2010

Communicated by Thomas Nalepa

Index words:
Disturbance
Dispersal
Ephemeroptera
Hexagenia
Lake Erie
Oviposition
Recolonization

A B S T R A C T

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 increased 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 sediments 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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0380-1330/$ – see front matter © 2010 Elsevier B.V. All rights reserved.
doi:10.1016/j.jglr.2010.01.006

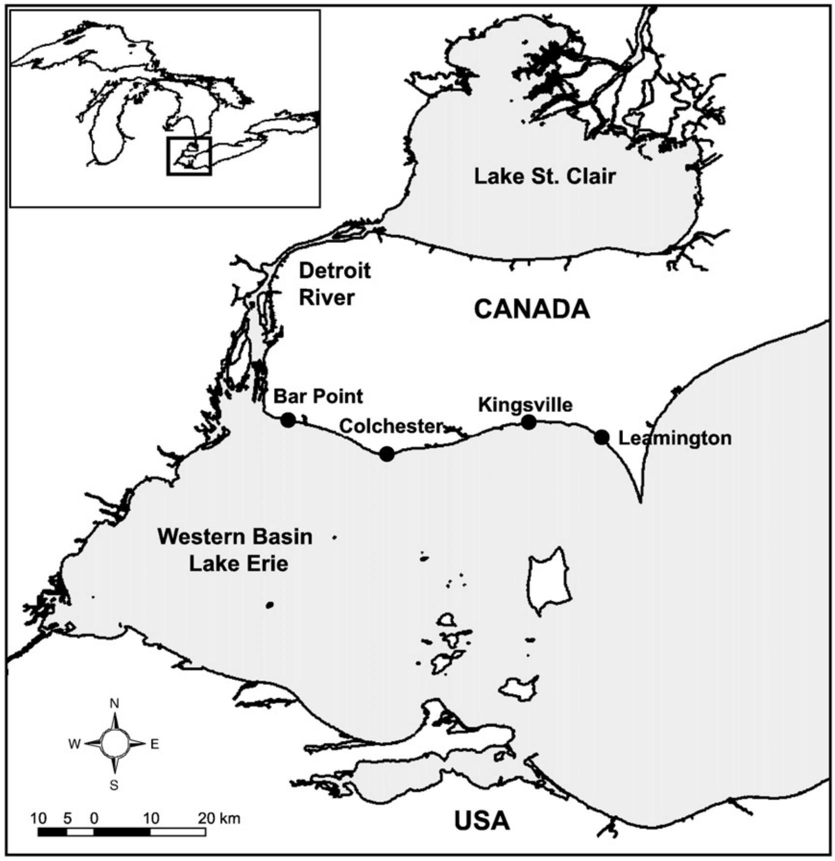

Fig. 1. Western basin of Lake Erie and upstream waterbodies (Detroit River and Lake St. Clair), indicating the four sites (Bar Point; Colchester; Kingsville, and Leamington) sampled for adult male *Hexagenia limbata* and *H. rigida*.

(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).

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