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The effect of mayfly (*Hexagenia* spp.) burrowing activity on sediment oxygen demand in western Lake Erie

William J. Edwards [a,*], Frederick M. Soster [b,1], Gerald Matisoff [c,2], Donald W. Schloesser [d,3]

[a] Department of Biology, Niagara University, Lewiston, NY 14109, USA
[b] Department of Geosciences, DePauw University, 602 South College Avenue, Greencastle, IN 46135, USA
[c] Department of Geological Sciences, Case Western Reserve University, Cleveland, OH 44106-7216, USA
[d] USGS, Great Lakes Science Center, 1451 Green Road, Ann Arbor, MI 48105-2807, USA

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ABSTRACT

Previous studies support the hypothesis that large numbers of infaunal burrow-irrigating organisms in the western basin of Lake Erie may increase significantly the sediment oxygen demand, thus enhancing the rate of hypolimnetic oxygen depletion. We conducted laboratory experiments to quantify burrow oxygen dynamics and increased oxygen demand resulting from burrow irrigation using two different year classes of *Hexagenia* spp. nymphs from western Lake Erie during summer, 2006. Using oxygen microelectrodes and hot film anemometry, we simultaneously determined oxygen concentrations and burrow water flow velocities. Burrow oxygen depletion rates ranged from 21.7 mg/nymph/mo for 15 mm nymphs at 23 °C to 240.7 mg/nymph/mo for 23 mm nymphs at 13 °C. Sealed microcosm experiments demonstrated that mayflies increase the rate of oxygen depletion by 2–5 times that of controls, depending on size of nymph and water temperature, with colder waters having greater impact. At natural population densities, nymph pumping activity increased total sediment oxygen demand 0.3–2.5 times compared to sediments with no mayflies and accounted for 22–71% of the total sediment oxygen demand. Extrapolating laboratory results to the natural system suggest that *Hexagenia* spp. populations may exert a significant control on oxygen depletion during intermittent stratification. This finding may help explain some of the fluctuations in *Hexagenia* spp. population densities in western Lake Erie and suggests that mayflies, by causing their own population collapse irrespective of other environmental conditions, may need longer term averages when used as a bio-indicator of the success of pollution-abatement programs in western Lake Erie and possibly throughout the Great Lakes.

Introduction

A major goal of the 1972 Great Lakes Water Quality Agreement was to restore year-round aerobic conditions in Lake Erie's central basin by reducing phosphorus loads to the lake to less than 11,000 metric tonnes per year. By the late 1980s, this goal was achieved (Hawley et al., 2006) and decreasing trends in both total phosphorus and hypolimnetic oxygen depletion rates in Lake Erie were apparent (Bertram, 1993). Following this period of improved water quality, total phosphorus concentrations increased and extensive hypoxic events began to recur (Hawley et al., 2006). Moreover, hypoxia in the western basin during periods of calm weather also has been observed (Bridgeman et al., 2006; Krieger et al., 2007).

Reasons for the recurrence of hypoxia in Lake Erie remain unknown despite considerable efforts to understand its cause (e.g., Matisoff and Ciborowski, 2005). Potential causes include higher temperatures due to climate change, lower water levels, natural variability, and changes induced by zebra mussels (Hawley et al., 2006). Because much of the oxygen depletion in Lake Erie is caused by sediment oxygen demand (SOD; defined here as the total flux of oxygen from the water column into the sediment via all processes; Snodgrass, 1987), a thorough understanding of processes that impact SOD is essential to understand recurrences of hypoxic conditions in the lake. Infaunal benthos may significantly increase SOD and thus impact hypolimnetic dissolved oxygen concentrations through their burrowing activity. Two taxa in particular—the mayfly *Hexagenia* spp. and the chironomid *Chironomus plumosus*—construct vertically-oriented, U-shaped burrows that extend as much as 8 cm into the sediment (Walshe, 1947; Hilsenhoff, 1966; Charbonneau and Hare, 1998). *Hexagenia* nymphs pump water through their burrows to maintain high oxygen concentrations for respiration (Eriksen, 1963) and *Chironomus* larvae pump water through their burrows to feed on algae and detritus (Walshe, 1947). Irrigation of U-shaped burrows extending deep into reduced, anoxic sediment by these infauna

* Corresponding author. Tel.: +1 716 286 8250.
E-mail addresses: wje@niagara.edu (W.J. Edwards), fsoster@depauw.edu (F.M. Soster), gerald.matisoff@case.edu (G. Matisoff), dschloesser@usgs.gov (D.W. Schloesser).
[1] Tel.: +1 765 658 4670.
[2] Tel.: +1 216 368 3677.
[3] Tel.: +1 734 214 7223.

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enhances the exchange of solutes between sediments and overlying water (Matisoff and Wang, 1998), produces oxidized halos around burrows (Matisoff et al., 1985), and introduces additional oxygen into the sediment. As a result, both bacterial respiration and biogeochemical oxygen demand may be increased.

Hexagenia spp. abundances in western Lake Erie declined catastrophically from high densities prior to the early 1950s (ca. 350/m^2) to being rare or absent in much of the basin by 1960 (Reynoldson et al., 1989). The onset of hypoxic conditions near the sediment–water interface (SWI) during periods of thermal stratification has been implicated as the likely cause for this decline (Britt, 1955). Recent improvements in water quality of western Lake Erie have resulted in a recovery of the benthic community and the return of *Hexagenia* spp. nymphs (Krieger et al., 1996, 2007; Schloesser and Nalepa, 2001). Densities of mayflies in western Lake Erie increased exponentially between 1991 and 1997 (Madenjian et al., 1998), and by 1997–1998 were greater or similar to densities found in 1929–1930 (Schloesser et al., 2000). The return of large populations of burrow-irrigating *Hexagenia* spp. nymphs might be expected to increase SOD, and thus contribute to hypolimnetic oxygen depletion. Because even small changes in SOD are predicted to have large impacts on the frequency and severity of hypoxia events (Edwards et al., 2005), it is important to evaluate and quantify the impact nymphs may have on SOD as a result of burrow irrigation.

Conversely, it appears that the population dynamics of *Hexagenia* spp. nymphs may be controlled, in part, by oxygen concentrations in the water column. In western Lake Erie, *Hexagenia* spp. population densities in the late 1990s exhibited two seasonal patterns: one pattern where densities were high in spring and gradually decreased through fall (1997) and a second pattern where densities were high in the spring, declined abruptly in summer, and then increased in the fall (1998 and 1999) (Schloesser and Nalepa, 2001). Nymph length–frequency data indicate that these patterns were attributable to either a failed (first pattern) or a successful (second pattern) young-of-the-year recruitment (Schloesser and Nalepa, 2001). Subsequently, Bridgeman et al. (2006) found a relationship between *Hexagenia* spp. recruitment success and frequency of weather-induced stratification in western Lake Erie. The highest reproductive success occurred in the year 2000, which had the fewest periods of stratification. Recruitment failures occurred in years with the most frequent or longest periods of stratification (1997 and 2002), which caused low oxygen concentrations over sediments where nymphs would emerge and where incubating eggs occur. It was not known if low dissolved oxygen caused nymph or egg mortality; however, substantial decreases in *Hexagenia* spp. densities appeared to occur immediately after peak densities, indicating a density dependent factor that may have contributed to *Hexagenia* spp. mortality (Schloesser et al., 2006). If nymphs increase SOD, then it is possible that large populations of nymphs may facilitate the onset of hypoxic conditions in areas of the western basin that are periodically stratified. We examine this possibility using the Bridgeman et al. (2006) model to hindcast potential periods of stratification in western Lake Erie. We then estimate the rates of hypolimnetic oxygen depletion during these stratified periods using *Hexagenia* spp. abundances from faunal surveys and data from laboratory experiments that quantified hypolimetic oxygen depletion rates by *Hexagenia* nymphs.

The purpose of this study was to test whether *Hexagenia* spp. nymphs may enhance the onset of hypoxia during episodic stratification in western Lake Erie via laboratory oxygen depletion experiments, field surveys of *Hexagenia* spp. abundances, and application of a thermal stratification model. We prepared laboratory sediment microcosms with and without nymphs and monitored the oxygen concentrations and flow velocities in burrows to quantitatively determine the oxygen consumption rates as water moved through burrows. We also obtained vertical profiles of oxygen concentrations in sediment microcosms and obtained X-rays of those microcosms to characterize the size and extent of the burrow system. The decrease in oxygen concentrations in water overlying sediments with and without nymphs in sealed microcosms was monitored to directly compare the difference in SOD. Vertical profiles of bromide, a solute tracer added to the overlying water, were used to model the enhancement of solute fluxes, and by inference the enhanced oxygen demand caused by *Hexagenia* spp. nymphs. Field surveys were conducted to determine *Hexagenia* spp. distribution and abundance patterns in western Lake Erie and our experimental results were applied to these data with a thermal stratification model to estimate the potential effects of mayflies on Lake Erie hypoxia during periods of stratification.

Methods

Field area

Sampling was conducted in western Lake Erie (Fig. 1). The basin has a surface area of 3080 km^2 and extends about 60 km east to west, and about 40 km north to south (Mortimer, 1987). The entire basin is shallow (7.4 m average depth; Mortimer, 1987) and has a maximum depth of 12 m at the east end. Post-glacial mud and sand mixtures, derived mostly from the Detroit River and the Maumee River, make up most of the substrate in the western basin. These sediments generally consist of less than 10% sand, between 20% and 60% silt, and greater than 40% clay (Thomas et al., 1976; Kemp et al., 1976; Soster, 1984). Surficial water temperatures range from a winter low of 0 °C (surface ice) to a typical summer high of about 25 °C. Surface and bottom water temperatures usually differ by only a few degrees, but short periods of thermal stratification in some cases accompanied by oxygen depletion of bottom water can occur (Britt, 1955; Carr and Hiltunen, 1965; Bridgeman et al., 2006).

Hexegenia surveys and collection

Densities of *Hexagenia* spp. nymphs were obtained at five sites (2L, 6L, 7L, 4P, and 7P; Schloesser et al., 2000) in the western basin of Lake Erie during April–May 1999–2004 to monitor *Hexagenia* spp. abundance patterns (Fig. 1) within the area modeled by Bridgeman et al. (2006). Three replicate ponar grab samples (484 cm^2 each) were

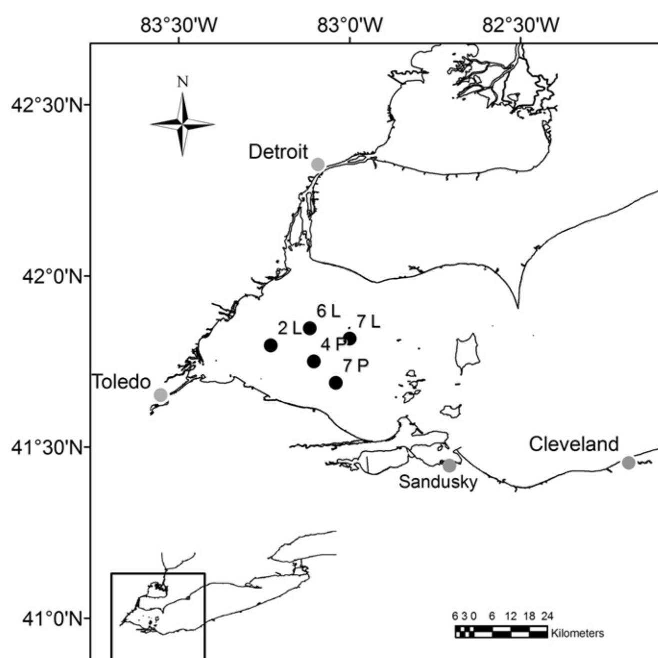

Fig. 1. Field area in western Lake Erie. Shown are the five abundance survey locations.