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Hypoxia Effects on Burrowing Mayfly (*Hexagenia*) Recolonization of Lake Erie's Central Basin

FINAL REPORT

LAKE ERIE PROTECTION FUND PROJECT SG 202-03

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Executive Summary

Nymphs of two native species of burrowing mayflies, *Hexagenia limbata* and *H. rigida*, were important in the food web of the western basin and several other areas of Lake Erie until the 1950s, when worsening pollution brought about their demise. Following a number of changes in the lake, including a reduction of pollution and invasion of the zebra mussel (*Dreissena polymorpha*), *Hexagenia* nymphs returned to western basin sediments beginning in the early 1990s. An annual sampling program was begun in 1997 to survey the distribution and abundance of *Hexagenia* nymphs in the central basin of Lake Erie, in a manner similar to efforts in the western basin that started in 1995 funded by the Ohio Lake Erie Protection Fund. The purpose of this project was to continue the annual sampling program in the central basin in 2003 and conduct limited sampling in the western basin to permit comparison between the basins. The survey addresses a requirement of the Lake Erie Protection and Restoration Plan to monitor long-term trends in Lake Erie water quality, including biological components, on a regular schedule. Furthermore, *Hexagenia* nymphs comprise a metric of the Lake Erie Quality Index.

Sediment grab samples were collected with the assistance of US Geological Survey personnel at 33 stations in the nearshore zone of the central basin from Sandusky to Conneaut, Ohio, in late May and early June 2003. Samples were also collected at seven stations in the western basin ranging from Maumee Bay to the eastern edge of the island area.

Nymphs were almost entirely absent from the central basin samples in 2003, being found only in very low abundance at two stations, one near Sandusky (5 nymphs/m^2) and the other immediately east of Ashtabula Harbor (23 nymphs/m^2). Thus, the distribution and abundance of nymphs in the central basin was about the same as in 2001 and 2002 and represented a return to the status of the population in 1997. The intervening years 1998 through 2000 had revealed a gradual increase in distribution and abundance in the central basin. Nymphs in the western basin were found at five of seven stations and in typical abundance, with as many as 1,278 /m^2.

The absence of nymphs at two western basin stations and 31 of 33 central basin stations appears to be directly or indirectly related to seasonally low dissolved oxygen conditions. The apparent decline in the abundance and distribution of nymphs in central basin sediments since May 2000 seems to correspond with reported changes in the basin that have resulted in a "dead zone" in summer nearly devoid of dissolved oxygen. Because some adult *Hexagenia* mayflies continue to be reported on shore each summer, the nymphs must be completing their life cycle successfully in some areas. Given the general absence of nymphs in the sediments of the open lake, it seems advisable that subsequent annual surveys should place special effort in areas that may be serving as refugia for the mayflies, such as river mouths, harbors, marinas, and other protected or semi-protected areas. Furthermore, a version of the mayfly metric of the Lake Erie Quality Index should be extended to the central basin.

Introduction

Nymphs of burrowing mayflies (Ephemeridae: *Hexagenia limbata* and *H. rigida*) are native members of the animal community in the bottom sediments of the western basin of Lake Erie and parts of the central and eastern basins. They were important in the diets of several kinds of fish (Boesel 1937, French 1994, Price 1963) until the 1950s, when they rapidly disappeared as the result of oxygen depletion in the water overlying their burrows (Britt 1955a, 1955b). Oxygen depletion resulted from chronic and worsening enrichment of the lake with organic and inorganic nutrients in the first half of the twentieth century that apparently led first to a large increase in the abundance of the burrowing mayflies (Reynoldson and Hamilton 1993) as their food supply increased, and later to their demise when dissolved oxygen was depleted in summer from the decomposition of organic matter. The accumulation of toxic contaminants within the sediments during the same time period may have contributed to the disappearance of the mayflies, although evidence apparently does not support that possibility (Burns 1985).

Following extensive efforts to reduce pollution in Lake Erie, *Hexagenia* began to repopulate most parts of the western basin in the 1990s (Krieger 1999, 2000, 2001; Krieger *et al.* 1996; Madenjian *et al.* 1998; Schloesser *et al.* 2000). With the expectation that burrowing mayflies would respond similarly in shallow sedimented areas of the central basin, nearshore sediments of the central basin in Ohio were sampled annually beginning in 1997 to document their colonization of that region (Krieger 2000, 2004). A summary of the changes in *Hexagenia* distribution and abundance in the western and central basins, from a recent report to the Ohio Lake Erie Commission (Krieger 2004) is quoted as follows.

> Sediment samples collected in the central basin in June of 1997 through 2000 revealed *Hexagenia* nymphs at more stations and generally in greater abundance each year, and this was especially notable in the Cleveland vicinity in 1999 and the Ashtabula-Conneaut area in 2000. In 2001, however, the nymphs disappeared almost completely from sediment samples. Therefore, we sampled the central basin again in 2002 in order to document whether the nymphs could be found throughout the sampling area or continued to be rare in our samples. It was also important to compare our central basin results with the *Hexagenia* population in the western basin in order to understand whether the observed changes in the central basin populations might be linked to lake-wide environmental conditions. For that purpose, we sampled seven stations in the western basin in May 2002 extending from Maumee Bay to the eastern edge of the basin.
>
> Five of the seven western basin stations yielded numerous nymphs. The greatest densities were near Maumee Bay State Park and between Kelleys and Pelee islands (251 to 288 nymphs/m^2), while no nymphs were found at two stations where they have been absent or rare over the past decade. Only three nymphs (at two stations) were present in the 144 samples (36 stations) collected from the central basin. The central basin results indicate that a major change in conditions, or one or more short-term events, such as an intrusion of oxygen-depleted hypolimnion water into shallower nearshore water overlying sediments occupied by *Hexagenia*, occurred between the sampling periods in 2000 and 2001. Hypolimnion intrusion would disrupt colonization by *Hexagenia* and reset the colonization process to an earlier phase. (Krieger 2004, pp. ii-iii)

The objective of the project reported here was to perform an annual survey in 2003 of the distribution and abundance of *Hexagenia* nymphs in the Ohio part of the central basin within about five miles of shore and at seven stations in the western basin. The data, when compared with the annual surveys from 1997 through 2002, would provide evidence of change or stability in the water and sediment quality of the two basins. This project relates to the Strategic Objective of the Lake Erie Protection and Restoration Plan to "adequately monitor long-term trends in Lake Erie water quality parameters" (OLEC 2000, p. 16). It also addresses WQ-13 "in establishing monitoring stations and regular sampling schedules that include . . . water chemistry and biological sampling" (OLEC 2000, p. 16). The project also is related to the "Biological Indicator" of the Lake Erie Quality Index (OLEC 1998), which includes a metric consisting of the abundance of *Hexagenia* nymphs in western basin sediments but which also could be extended in modified form to the central basin (Krieger 2004).

Methods

Transportation to the sampling stations was provided aboard the *R/V Pike* by Mr. Kip Powell of the U.S. Geological Survey's Lake Erie Biological Station in Sandusky, Ohio. The stations were sampled from west to east on 14, 19 and 23 May (7 stations in the island area of the western basin), 27-30 May (26 stations), and 2-3 June 2003 (7 stations), for a total of 40 stations varying in depth from 19 feet (5.8 m) to 61 feet (18.5 m) (Table 1). Four replicate sediment samples were collected at each station using a Ponar grab (21 cm x 21 cm). At those stations where *Hexagenia* nymphs were seen in the samples, four samples were also taken with an Ekman grab in order to provide comparative data on the relative efficiency of the two types of sampler at collecting the nymphs. The Ekman grab had been used prior to 2002, and the Ponar grab was made the primary sampler in 2002 and 2003 to ensure that the sampling results were directly comparable to data on Lake Erie being produced by researchers at several other laboratories. Each sample was rinsed through a U.S. Standard No. 30 screen (0.60 mm mesh openings), and the presence of nymphs in the sample residues was noted on field sheets. The residues were put into 500-mL wide-mouth plastic jars, were preserved in ~5% formaldehyde and were returned to the Water Quality Laboratory. The samples were stained in the laboratory with Phloxine B to enhance the visibility of small nymphs, and after at least 48 hours all nymphs were removed from each sample and counted.

Results and Discussion

Hexagenia nymphs were present at five of the seven stations sampled in the western basin in 2003 (Table 2, Figure 1), being absent from stations 6B and 5P, where they have been either absent or present in very low abundance through the 1990s and early 2000s. Those two stations have been included in yearly sampling in order to monitor their progress in sustaining a population of nymphs as the surrounding areas of the basin already do. Nymph abundance at the remaining five stations varied widely from 1,278 nymphs/m^2 at 6K to 32.5 nymphs/m^2 at 7K. Station 7M near Maumee Bay, which has had the highest abundance some years, revealed 190.5 nymphs/m^2 (Table 2).

Table 1. Coordinates and depths of stations sampled for *Hexagenia* nymphs in the western basin in 2003 and the nearshore zone of the central basin of Lake Erie, 1998 through 2003 (1997 omitted). Stations successfully sampled are indicated with a check mark (√); stations where satisfactory samples could not be obtained are shown with an "a". Coordinates indicate initial sampling station each year; in some years it was necessary to move some distance off station in order to obtain satisfactory sediments.

Western Basin				Central Basin				Years Successfully Sampled					
Station	N latitude	W longitude	Depth, 2003 ft (m)	Station	N latitude	W longitude	Depth, latest yr ft (m)	98	99	00	01	02	03
5B	41°41.50'	82°46.00'	29 (9.0)	BRD15	41°24.37'	82°29.52'	26 (7.8)	√	√	√	√	√	√
				BRD15N	41° 29.25'	82°29.52'	44 (13.4)					√	√
6B	41°52.00'	82°49.00'	37 (11.5)	CP1	41°30.01'	82°38.07'	34 (10.3)	√	√	√	√	√	√
				CP2	41°26.60'	82°.35.00'	34 (10.4)	√	√	√	√	√	√
6K	41°40.00'	82°40.00'	37 (11.3)	CP3	41°25.71'	82°35.04	26 (8.0)	√	√	√	√	√	√
7K	41°34.00'	82°40.00'	39 (11.9)	LV52	41°27.30'	82°24.00'	45 (13.8)		√	√	√	√	√
7M	41°44.00'	83°17.83'	19 (5.9)	LV56	41°27.30'	82°21.10'	40 (12.2)		√	√	√	√	√
				LV66	41°28.75'	82°11.17'	29 (9.0)	√	√	√	a	√	√
1P	41°32.92'	82°55.00'	19 (5.8)	LH1	41°28.50'	82°11.10'	29 (8.9)			√	√	√	√
5P	41°44.00'	82°58.25'	32 (9.8)										
				BRD16B	41°29.57'	82°09.46'	41 (12.5)	√	√	√	a	√	√
				BRD16C	41°31.64'	82°09.46'	48 (14.6)					√	√
				AV1	41°32.50'	82°01.00'	50 (15.3)		√	√	√	√	√
				RR1B	41°29.83'	81°51.72'	35 (10.7)	√	√	√	√	√	√
				BRD17S	41°30.44'	81°48.00'	39 (11.8)					√	√
				BRD17I	41°31.25'	81°48.00'	46 (14.2)					√	√
				BRD17D	41°35.78'	81°48.00'	58 (17.8)					√	√
				CW81	41°30.80'	81°45.33'	42 (12.7)	√	√	√	√	√	√
				CW82	41°32.88'	81°45.84'	49 (15.2)		√	√	√	√	√
				CE84	41°29.83'	81°43.50'	28 (8.5)	√	√	√	√	√	√
				CE85	41°30.30'	81°42.75'	31 (9.4)	√	√	√	√	√	√
				CW88	41°31.50'	81°42.70'	40 (12.2)	√	√	√	√	√	
				CE91	41°32.25'	81°39.33'	25 (7.7)	√	√	√	√	√	√
				CE92	41°32.70'	81°40.50'	41 (12.6)		√	√		√	√
				CE100	41°36.20'	81°35.83'	44 (13.4)	√	√	√	√	√	√
				BRD18	41°45.47'	81°19.22'	30 (9.3)	√	√	√	a	a	a
				BRD18B	41°47.79'	81°19.22'	50 (15.2)					a	
				BRD18C	41°49.22'	81°19.22'	61 (18.5)					√	√
				FP111	41°46.10'	81°18.40'	35 (10.7)	√	√		√	a	a
				FH1	41°45.95'	81°16.91'	16 (5.0)	√	√	√	√	√	√
				FP116B	41°46.92'	81°16.87'	34 (10.4)	√	√		a	a	a
				FH3 (FC57J)	41°48.30'	81°15.15'	49 (15.0)				√	√	√
				AS124B	41°53.02'	80°59.35'	37 (11.4)	√	√		√	√	√
				BRD19	41°54.38'	80°49.42'	29 (8.8)					a	a
				BRD19B	41°54.55'	80°49.49'	36 (11.0)	√	√	√	√	√	√
				BRD19C	41°55.86'	80°49.49'	49 (15.0)					√	√
				BRD19D	41°57.24'	80°49.49'	58 (17.8)					√	
				AS135S	41°53.96'	80°55.82'	49 (15.0)	√	√	√	√	√	√
				AS139C	41°54.89'	80°48.31'	29 (8.7)	√	√	√	√	√	a
				AH1B	41°55.15'	80°47.70'	34 (10.4)	√	√	√	√	√	√
				AH2B	41°54.92'	80°47.36'	30 (9.0)	√		√	√	√	√
				CN1	41°59.90'	80°34.00'	47 (14.4)		√	√	√	√	√

a = attempted but no useful samples obtained

Nymphs were almost entirely absent from the central basin samples and were found only at the westernmost station near Sandusky (1CP) and a station immediately east of Ashtabula Harbor (AH2B). They were present at both stations in very low numbers, 4.6 nymphs/m^2 at 1CP, and 23.2 nymphs/m^2 at AH2B. Thus, in 2003 the distribution and abundance of *Hexagenia* nymphs in the central basin appeared to be the same as in the prior two years and in 1997, before the spread of the mayflies in that basin in the years 1998 through 2000 (Figure 1).

Despite the general absence of nymphs in our samples, we received several communications that winged *Hexagenia* had appeared on the sides of buildings in the Cleveland area as early as 28 June 2003 (K. Linn, Northeast Ohio Regional Sewer District, personal communications, 30 June 2003 and later). We received similar reports from that source in 2001 and 2002. Thus, it appears that the nymphs are completing their life cycle successfully in parts of the central basin and perhaps the mouths of its tributaries where we have not sampled. We are continuing to attempt to develop a sampling scheme that will more effectively demonstrate the presence and abundance of nymphs in the central basin. It may well be that attention should be devoted specifically to sampling in river mouths, harbors, marinas, and other protected or semi-protected areas with sedimented bottoms while temporarily abandoning most of our open-lake stations. It is important to link the nursery areas of the *Hexagenia* nymphs to the sightings of adults on shore so that the distribution and abundance of the nymphs can be monitored for the purposes of judging localized and regional lake quality.

Table 3 compares the average abundance of nymphs from 1997 through 2003 west and east of Euclid, Ohio, which is approximately at the midpoint of the study area in the central basin. Also shown for each year is the proportion of stations where nymphs were found. It should be noted that because fewer stations were sampled east of Euclid, a single station in 2003 accounted for 10% of stations to the east but only 4.3% of stations to the west. The abundance of nymphs peaked west of Euclid in 1999 and has declined since, while east of Euclid, abundance peaked in 2001. In both parts of the study area, abundance even in the peak years was extremely low compared to the western basin. The distribution of nymphs (percent of stations where they were found) peaked in 1999 in the western half as did abundance, but in the eastern half distribution peaked in 2000 as opposed to the abundance peak occurring in 2001. In each of the years 2001, 2002, and 2003, nymphs were only found at one station toward each end of the study area (Figure 1, Table 3).

During the season when nymphs are sampled each year, in May and June, dissolved oxygen levels near the sediment are at or near saturation. This is because thermal stratification becomes established later, and at greater depths than most of our stations. Schertzer *et al.* (1987) showed that in 1979 the hypolimnion formed near mid-June with an upper boundary in both 1979 and 1980 near 15 m to 20 m. Only 10 of our 33 central basin stations had a depth in that range (Table 1). Dissolved oxygen recorded in the western and central basins at several representative stations at the time we sampled for nymphs showed that in 2003 dissolved oxygen ranged from slightly below to slightly above saturation at 1 m above the lake bottom (Table 4).

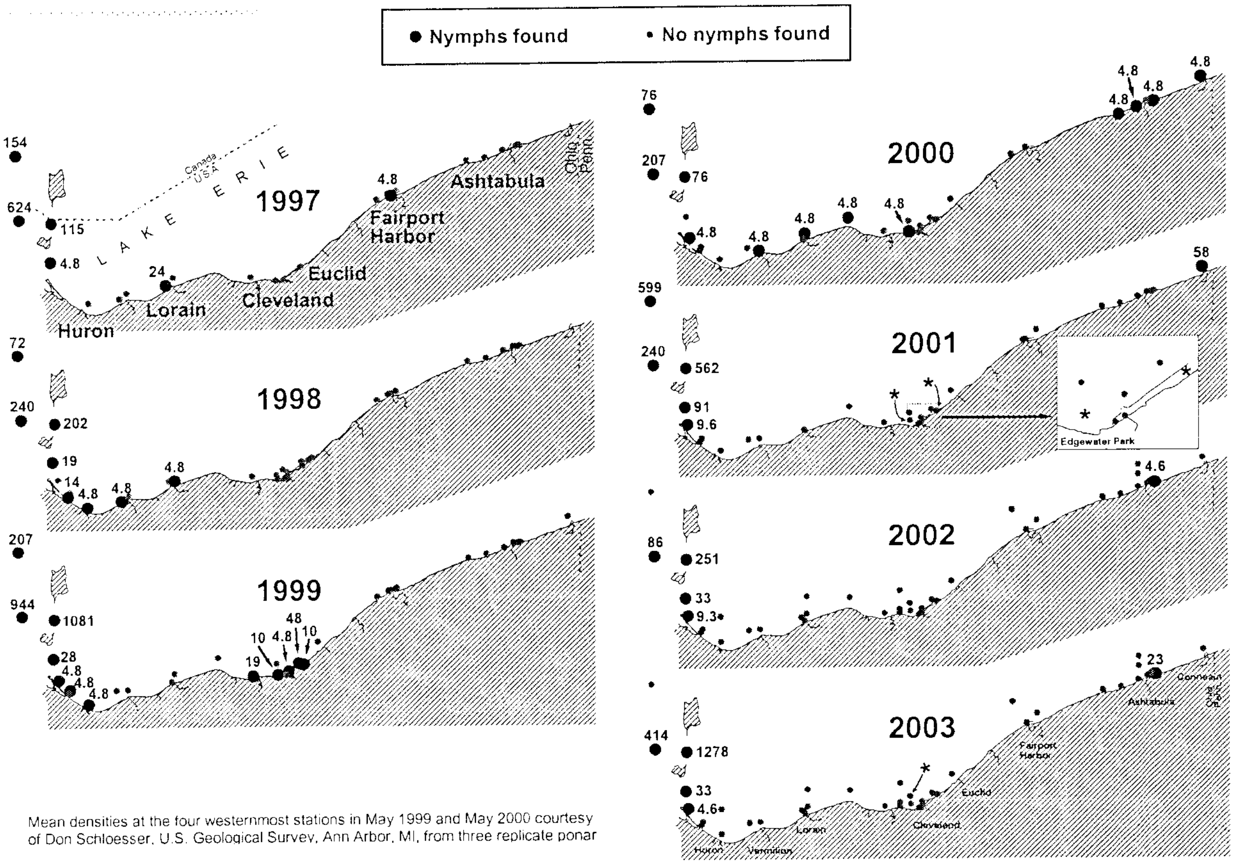

Figure 1. Stations successfully sampled for *Hexagenia* nymphs in May-June 1997 through 2003, and the mean abundance (individuals/m^2) of nymphs where they were found. Low densities in 2000 probably resulted from sampling after the emergence of adults had begun. Asterisks show stations where apparent mayfly burrows were seen in samples in 2001. Mean abundances at the four westernmost stations in May 1999 and 2000 were provided by Don Schloesser, U.S. Geological Survey, Ann Arbor, Michigan, from three replicate Ponar samples collected at each station.

Even though highly oxygenated water is present near the sediment in both the western and central basins in spring and early summer, past and current evidence indicates that the concentration of oxygen declines many years to less than 2 mg/L in parts of the western basin (Krieger *et al.* 1996; Bridgeman and Schloesser in preparation; M. Thomas, Stone Laboratory, personal communications, June 1996 and later) and less than 1 mg/L in much of the central basin hypolimnion (bottom layer of water) (USEPA 2004). Bridgeman and Schloesser (in preparation) have linked climatic conditions that affect dissolved oxygen concentrations to the relative success or failure of recruitment of the new cohort of nymphs in the western basin in a given year. *Hexagenia* nymphs cannot survive at dissolved oxygen concentrations below about 1 mg/L (Eriksen 1963),

Table 2. Abundance of *Hexagenia* nymphs in samples collected May-June 2003 in the western and central basins.

	Replicate -- PONAR						Replicate -- EKMAN					
Station	**1**	**2**	**3**	**4**	**Mean**	**#/m²**	**1**	**2**	**3**	**4**	**Mean**	**#/m²**
5B	27	16	26	20	22.25	**413.6**	16	6	7	10	9.75	**187.2**
6B	0	0	0	0	0.00	**0.0**						
6K	82	52	61	80	68.75	**1278.1**	47	31	36	44	39.50	**758.4**
7K	2	3	1	1	1.75	**32.5**						
7M	10	7	13	11	10.25	**190.5**	7	8	2	8	6.25	**120.0**
1P	11	7	9	8	8.75	**162.7**	8	7	12	3	7.50	**144.0**
5P	0	0	0	0	0.00	**0.0**						
1CP	1	0	0	0	0.25	**4.6**	0	0	0	0	0.00	**0.0**
2CP	0	0	0	0	0.00	**0.0**						
3CP	0	0	0	0	0.00	**0.0**						
BRD15	0	0	0	0	0.00	**0.0**						
BRD15N	0	0	0	0	0.00	**0.0**						
LV52	0	0	0	0	0.00	**0.0**						
LV56	0	0	0	0	0.00	**0.0**						
LV66	0	0	0	0	0.00	**0.0**						
LH1	0	0	0	0	0.00	**0.0**						
BRD16B	0	0	0	0	0.00	**0.0**						
BRD16C	0	0	0	0	0.00	**0.0**						
AV1	0	0	0	0	0.00	**0.0**						
RR1B	0	0	0	0	0.00	**0.0**						
CW81	0	0	0	0	0.00	**0.0**						
CW82	0	0	0	0	0.00	**0.0**						
CE84	0	0	0	0	0.00	**0.0**						
CE85	0	0	0	0	0.00	**0.0**						
CW88*												
CE91	0	0	0	0	0.00	**0.0**						
CE92	0	0	0	0	0.00	**0.0**						
BRD17	0	0	0	0	0.00	**0.0**						
BRD17M	0	0	0	0	0.00	**0.0**						
BRD17 D	0	0	0	0	0.00	**0.0**						
CE100	0	0	0	0	0.00	**0.0**						
BRD18[a]												
BRD18C	0	0	0	0	0.00	**0.0**						
FP111[a]												
FP116B[a]												
FH1	0	0	0	0	0.00	**0.0**						
FH3 (FC57J)	0	0	0	0	0.00	**0.0**						

Table 2. Continued.

AS124B	0	0	0	0	0.00	**0.0**						
AS135S	0	0	0	0	0.00	**0.0**						
BRD19[a]												
BRD19B	0	0	0	0	0.00	**0.0**						
BRD19C	0	0	0	0	0.00	**0.0**						
BRD19D*												
AS139C[a]												
AH1B	0	0	0	0	0.00	**0.0**						
AH2B	1	1	2	1	1.25	**23.2**	0	1	0	2	0.75	**14.4**
CN1	0	0	0	0	0.00	**0.0**						

* Not sampled. [a]Samples attempted but hard bottom.

Table 3. Average density of *Hexagenia* nymphs and the proportion of sampling stations where they were found in the central basin of Lake Erie between Sandusky and Conneaut, Ohio, 1997 through 2003.

	Average Number nymphs per square meter		Percent of Stations with nymphs	
Year	West of Euclid	East of Euclid	West of Euclid	East of Euclid
1997	2.4	0.6	10%*	11%*
1998	1.5	0	21%	0%
1999	5.9	0	44%	0%
2000	1.3	2.4	26%	50%
2001	0.6	5.8	5.9%*	10%*
2002	0.4	0.4	5.6%*	8.3%*
2003	0.2	2.3	4.3%*	10%*

*nymphs collected at a single station

Table 4. Temperature and dissolved oxygen at 1 m above the lake bottom at the time of sediment collections at five stations in May 2003.

Date	Time	Station	Temp. °C	Dissolved Oxygen, mg/L	Dissolved Oxygen % saturation
14 May 03	09:45	7M	14.0	8.8	85
23 May 03	11:05	6K	13.1	10.5	100
29 May 03	10:00	CW81	13.2	10.8	112
29 May 03	10:50	CE84	14.5	9.1	92
29 May 03	12:20	CE91	14.5	9.0	90

especially at warmer temperatures (Winter *et al.* 1996). Thus, it appears probably that the absence of nymphs at the two western basin stations and most of the central basin stations is directly or indirectly related to seasonally low dissolved oxygen conditions. It seems reasonable to hypothesize that their absence even in shallow areas (above the hypolimnion) with suitable sediments that have been sampled in the central basin are the result of internal seiches, that is, the sloshing of hypolimnionic water from deeper areas into shallower areas that normally remain sufficiently oxygenated. Bartish (1987) reported incursions of anoxic central basin water from the hypolimnion into the western basin at depths as shallow as nine meters. Given the sensitivity of *Hexagenia* nymphs to low dissolved oxygen concentrations, this organism appears to be an important bioindicator of the status of summer oxygen conditions in both the western and central basins of Lake Erie, and as such, this insect should be incorporated into a metric that would be applied specifically to the central basin.

Benefits and Information Dissemination

The project results directly benefit the development and application of the Lake Erie Quality Index to the central basin of the lake. Data since 1997 have shown that *Hexagenia* began to increase its distribution and abundance in the open lake sediments but regressed to very low numbers in that large area. Their apparent decline in the open lake after 2000 indicates that overall lake conditions are not as conducive to their survival and growth as in the two to three years prior to 2000, and may be indicative primarily of a change in summer dissolved oxygen conditions near the lake bottom (USEPA 2004).

The project results were disseminated via a poster presentation at the annual conference of the International Association for Great Lakes Research held in June 2003 at DePaul University in Chicago. That poster and this report will be posted on the Water Quality Laboratory web site (http://www.heidelberg.edu/offices/wql/mayflies-in-erie.html) to provide ready access to all interested individuals.

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Mr. Kip Powell, USGS Sandusky, Ohio, provided transportation to all sampling stations, assisted in sample collection, and made the difficult decisions regarding suitable weather for sampling. Mr. Mike Bur, USGS Sandusky, and Heidelberg College student technicians Natalie Johnson and Ronald Maichle assisted in the field collections, and Ms. Johnson processed and analyzed the samples in the laboratory. Nancy Miller of the Water Quality Laboratory provided administrative assistance.

Literature Cited

Bartish, T. 1987. A review of exchange processes among the three basins of Lake Erie. *Journal of Great Lakes Research* 13:607-618.

Boesel, M. W. 1937. The food of nine species of fish from the western end of Lake Erie. *Transactions of the American Fisheries Society* 67:215-233.

Bridgeman, T. B., and D. W. Schloesser. In Preparation. Recruitment of *Hexagenia* mayfly nymphs in western Lake Erie linked to environmental variability.

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

Britt, N. W. 1955b. *Hexagenia* (Ephemeroptera) population recovery in western Lake Erie following the 1953 catastrophe. *Ecology* 36:520-522.

Burns, N. M. 1985. *Erie, the lake that survived.* Rowman & Allanheld Publ., Totawa, New Jersey.

Eriksen, C. H. 1963. Respiratory regulation in *Ephemera simulans* Walker and *Hexagenia limbata* (Serville) (Ephemeroptera). *Journal of Experimental Biology* 40:455-467.

French, J. R. P. III. 1994. Burrowing mayflies (*Hexagenia* spp.) consumed by freshwater drum (*Aplodinotus grunniens*) in western Lake Erie, 1990-1992. (Abstract). 37th Annual Conference of the International Association for Great Lakes Research, Windsor, Ontario.

Krieger, K. A. 1999. *Ecosystem change in western Lake Erie: cause and effect of burrowing mayfly recolonization*. Final Rept. to Ohio Lake Erie Office, Project LEPF-08-94. Toledo, Ohio. 18 pp. + app. http://www.epa.state.oh.us/oleo/lepf/lepf_08-94_final.htm.

Krieger, K. A. 2000. *Ecosystem change in Lake Erie: recolonization by burrowing mayflies and their contribution to fish diets.* Final Rept. to Ohio Lake Erie Office, Project LEPF-97-30. Toledo, Ohio. 31 pp. http://www.heidelberg.edu/wql/mayflies-in-erie.html

Krieger, K. A. 2001. *Tracking rapid population change of burrowing mayflies in the central basin of Lake Erie*. Final Rept. to Ohio Lake Erie Office, Project SG 129-00. Toledo, Ohio. 8 pp. + app. http://www.heidelberg.edu/wql/mayflies-in-erie.html

Krieger, K. A. 2004. *Mayfly metric of the Lake Erie Quality Index: design of an efficient censusing program, data collection, and development of the metric.* Final Rept. To Ohio Lake Erie Office, Project LEQI 01-03. Toledo, Ohio. 33 pp.

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

Madenjian, C. P., D. W. Schloesser, and K. A. Krieger. 1998. Population models of burrowing mayfly recolonization in western Lake Erie. *Ecological Applications* 8:1206-1212.

OLEC (Ohio Lake Erie Commission). 1998. *State of Ohio 1998 state of the lake report: Lake Erie Quality Index.* 88 pp.

OLEC (Ohio Lake Erie Commission). 2000. *Lake Erie protection and restoration plan.* Toledo, Ohio. 48 pp.

Price, J. W. 1963. A study of the food habits of some Lake Erie fishes. *Bulletin of the Ohio Biological Survey* 11(1). 89 pp.

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

Schertzer, W. M., J. H. Saylor, F. M. Boyce, D. G. Robertson, and F. Rosa. 1987. Seasonal thermal cycle of Lake Erie. *Journal of Great Lakes Research* 13:468-486.

Schloesser, D. W., K. A. Krieger, J. J. H. Ciborowski, and L. Corkum. 2000. Recolonization and possible recovery of burrowing mayflies (Ephemeroptera: Ephemeridae: *Hexagenia* spp.) in Lake Erie of the Laurentian Great Lakes. *Journal of Aquatic Ecosystem Stress and Recovery.* 8:125-141.

USEPA (U.S. Environmental Protection Agency), Great Lakes National Program Office. 2004. Lake Erie "Dead Zone". www.epa.gov/glnpo/lakeerie/eriedeadzone.html. Accessed July 2004.

Winter, A., J. J. H. Ciborowski, and T. B. Reynoldson. 1996. Effects of chronic hypoxia and reduced temperature on survival and growth of burrowing mayflies, *Hexagenia limbata* (Ephemeroptera: Ephemeridae). *Canadian Journal of Fisheries and Aquatic Sciences* 53:1565-1571.