

Distribution and Abundance of Burrowing Mayflies (*Hexagenia* spp.) in Lake Erie, 1997–2005

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ABSTRACT. *Burrowing mayflies* (*Hexagenia limbata* and *H. rigida*) recolonized sediments of the western basin of Lake Erie in the 1990s following decades of pollution abatement. We predicted that *Hexagenia* would also disperse eastward or expand from existing localized populations and colonize large regions of the other basins. We sampled zoobenthos in parts of the western and central basins yearly from 1997–2005, along the north shore of the eastern basin in 2001–2002, and throughout the lake in 2004. In the island area of the western basin, *Hexagenia* was present at densities $\leq 1,278$ nymphs/m² and exhibited higher densities in odd years than even years. By contrast, *Hexagenia* became more widespread in the central basin from 1997–2000 at densities ≤ 48 nymphs/m² but was mostly absent from 2001–2005. Nymphs were found along an eastern basin transect at densities ≤ 382 /m² in 2001 and 2002. During the 2004 lake-wide survey, *Hexagenia* was found at 63 of 89 stations situated throughout the western basin ($\leq 1,636$ nymphs/m², mean = 195 nymphs/m², SE = 32, N = 89) but at only 7 of 112 central basin stations, all near the western edge of the basin (≤ 708 nymphs/m²), and was not found in the eastern basin. *Hexagenia* was found at 2 of 62 stations (≤ 91 nymphs/m²) in harbors, marinas, and tributaries along the south shore of the central basin in 2005. Oxygen depletion at the sediment-water interface and cool temperatures in the hypolimnion are probably the primary factors preventing successful establishment throughout much of the central basin. *Hexagenia* can be a useful indicator of lake quality where its distribution and abundance are limited by anthropogenic causes.

INDEX WORDS: *Hexagenia*, Ephemeroptera, mayfly, bioindicator, pollution, hypoxia, Great Lakes.

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INTRODUCTION

The Lake Erie ecosystem has undergone major changes since Europeans began to exploit its resources in the eighteenth century. These changes included a long-term, increasing degradation of lake water and sediment quality that disrupted aquatic ecosystem integrity and threatened public health (Burns 1985, Makarewicz and Bertram 1991).

Until the middle of the twentieth century, two native species of burrowing mayflies, *Hexagenia limbata* (Serville) and *H. rigida* McDunnough, were widespread and abundant in sediments of the western basin of Lake Erie (Britt 1955) and probably parts of the nearshore regions of the central and eastern basins (Fig. 1) (Reynoldson and Hamilton 1993) as well as shallow, mesotrophic regions of other Laurentian Great Lakes such as Green Bay, Lake Michigan (Howmiller 1971), and Saginaw Bay, Lake Huron (Surber 1955, Schneider *et al.* 1969). Between 1930 and the early 1950s, densities of *Hexagenia* nymphs in the sediments of the western basin averaged about 150–200 nymphs/m² (Schloesser *et al.* 2000), and at some locations in the island area, densities occasionally exceeded 1,000 nymphs/m² (Britt 1955, Wright *et al.* 1955). In western Lake Erie *Hexagenia* nymphs were an important component of the aquatic food web because they were consumed in large numbers by numerous fishes including yellow perch (*Perca flavescens*), white perch (*Morone americana*), freshwater drum (*Aplodinotus grunniens*), and channel catfish (*Ictalurus punctatus*) (Boesel 1937, Daiber 1952, Price 1963). Nuisance swarms of the subimagos and imagos were widely reported in the 1940s and early 1950s (Teale 1960, Burns 1985).

Hexagenia populations were devastated in September 1953 as a result of depletion of dissolved oxygen above the sediments (Britt 1955). Other factors, particularly increased application of insecticides in the Great Lakes basin, have been suggested, with little evidence, as additional mechanisms in the demise of burrowing mayflies in Lake Erie (Burns 1985). Oxygen depletion was known to be an increasing problem in much of the central basin (Burns 1985), but until the 1950s the shallowness of the polymictic western basin seemed to ensure a sufficient supply of dissolved oxygen at the sediment-water interface. Localized populations of *Hexagenia* survived from the 1960s through 1980s within a few km of shore or lakeward of the Detroit River mouth (Krieger *et al.* 1996) but apparently were absent from the rest of the western basin.

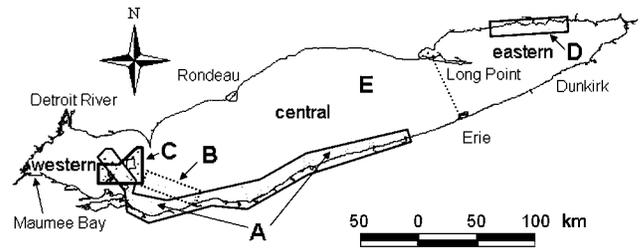


FIG. 1. Study areas of the independent surveys of *Hexagenia* in Lake Erie. A. Southern nearshore stations of central basin and island area of western basin, 1997–2003, and central basin inshore stations, 2005; B. Southwestern central basin, 2004; C. Bass and Pelee islands area; D. North shore transects in eastern basin, 2001–2002; E. Entire lake at depths ≥ 1.5 m, Erie Collaborative Comprehensive Survey, 2004. Dashed line represents approximate boundary between central and eastern basins.

Under the Great Lakes Water Quality Agreement of 1972 signed by Canada and the U.S., an extensive binational effort was undertaken to reduce and eliminate sources of pollution to Lake Erie. Water quality in the lake responded to those measures (Makarewicz and Bertram 1991). The percent of western basin stations colonized by *Hexagenia* began to increase around 1982, especially near shore, and densities began to increase around 1995 (Schloesser *et al.* 2000).

The history of *Hexagenia* in the central basin is not well documented. Limited paleolimnological evidence indicates that mayflies never populated offshore sediments of the basin beneath the hypolimnion (Reynoldson and Hamilton 1993). Brown (1953), who collected benthic samples at river mouths along the Ohio shore in May 1950, reported *Hexagenia* sp. in < 15% of the samples from the Huron and Vermilion rivers and none from the Sandusky, Grand, and Ashtabula rivers and Conneaut Creek (Fig. 2). Residents along the central basin south shore report large swarms of *Hexagenia* in the 1950s and perhaps 1960s (K.A. Krieger, *pers. observ.*). Only one nymph was found south of Long Point among all samples from the central basin collected during 24 cruises in the years 1963–65 by the Great Lakes Institute, University of Toronto (Barton 1988a). *Hexagenia* was very rare or absent from the central basin in the 1970s. Hundreds of sedi-

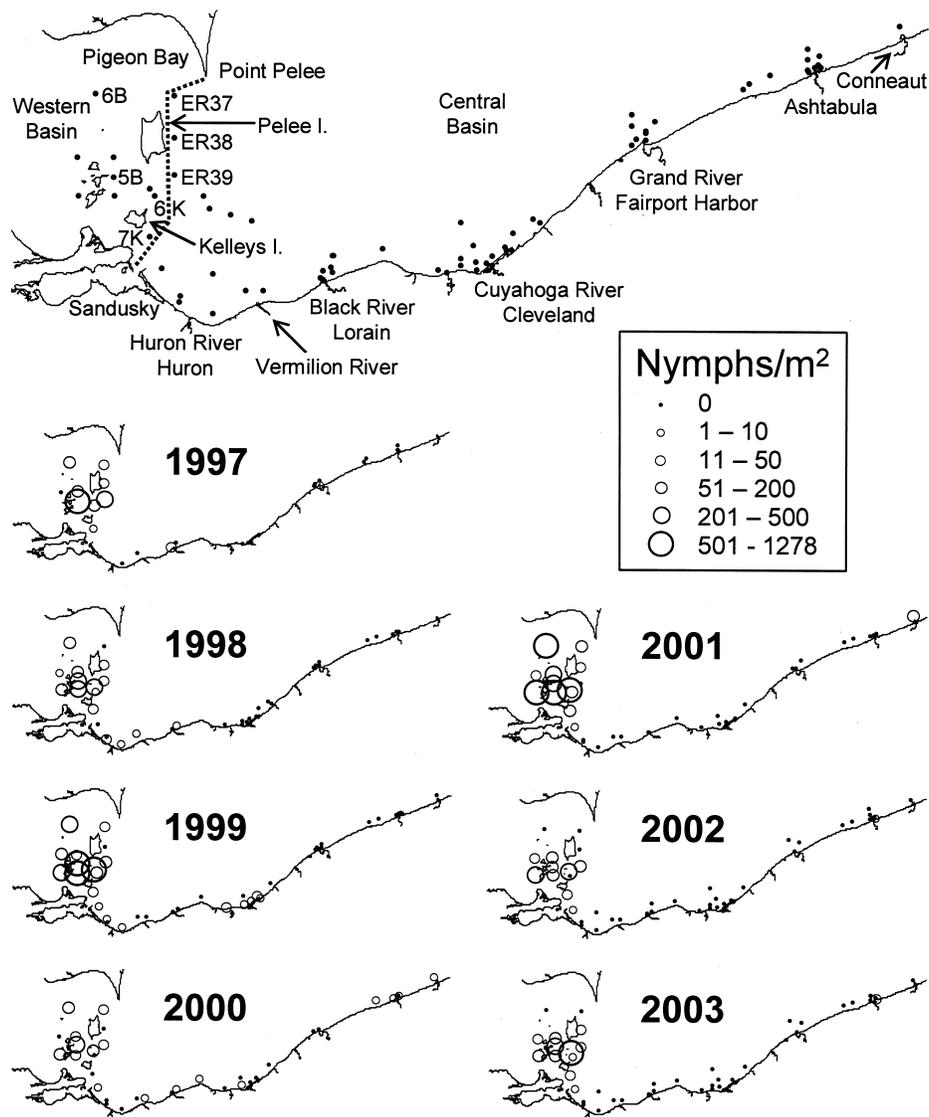


FIG. 2. Top panel: Stations sampled for *Hexagenia* in the central basin and island area of the western basin one or more years, 1997 through 2003. Dashed line shows approximate boundary between the western and central basins. Lower panels: Mean densities of *Hexagenia* at individual stations each year.

ment samples collected at depths of 2–17 m in the southern nearshore zone of the basin in 1971–1972 (Cleveland area: R.G. Rolan, unpublished data), 1978 and 1979 (Huron to Conneaut, Ohio: Krieger 1984), 1987 (Huron to Ashtabula, Ohio: M.T. Bur, unpublished data), 1988 and 1989 (Cleveland Harbor vicinity: Krieger and Ross 1993), and 1995 (Huron to Ashtabula: Pira 2003) lacked *Hexagenia* nymphs. Unlike the western basin, no summer swarms of *Hexagenia* had been reported along the

central basin shores by the mid-1990s. However, Corkum *et al.* (1997) conducted light trap surveys around the lake in 1994. They reported collecting adults at all 12 western basin sites, at Vermilion, Ohio, and Rondeau, Ontario, in the central basin, and at Dunkirk, New York, in the eastern basin (Fig. 1). No adults were observed at five central basin sites between Vermilion and Erie, Pennsylvania, in the U.S. or at four eastern basin sites in Ontario.

The zoobenthos of the eastern basin has received little study. Nymphs of *Hexagenia* were found fairly consistently but at low densities (26 nymphs/m² to 107 nymphs/m²) at depths of 4 m to 10 m in Long Point Bay from 1963–1972 (Veal and Osmond 1968; Barton 1988a,b). Flint and Merckel (1978) collected samples from 1973–1976 at 26 stations throughout the basin encompassing all depths. They did not report the presence of mayflies among a wide diversity of macroinvertebrates even though many stations had soft sediments. They also noted that hypoxia did not develop during the four years of study. Masteller and Felege (2003) found *Hexagenia* nymphs from 1999–2001 in benthic samples from as deep as 14 m in the nearshore area north and east of Presque Isle near Erie, Pennsylvania, where favorable habitat was interspersed among outcrops of shale and beds of *Dreissena* sp. (zebra or quagga mussels) and sand. Weather radar in Erie, Pennsylvania, recorded the relative density and movement of large *H. rigida* swarms over the lake along 134 km of shoreline in 2001 (Hagenbuch and Masteller 2003). However, the swarms were not detected after 2001 and few winged individuals were found onshore in the following summers (E. Masteller, Pennsylvania State University, pers. commun., 11 May 2006). Nymphs were collected from multiple locations in New York and Ontario waters in 1998; adult swarms were found in those same locations in 1999 (S.L. Parker, Cornell University, unpublished data).

In anticipation that *Hexagenia* would disperse from the western basin into the central basin, we conducted annual surveys from 1997–2003 in the nearshore zone of the central basin in Ohio. These were complemented with annually collected samples from sites around Pelee Island (Fig. 2). In addition, the zoobenthos in all three basins was sampled in 2004 as part of the Lake Erie Collaborative Comprehensive Survey (ECCS) sponsored by Environment Canada and U.S. EPA. In this paper we (1) integrate several independent studies that document the distribution and abundance of *Hexagenia* in the central basin from 1997–2005, (2) compare those data with population changes in the island area of the western basin, (3) present the lake-wide distribution and abundance of *Hexagenia* in 2004, (4) discuss factors that may prevent *Hexagenia* from successfully colonizing large areas of Lake Erie, and (5) address the potential of these mayflies to serve as a bioindicator in the Laurentian Great Lakes.

STUDY AREA

We sampled sediments from May to mid-June 1997–2003 at 16 to 36 stations in the southern nearshore zone of the central basin and, for comparison, four stations in the southeastern island area of the western basin (Fig. 1). Most stations were sampled every year. When we encountered a hard substratum where previously we had found soft sediment, primarily east of Cleveland, we searched for penetrable sediment nearby. In addition, we collected samples annually from four stations off the east side of Pelee Island and four stations surrounding the Bass Islands (Fig. 1). In the eastern basin, we sampled five transects in late May or early June and August 2001 and 2002 (three transects in August 2002) at 2, 5, 10, and 20 m perpendicular to the north shore (Fig. 1).

In 2004, numerous organizations collaboratively sampled 284 ECCS stations on hard and soft substrata in all three basins at depths ≥ 1.5 m. Also in 2004, we sampled several offshore central basin stations (Fig. 1). To determine whether semi-enclosed inshore habitats provide localized refugia for *Hexagenia*, in 2005 we visited 62 stations in harbors (16 stations), marinas (31), slips (4), lower tributaries at lake level (9), and open lake (2) along the central basin shoreline from Huron to Ashtabula, Ohio (Fig. 2).

METHODS

Sampling was completed most years in May and June prior to the beginning of the seasonal emergence of subimagos (Table 1). Some sampling in 2000 was delayed because of storms, and nymphal exuviae were noted on the lake surface while sampling. Most of the 284 ECCS stations were sampled between 10 May and 25 June 2004 prior to *Hexagenia* emergence, although four eastern basin and one central basin stations were sampled 20–21 September 2004 and six western basin stations were sampled on 29 August, 1 September, and 5 October 2004. In addition to ECCS sampling, five stations in the central basin were sampled in May and June, and three stations in October 2004 (Fig. 1).

In the central basin and island area of the western basin from 1997 through 2004, we collected four or five replicate samples at each station. An Ekman grab (24 cm \times 24 cm) was used at most stations in 1997 and 1998, and a Ponar grab (21 cm \times 21 cm) from 1999–2003. A petite Ponar grab (15 cm \times 15 cm) was used at other stations. For ECCS, three replicate samples were collected by Ponar (penetra-

TABLE 1. Number of stations, dates sampled, station depths, and depths of stations possessing nymphs each year of the surveys in the island area of the western basin (W) and southern nearshore central basin (C), 1997–2005. Abbreviation: NS = not sampled.

Year	Stations	Dates	Station Depths, m	Stations with Nymphs	Depths with Nymphs, m	Nymphs/m ²
1997	26	22 May–4 June	4.6–17.1	10	5.0–12.0	W: 5–624 C: 0–24
1998	41	29 Apr–11 June	7.3–14.0	15	7.8–13.8	W: 0–240 C: 0–14
1999	41	5 May–10 June	8.2–18.3	19	7.8–12.7	W: 0–1,081 C: 0–48
2000	39	16 May–30 June	8.5–16.8	17	9.0–15.3	W: 0–207 C: 0–5
2001	39	31 May–14 June	7.0–15.5	13	9.0–14.4	W: 0–1,244 C: 0–58
2002	48	28 May–13 June	4.6–19.3	10	9.0–12.0	W: 0–302 C: 0–9
2003	45	19 May–22 June	7.6–18.6	12	9.0–12.7	W: 0–1,278 C: 0–23
2004	7	27 May–13 October	11.6–15.1	4	13.7–14.9	W: NS C: 0–161
2005	62	15 May–2 June	1.5–9.0	2	2.5–4.0	W: NS C: 0–91

ble sediments) or air lift sampler (hard substrata). In 2005, only one Ponar sample was collected per station.

In the eastern basin, three replicates were collected at depths of 2 m, 5 m, 10 m, and 20 m along five transects perpendicular to the north shore during early June and August 2001 and 2002, using an Ekman grab where possible (most 10-m and 20-m sites) or an air lift on rocky substrata (Patterson *et al.* 2005). These samples were concentrated using a 0.25-mm aperture mesh and were preserved in 4% formaldehyde.

To compare the relative efficiencies of the Ponar and Ekman samplers for collecting *Hexagenia*, four replicate Ekman samples were collected in 2002 and 2003 immediately after field-sieving the Ponar samples at 13 stations where nymphs were observed. Overall, the Ponar collected 1.54 times as many nymphs/m² as the Ekman (linear regression: $r^2 = 0.92$, $P < 0.01$), which is similar to the seasonal sampling efficiency (1.47–1.74) reported by

Schloesser and Nalepa (2002). The Ponar grab collected approximately 1.25 times as many *Hexagenia* nymphs/m² as the petite Ponar (Paonessa 1998). Because the Ekman occasionally yielded a greater density of nymphs, and to permit direct comparison with earlier studies that reported densities from a variety of samplers (*e.g.*, Britt 1955, Krieger *et al.* 1996), we present the data produced by all samplers without adjustment to “Ponar equivalents.”

All central basin replicates in 1997–2005, except ECCS in 2004, were individually rinsed onboard through a 0.60-mm aperture sieving bucket with a stream of lake water from a hose. The 2004 samples were rinsed in bags with 0.25-mm mesh openings. These differences in mesh size do not affect the estimated density of *Hexagenia* nymphs (Paonessa 1998). The sample residues were preserved with < 5% formaldehyde.

In the laboratory, the 1997–2003 and 2005 samples were stained with Phloxine B to aid recognition of nymphs. Residues from all years were rinsed

through a sieve of the same or smaller mesh aperture as used in the field and all nymphs were removed during two systematic passes under a dissecting microscope. For the ECCS samples, two of the three replicates for each station were randomly selected. One-third of the 568 selected replicates was randomly assigned to each of three laboratories so that only one replicate per station was processed by a given laboratory. In 2005, sample residues were observed with a single pass under a dissecting microscope. Specimens were only identified to genus because the species can be distinguished only for mature male nymphs, which typically contributed few if any individuals to any given sample.

Temperature and dissolved oxygen (DO) concentration were measured at some or all stations during a given study using a DO meter calibrated in saturated air. Most measurements were about 1 m off the bottom.

RESULTS

Distribution and Abundance

Nearshore Surveys 1997–2003, 2005

The densities of *Hexagenia* nymphs fluctuated greatly from year to year in the island area (Fig. 2). The highest densities were usually between Kelleys and Pelee islands and occasionally exceeded 1,000 nymphs/m². Densities were higher in odd years than in even years (Table 2). Nymphs were only occasionally found at some stations, most notably north and northwest of Pelee Island in 2002 and 2003. Northwest of Pelee Island (Station 6B), the density peaked at 599 nymphs/m² in 2001 followed by no nymphs in 2002 and 2003. Nymphs also were usually collected along the east shore of Pelee Island (Fig. 2). Densities increased from north to south, largely reflecting suitability of substrate for the construction of burrows.

In contrast to the island area stations, nymphs were found in the central basin in 1997 only at two

stations: outside both Fairport Harbor (one individual) and Lorain Harbor (five individuals) (Fig. 2). In 1998, no nymphs were found east of Lorain but they were found at four stations from Lorain to west of Huron. In 1999, all nymphs collected were clustered at three stations near Huron and five stations in the Cleveland area. Thus, *Hexagenia* apparently began to repopulate nearshore sediments at low densities from Sandusky to Cleveland from 1997 through 1999 but either was not repopulating the sediments east of Cleveland or was doing so more slowly.

In 2000, the maximum density in samples was 5 nymphs/m² (*i.e.*, 1 nymph in 4 replicates). The geographic range of nymphs was much greater than in the 3 previous years, extending from Sandusky to Conneaut, Ohio, except in the Fairport Harbor area (Fig. 2). Delayed sampling in June 2000 contributed to the low densities found because nymphs had already begun to emerge. Therefore, nymph densities and probably the number of locations where nymphs appeared were lower than they would have been prior to the onset of emergence.

The results of sampling in the central basin in 2001 contrasted sharply with the yearly increases in distribution and abundance seen from 1997–2000, as nymphs were only found at the easternmost and westernmost stations. The presence of apparently abandoned nymph burrows at two Cleveland stations may indicate that nymphs had emerged prior to our sampling there, although winged *Hexagenia* were not observed swarming on shore until later in the season (K. Linn, Northeast Ohio Regional Sewer District, pers. commun. 20 June 2001). *Hexagenia* was found in the eastern basin in 2001 and 2002 along only one of the three north shore transects at three depths: in June, 138 nymphs/m² at 5 m, 191 nymphs/m² at 10 m, and 0 nymphs/m² at 19 m; in August, 42 nymphs/m² at 5 m, 382 nymphs/m² at 10 m, and 26 nymphs/m² at 19 m. In June 2002, 170 nymphs/m² were found at 19 m.

To test our hypothesis that some nymphs may be residing in deeper waters than we had sampled, in

TABLE 2. Mean (SE), median, and maximum densities of *Hexagenia* nymphs/m² in the island area of the western basin of Lake Erie, 1997–2003. N is number of stations sampled.

	1997	1998	1999	2000	2001	2002	2003
Mean (SE)	183 (94)	115 (31)	367 (133)	60 (22)	427 (126)	107 (37)	248 (136)
Median	135	107	207	44	267	86	107
Maximum	624	240	1,081	207	1,244	302	1,278
N	6	9	9	9	9	9	9

TABLE 3. Ranges of temperature and dissolved oxygen (DO) measured near 1 m off the bottom at stations (N) at various depths < 15 m in the island area of the western basin (W), central basin (C), and eastern basin (E) within the time periods listed in Table 1. Abbreviation: NR = not recorded.

Year	Basin	N	Temperature (°C)	DO (mg/L)	DO (% saturation)
1997	W	2	16.4–16.4	10.5–10.7	NR
	C	1	12.2–12.2	12.2	NR
1998	W	4	10.0–10.8	NR	NR
	C	29	17.0–21.0	NR	NR
1999	W	0			
	C	11	15.3–22.6	7.3–11.0	73–121
2000	W	0			
	C	8	16.3–23.4	1.3–10.0	11–119
2001	W	2	14.8–15.8	9.0–9.2	92–92
	C	23	12.5–17.7	8.0–11.1	82–107
2002	W	3	5.3–5.4	11.8–12.6	132–136
	C	31	9.0–18.3	8.5–13.1	80–126
2003	W	1	13.1	10.5	100
	C	8	13.2–14.5	8.9–10.8	90–112
2004	W, C, E	214	4.4–24.5	2.7–14.6	NR
2005	C	57	12.5–19.6	2.5–11.0	39–133

2002 we incorporated several stations new to the series of annual surveys but along transects established decades ago by the USGS (Pira 2003) that were several km further offshore than other stations (Fig. 2). Most of those and a few other stations were sufficiently deep (≤ 19.3 m, Table 1) that the lake sediments most years would be within the metalimnion or hypolimnion (Burns 1985) and thus subject to lower temperatures and summer hypoxia. No nymphs were found at the deeper stations, although one individual (5 nymphs/m²) was found in Ashtabula Harbor and two (9 nymphs/m²) at the westernmost central basin station.

Nymphs were again almost entirely absent from central basin samples in 2003, being found only at the westernmost station (5 nymphs/m²) and immediately east of Ashtabula Harbor (23 nymphs/m²). Thus, in 2003 the distribution and abundance of nymphs in the central basin appeared to be similar to those in the prior 2 years and in 1997 (Fig. 2).

Despite apparently suitable sediment and high dissolved oxygen concentrations at most stations

during the inshore survey in 2005 (Table 3), *Hexagenia* nymphs were found at only two stations. Four nymphs (91 nymphs/m²) were found at a marina in the lower Vermilion River, and three nymphs (68 nymphs/m²) were found at one of two stations in Lorain Harbor.

Lake-wide Survey, 2004

Hexagenia was found at 63 (71%) of 89 western basin stations in 2004 (Fig. 3) at a mean density for all stations on both hard and soft substrata of 195 (SE = 32) nymphs/m² and a median of 48 nymphs/m². Stratified random selection of stations resulted in no stations in the area beyond Maumee Bay in the southwestern part of the basin or near the mouth of the Detroit River. Those regions, which consist of soft sediment, have had the highest densities of nymphs in the basin some years (Schloesser *et al.* 2000).

By contrast, *Hexagenia* was found at only seven (6%) of 112 central basin stations. Of those sta-

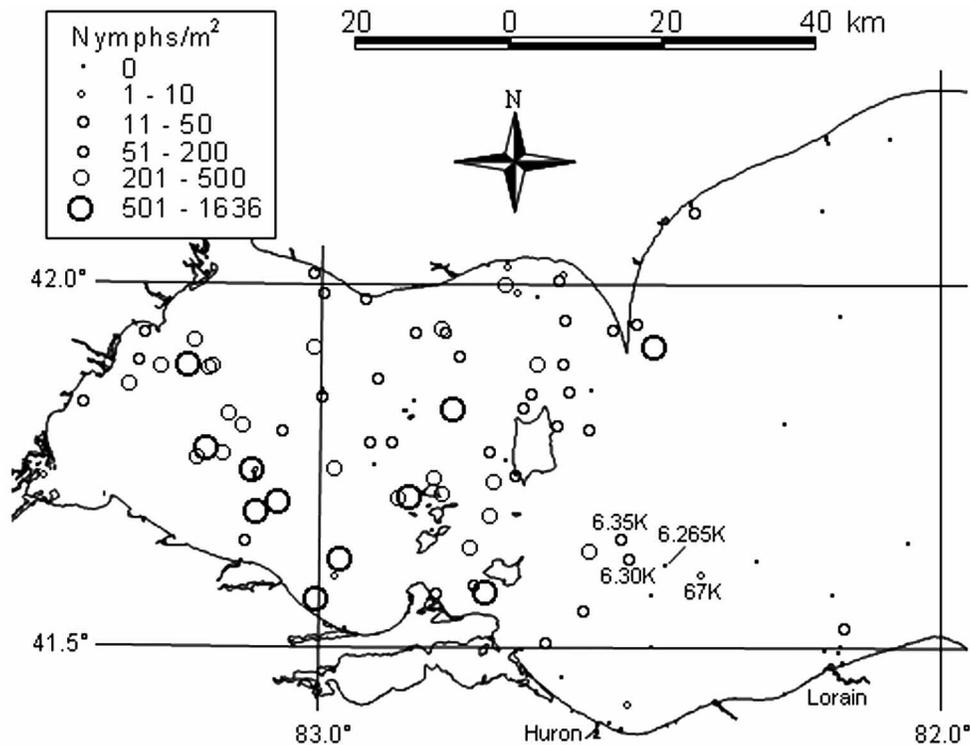


FIG. 3. Mean densities of *Hexagenia* nymphs in the central and western basins of Lake Erie in 2004 in samples from the Erie Collaborative Comprehensive Survey and additional stations in the southwestern central basin (Fig. 1B). No nymphs were found east of 82°. Four stations (e.g., 6.35K) mentioned in the text are labeled.

tions, most were < 20 km east of the western basin or < 10 km from the north or south shores near Point Pelee, Ontario, and Huron and Lorain, Ohio (Fig. 3), and at depths of 10.0–13.3 m. Mean densities at the seven stations ranged from 6 to 708 nymphs/m² (median 19/nymphs/m²). No nymphs were found east of 82° W. In a separate survey, small nymphs were found east of Kelleys Island in May 2004 at depths of 13.7 m (station 6.35K) and 14.9 m (67K) at densities of 50 nymphs/m² and 6 nymphs/m², respectively (Fig. 3). In October 2004, no nymphs were found at station 67K or nearby station 6.265K (14.6 m), but 161 nymphs/m² were obtained at station 6.30K (13.9 m) a few km south of station 6.35K. No nymphs were found at the 83 eastern basin stations.

Environmental Variables

Station depths in the central basin during the annual surveys in 1997–2004 ranged from 4.6–19.3 m

and *Hexagenia* was found at depths of 5.0–15.3 m (Table 1). Station depths in the 2004 lake-wide study ranged from 1.5 m close to shore to 60.5 m in the eastern basin, and nymphs were found at depths of 2.0–13.3 m. Depths at the 62 inshore stations in 2005 ranged from 1.5 m to 9.0 m and nymphs were collected at 2.5 and 4.0 m.

Water temperature 1 m above the bottom at representative stations visited during 1997 through 2005 ranged from 4.4°C to 24.5°C, depending on time of year and depth (Table 3). Temperatures at stations where nymphs were found ranged from 8.9°C to 24.5°C.

Similarly, DO concentrations 1 m above the bottom varied among stations and times of the year (Table 3). In general, concentrations were high (> 7 mg/L) when the lake was not thermally stratified. Low values (1.3–3.0 mg/L) were recorded occasionally during summer at offshore stations in the western basin and a few nearshore stations in the central basin.

Physical characteristics of the island area and nearshore central basin sediments varied from a homogeneous soft, cohesive clay typical of the densest nymph populations to various proportions of clay, sand, gravel, and shells of native clams and *Dreissena* spp. In the densely populated western basin and eastward to Huron, Ohio, in the central basin, nymphs were often found in substrata such as loose sand and sand-silt-shell mixtures while they were generally only found in fine-grained sediment east of Huron.

The sediment of most inshore (marina, tributary) samples in 2005 appeared suitable for *Hexagenia* nymphs in that it consisted mostly of silt and clay with varying but small proportions of gravel, sand, shells, and detritus. However, the sediment at 14 (23%) of the 62 stations was comprised mostly or entirely of sand, gravel, or detritus such as leaves and twigs. These materials provide poor habitat for *Hexagenia* because they are not suitable for burrowing. The Vermilion River station where nymphs were found had a thin layer of mud above a 1.5-cm layer of leaves, with more mud beneath. The Lorain Harbor station with nymphs possessed sediment typical of areas of the western basin with the greatest *Hexagenia* densities.

Contaminants were only infrequently observed in the field or laboratory. Occasional taconite (iron ore) pellets and bits of coal, coal cinders, and plastic were found, especially in and near harbors, and oil was occasionally seen. At several inshore stations in 2005, oil was visible in sediment in the Black River, southwestern Cleveland Harbor, the old Cuyahoga River channel, and the eastern Cleveland area; and an apparent sewage odor was noted at one station in a slip off the Cuyahoga River. No samples of visibly contaminated sediment yielded *Hexagenia*.

DISCUSSION

Distribution and Abundance

Our study and related studies (Corkum *et al.* 1997, Masteller and Felege 2003, Hagenbuch and Masteller 2003) reveal that *Hexagenia* nymphs (1) were relatively abundant in the island area of the western basin from 1997 through 2004, (2) were present in the southern nearshore zone of the central basin from 1997 through 2000 but were rarely collected there from 2001 through 2004, (3) were present in 2001 and 2002 in localized northern nearshore areas of the eastern basin, (4) primarily inhabited the western basin and the contiguous

western edge of the central basin in 2004, and (5) were largely absent from harbors, marinas, and tributary mouths along the southern shore of the central basin in 2005.

The varying densities from 1997 through 2003 at the island area stations, several of which lie at the juncture of the central and western basins (Fig. 2), indicate that conditions in the western basin were suitable for survival and maturation of nymphs during each preceding year. However, the absence of nymphs north and northwest of Pelee Island in 2002 and 2003 is consistent with their absence in other parts of the western basin, particularly Pigeon Bay to the north of Pelee Island (Schloesser *et al.* 2000). Higher densities in alternate years, as seen in the island area, were also observed for *H. limbata* in a small northwestern Ontario lake, where the pattern appeared to be related to a 2-year life cycle (Riklik and Momot 1982).

Small swarms of winged *Hexagenia* that occurred along the central basin lakeshore every year (K.A. Krieger, pers. observ.), even in years when almost no nymphs could be found, indicated that the nymphs were growing successfully in some parts of the central basin or in nearby smaller inland water bodies. The apparently expanding distribution of nymphs along the south shore of the central basin from 1997 through 2000 confirmed their ability to survive there, but their near-absence from 2001 through 2004 indicates that at least one environmental factor was limiting the establishment or survival of mayfly populations. The small numbers of winged *Hexagenia* on shore indicate that densities in the lake were very low. This was confirmed by our inshore sampling in 2005, which revealed only small, scattered populations of *Hexagenia*. For example, nymphs were found at a station in eastern Lorain Harbor but not at a nearby marina or on the western side of the harbor. The presence of a localized population of nymphs in 2001 and 2002 at one of three transects perpendicular to the northern shoreline of the eastern basin reveals a pattern similar to that observed along the southern central basin shoreline except that the eastern basin population density was much greater than the densities in the central basin. Although our data are not extensive, they begin to establish a record of the distribution and abundance of nymphs in the eastern basin.

Predation by round gobies (*Neogobius melanostomus*) may be another factor limiting the abundance of *Hexagenia* in Lake Erie. Johnson *et al.* (2005) estimated that the round goby population reached 9.9×10^9 individuals in the western basin

in 2002. Densities of round gobies were also very high (9–15 fish/m²) in the nearshore zone of the eastern basin that same year (Barton *et al.* 2005), but comparable estimates for the other basins and other years are lacking. When available, *Hexagenia* can be an important component of the diet of round gobies (French and Jude 2001).

Limiting Factors

Reynoldson and Hamilton (1993) attributed the historical absence of *Hexagenia* tusks from sediments in deep parts of the central basin to a possible combination of water depth, distance from shore, temperature requirements, or periodic anoxia. Of these, they felt that episodic anoxia was the most likely explanation. They reported that this was consistent with assessments of the relative frequency of species of subfossil ostracode shells made by Delorme (1982), who found remains of a species tolerant of low dissolved oxygen concentrations but not two species that require high levels of dissolved oxygen. However, laboratory studies suggest that Lake Erie populations of *Hexagenia* are unlikely to be able to develop to maturity given the thermal phenology of the hypolimnetic zone of Lake Erie's central basin. Both egg (Gerlofsma 1998) and larval development times (Corkum and Hanes 1992) are strongly temperature regulated. *Hexagenia* has a developmental temperature threshold as low as 8°C, requires as few as 1,400 degree days above the growth threshold, and can emerge when water temperatures reach 12°C near the northern limit of its geographical range (Giberson and Rosenberg 1992, 1994). However, more-southern populations have a higher threshold, requiring from > 1,700 degree days above 10°C in southern Manitoba to > 2,500 degree days for a laboratory-reared Midwest U.S. population (Heise *et al.* 1987). In Lake Erie, *Hexagenia* subimagos do not emerge in large numbers until the water temperature reaches 20°C (Corkum *et al.* in press).

Schertzer *et al.* (1987) provided a continuous record of near-bottom temperature readings from a 23 m deep central basin site between June and December 1979. Temperature rose to about 10°C in mid-July, reached 12°C during the first week in August, and remained constant until early September, when summer stratification ended. The near-bottom temperature then rose more quickly, reaching 18°C for 1 week at the end of September. Thereafter, temperature declined linearly through time, falling below 10°C by the beginning of November. We

converted those data into cumulative degree days to estimate the time needed for *Hexagenia* to develop from an egg (oviposited in early July by a western-basin gravid female) to an emergent subimago under prevailing temperatures in the hypolimnetic region. In all, 512 degree days above 10°C were accumulated.

Laboratory data from Gerlofsma (1998) indicate that Lake Erie *Hexagenia* eggs require 100 degree days above 10°C to hatch. Therefore, eggs deposited in early July could hatch in mid-August of the year of oviposition. However, if we assume that *Hexagenia* larvae require 1,900 degree days over 10°C (Corkum and Hanes 1992) and a threshold temperature of 12°C to stimulate emergence (Giberson and Rosenberg 1994), the first opportunity for nymphs to transform into subimagos would be in November, 3 years after they hatched. The earliest opportunity for emergence in the subsequent year would be early August. Although *Hexagenia* adults are occasionally observed as late as August in Lake Erie, this is well past the time when mass swarms are observed (Corkum *et al.* in press; K.A. Krieger, unpublished data). Such developmental rates pertain to growth under normoxic conditions, but even mild hypoxia slows *Hexagenia* growth (Winter *et al.* 1996) and would likely delay development further. Consequently, we conclude that *Hexagenia* is unlikely to have ever successfully developed in the deep areas of the central basin whether or not it has always been subject to episodic hypoxia.

When we sampled nymphs each year (late April to mid-June), DO concentrations above the sediment were often at or near saturation. Thermal stratification only becomes established later (mid-June to July) and at greater depths (15–20 m; Schertzer *et al.* 1987) than all but 10 of our central basin stations.

Even though DO concentrations are high in spring and early summer in both the western and central basins, they often decline later in summer to < 2 mg/L in parts of the western basin (Krieger *et al.* 1996; Bridgeman *et al.* 2006; M. Thomas, Stone Laboratory, personal communications, June 1996 and later) and < 1 mg/L in much of the central basin hypolimnion (Burns *et al.* 2005). Bridgeman *et al.* (2006) have linked climatic conditions that affect DO concentrations in June to the relative success or failure of recruitment of the subsequent cohort of nymphs in the western basin in a given year. *Hexagenia* nymphs cannot survive for more than 24 h at DO concentrations below about 1 mg/L (Eriksen 1963), especially at warmer temperatures (Winter *et*

al. 1996). Thus, the absence of nymphs some years at several island area stations and most of the shallow central basin stations is probably related to seasonally low DO. Their absence in shallow areas of the central basin above the hypolimnion may be the result of internal seiches that cause episodic upwelling of hypoxic water into those areas. Bartish (1987) reported incursions of hypoxic central basin water into the western basin at depths as shallow as 9 m. Given the sensitivity of *Hexagenia* nymphs to hypoxia, 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.

The distributions and densities of *Hexagenia* populations should provide clues to the frequency, extent, or severity of episodes of hypoxia in parts of Lake Erie, especially in relation to the "dead zone" (hypoxic area of hypolimnion) that develops in the central basin. That hypothesis seems to be supported indirectly by the results of our 2004 sampling. As is typical prior to establishment of the thermocline, DO concentrations in May and June 2004 were high and nearly uniform from the top to the bottom of the water column, as they were in October 2004 after the thermocline dissipated. Therefore, our DO readings do not provide evidence of oxygen stress that may have been present much of the summer. We did not analyze the sediments for harmful or lethal concentrations of pollutants (e.g., DDT, PCBs, PAHs) that may be a factor in the absence of mayflies, though a number of studies (e.g., Burns 1985, Schloesser *et al.* 1991) have indicated that *Hexagenia* can tolerate elevated concentrations of most of such persistent organic contaminants.

Data that show the shoreward extent of hypoxia when the hypolimnion exists are lacking. However, zoobenthic taxa reflect the environmental conditions experienced throughout their life stages at the lake bottom. Therefore, the abundance or absence of oxygen-sensitive invertebrates such as burrowing mayflies may indicate the severity of summer hypoxia at the sediment-water interface. Because we found *Hexagenia* at a low density (50 nymphs/m²) in May 2004 at a 13.7-m deep station in the central basin and also found small nymphs (6 nymphs/m²) in May further east at 14.9 m, we sampled again in October to determine whether the young nymphs found in May had survived the summer. However, no nymphs were collected. The absence of *Hexagenia* at those stations in October 2004 was consistent with our hypothesis that hypoxia there during part of the summer prevented their survival.

Sediment composition also influences the distribution and abundance of *Hexagenia*. Soft, firm clay or clay-silt supports the greatest densities. Sand is a relatively poor habitat for nymphs, and associated water currents may frequently disturb and mix the sediments, thereby interfering with maintenance of burrows. Therefore, it is difficult to infer water and sediment quality from samples collected in suboptimal habitats.

The expansion of *Hexagenia*'s range along the southern nearshore zone of central Lake Erie from 1997 through 2000 appeared to reflect an eastward colonization from the western basin as well as the expansion of pre-existing small, disjunct populations that became more readily detectable as their size and density increased. However, the increased distribution and density were not sustained in most of the study area (Fig. 2). Nymphs remained abundant throughout much of the western basin, where relatively high densities were present between 1995 and 2006 (Schloesser *et al.* 2000; D.W. Schloesser and J.J.H. Ciborowski, unpublished data). This suggests that the failure of central basin populations to be maintained reflects local conditions rather than lake-wide or broader regional effects. Even in western Lake Erie, the anticipated restoration of nymphs is not complete in that nymphs do not presently occur throughout their former range (Schloesser *et al.* 2000; J.J.H. Ciborowski unpublished data). Indeed, the "recovery" could be temporary. Schloesser (unpublished data) recorded marked year-to-year fluctuations in western Lake Erie, with basin-wide mean densities of about 100 nymphs/m² following peaks that occasionally reach about 500 nymphs/m². Superficially, these patterns are consistent with density-dependence. However, Bridgeman *et al.* (2006) suggest that DO concentrations at the sediment-water interface, partially determined by weather conditions, play a role in controlling the success of annual cohort production and possibly the survival of the population. Similar processes may be operating in the central basin near shore.

Hexagenia as a Lake Quality Indicator

The failure of *Hexagenia* to establish persistent populations along the southern shore of central Lake Erie except in a few isolated locations, and other areas of the Laurentian Great Lakes where it had been present historically and was observed again in the early 1990s, has substantial implications for its use as an environmental indicator. *Hexagenia* can serve as an important indicator in its

historical ranges, including tributary mouths, harbors, bays, interconnecting channels, shallow basins of the Great Lakes, and certain nearshore areas such those bordering the north and south shores of Lake Erie's central and eastern basins. This taxon has been used historically as an indicator in the Laurentian Great Lakes and shallow waters elsewhere (Fremling 1964, Schloesser 1988, Schloesser *et al.* 1991, bij de Vaate *et al.* 1992, Edsall *et al.* 2005).

In the Laurentian Great Lakes, the Ohio Lake Erie Commission (OLEC 2004), Environment Canada and USEPA (2003), and USEPA (Detroit River-Western Lake Erie Basin Indicator Project) have adopted the abundance of *Hexagenia* as a bioindicator of lake quality. Presently these measures of recovery rely solely on data collected from western Lake Erie since 1995 (Krieger *et al.* 1996; Schloesser *et al.* 2000; D.W. Schloesser unpublished data). Target goals may change as the responses of *Hexagenia* to environmental perturbations in the basin are better understood. At present, Ohio's Lake Erie Quality Index (OLEC 2004) has established a set of density ranges based on a 3-y running average to determine a narrative score (e.g., Good = 101–200 nymphs/m²). Overall, western Lake Erie exhibited a mean density of 195 nymphs/m² in 2004, near the present index score of "Excellent" (201–300 nymphs/m²). Target densities unique to other areas of Lake Erie and other North American great lakes may be needed in order to reflect realistic expectations given the natural and anthropogenic constraints in each.

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