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DON W. SCHLOESSER[1] and THOMAS F. NALEPA[2]

[1]Great Lakes Science Center, U.S. Geological Survey, Ann Arbor, Michigan 48105, USA
[2]Great Lakes Environmental Research Laboratory, National Oceanic and Atmospheric Administration, Ann Arbor, Michigan 48105, USA

# Changing Abundance of *Hexagenia* Mayfly Nymphs in Western Lake Erie of the Laurentian Great Lakes: Impediments to Assessment of Lake Recovery?

*key words:* mayfly, lake recovery, recruitment, Laurentian Great Lakes

## Abstract

After an absence of 40 years, mayfly nymphs of the genus *Hexagenia* were found in sediments of western Lake Erie of the Laurentian Great Lakes in 1993 and, by 1997, were abundant enough to meet a mayfly-density management goal (ca. 350 nymphs $m^{-2}$) based on pollution-abatement programs. We sampled nymphs in western Lake Erie and Lake St. Clair, located upstream of western Lake Erie, to determine the importance of seasonal abundance and life-history characteristics of nymphs (e.g., emergence and recruitment) on density estimates relative to the mayfly-density management goal. Two types of density patterns were observed: (1) densities were relatively high in spring and gradually decreased through late summer (observed in Lake Erie and Lake St. Clair in 1997 and Lake St. Clair in 1999) and (2) densities were relatively high in spring, gradually decreased to mid summer, abruptly decreased in mid summer, and then increased between summer and late fall (Lake Erie and Lake St. Clair in 1998 and Lake Erie in 1999). Length-frequency distributions of nymphs and observations of adults indicate that the primary cause for the two density patterns was attributed to failed (first pattern) and successful (second pattern) reproduction and emergence of nymphs into adults in mid summer. Gradual declines in densities were attributed to mortality of nymphs. Our results indicate that caution should be used when evaluating progress of pollution-abatement programs based on mayfly densities because recruitment success is variable both between and within years. Additionally, the interpretation of progress toward management goals, relative to the restoration of *Hexagenia* populations in the Great Lakes and possibly other water bodies throughout the world, is influenced by the number of years in which consequtive collections are made.

## 1. Introduction

In 1992, swarms of adult burrowing mayflies (*Hexagenia limbata* and *H. rigida*) were observed in open waters of the western basin of Lake Erie after an absence of about 40 years (KRIEGER *et al.*, 1996). Subsequent studies of western Lake Erie revealed that nymphs were present in sediments in many parts of the basin in 1993, had become abundant enough to be noted by the general public in 1994, and by 1997 had reached a basin-wide density (350 $m^{-2}$) similar to those found in the 1930s and 1950s (BURNS, 1985; ASIKARI, 1994; MADENJIAN *et al.*, 1998; SCHLOESSER *et al.*, In review). Except, for a small, localized emergence of adult mayflies in an area with small islands in 1981 (BURNS, 1985), no large emergences over a broad geographic area were noted until 1996 when an *en masse* emergence was observed over a large portion of the basin (ASSOCIATED PRESS, 1996; THE BLADE, 1996). Between 1996 and 1999 emergences were similar to those observed in the 1930s and were large enough to disrupt electrical power generation, create automobile hazards and be of nuisance to nearshore residents and tourists (ASSOCIATED PRESS, 1996; THE BLADE, 1996; SCHABATH, 1998). The recovery of benthic species, such as mayfly nymphs in western Lake Erie, in waters throughout North America and other parts of Europe is attributed to pollution-abatement programs which were initiated near the middle of the 20[th] century (FREMLING and JOHNSON, 1990; EDMONDSON, 1991; BIJ DE VAATE *et al.*, 1992; LATHROP, 1992).

Little information exists concerning seasonal abundance and life-history information (e.g., period of recruitment) of burrowing mayflies in the Great Lakes and especially western Lake Erie because nymphs have been absent or occured in insufficient numbers to obtain life history information for about the past 40 years (BEETON, 1961; BRITT, 1955a, 1955b; SCHLOESSER *et al.*, 1991; SCHLOESSER and HILTUNEN, 1984; SCHLOESSER *et al.*, In review). The only information about density fluctuations and life-history characteristics of nymphs in western Lake Erie was obtained in 1942–1944 when CHANDLER (1963) combined data on densities and length-frequency distributions of nymphs with observations of adult (i.e., subimago) emergence patterns to examine the life history of nymphs.

Knowledge of seasonal densities and life-history characteristics of burrowing mayfly nymphs in western Lake Erie may be important because the abundance of nymphs has been established as a management goal for pollution-abatement programs initiated in the early–1970s (REYNOLDSON *et al.*, 1989; OHIO LAKE ERIE COMMISSION, 1998). Although a density of 1000 nymphs $m^{-2}$ has been suggested as a management goal for open waters of western Lake Erie, lake-wide means of 350 nymphs $m^{-2}$ for fair conditions, 400 $m^{-2}$ for good conditions and 450 to 500 $m^{-2}$ for excellent conditions have been adopted by one management agency (REYNOLDSON *et al.*, 1989; OHIO LAKE ERIE COMMISSION, 1998). In addition, recent colonization of mayflies throughout western Lake Erie as a result of pollution-abatement programs and impacts of zebra mussels have resulted in a hypotheses that mayflies are near full recovery, and to speculation that continued pollution-abatement programs may lead to lower system productivity and ultimately to lower fish production (ASSOCIATED PRESS, 1994; KRIEGER *et al.*, 1996; KOLAR *et al.*, 1997; HENRY, 1998; MADENJIAN *et al.*, 1998).

We determined the abundance and length-frequency distributions of *Hexagenia* spp. nymphs in western Lake Erie to examine the impact of life-history characteristics on the density of nymphs relative to basin-wide management goals. If density estimates of nymphs are strongly influenced by life-history characteristics, then our ability to use *Hexagenia* to assess progress toward management goals may be affected.

## 2. Methods

### *2.1. Sampling*

Sediment samples were collected monthly May–October 1997, March–November 1998 and April–October 1999 from one site in western Lake Erie (site 7M; 41°44′00″ N, 83°17′50″ W) where the population of *Hexagenia* spp. nymphs was recovering in the early 1990s, and at one site in Lake St. Clair (site 1; 42°25′00″ N, 82°45′00″ W) where nymph populations have been relatively stable for the past decade (Fig. 1) (SCHLOESSER *et al.*, 1991; KRIEGER *et al.*, 1996; SCHLOESSER *et al.*, In review; pers. comm., R. HAAS, Michigan Department Natural Resources, Mt. Clemens, Michigan). Sediments were soft and very similar (texture, color and composition) at the two sites with the exception that sediments in Lake St. Clair were a little firmer (as a result of loose clay) than those in Lake Erie. Thus, all sediment samples from Lake Erie filled the sampler, whereas in Lake St. Clair the sampler was full about 90% of the time and the remaining 10% of the time samples filled between 80% and 90% of the sampler.

Three Ponar grab samples (484 $cm^2$ each) were obtained at each site and date to determine density of nymphs per $m^2$. Additional grab samples were obtained during some sampling periods of low nymph abundance (e.g., in western Lake Erie in June 1998 when 13 samples were taken) to obtain additional

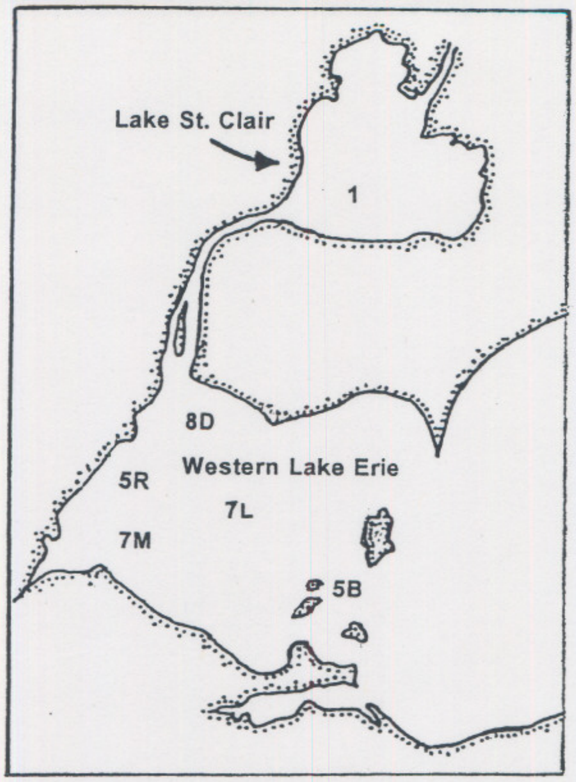


Figure 1. Locations of one study site in western Lake Erie (site 7M) and one in Lake St. Clair (site 1) where *Hexagenia* nymphs were collected monthly May-October 1997, March–November 1998 and April–October 1999, and at four sites in western Lake Erie (5B, 8D, 7L and 5R) where nymphs were collected May 1998 and 1999.

nymphs to aid in determining length-frequency distributions. In addition, 10 to 30 grab samples per site were collected at sites 8D, 5B, 7L, and 5R during other studies of western Lake Erie in May 1998 and 1999 to assess spatial variability in length-frequency distributions (Fig. 1; site coordinates in CARR and HILTUNEN, 1965; SCHLOESSER *et al.*, In review).

### 2.2. *Laboratory Processing*

Sediment samples were washed over a U.S. Standard No. 30 sieve (mesh size, 0.6 mm), and retained material was placed in individual jars and a cooler containing ice. Within 24 hours, each sample of retained bottom material was washed over a U.S. Standard No. 35 sieve (0.5 mm), placed in a white pan and live nymphs removed. Nymphs were enumerated and placed in 10% buffered formalin solution. Total length (whole mm sizes from the anterior tip of the head to the posterior end of the last abdominal segment; HUNT, 1953; SCHLOESSER and HILTUNEN, 1984) and identification to genus (EDMUNDS *et al.*, 1976) of individual nymphs were determined at 7–70X magnification. Life-history information was obtained from length-frequency distribution curves composed of individual nymph lengths.

Sex and species identifications were determined, but are not included here because the data indicated an inconsistent ability to determine these characteristics in all size ranges of nymphs (unpublished data are available from one of the authors, DWS). Consistent use of sexual and species characteristics is difficult for nymphs below 15 mm in length (MANNY, 1991; P. HUDSON, pers. comm., USGS Ann Arbor, Michigan). Separation of nymphs of the two species of adult mayflies (*Hexagenia limbata* (SER-

VILLE), 1829 and *Hexagenia rigida* MCDUNNOUGH, 1924) historically found before 1953 and those now being found along the shores of western Lake Erie is not possible at the present time (BRITT *et al.*, 1973; KRIEGER *et al.*, 1996). Many authors discuss the difficulty of separating species of *Hexagenia* based on nymphs and some believe an exhaustive description of nymphs needs to be undertaken before species separation of nymphs is possible (NEEDHAM, 1917–18; SPIETH, 1941; EDMUNDS, 1973; MCCAFFERTY, 1975). However, several studies have differentiated sex and species of medium and large (e.g., >ca. 8–10-mm length) *Hexagenia* spp. nymphs and assumed equal ratios of these characteristics for smaller nymphs (HEISE *et al.*, 1987; GIBERSON and ROSENBERG, 1994; pers. comm., D. GIBERSON, University of Prince Edward Sound, Charlottetown, Prince Edward Island, Canada). Species identification of nymphs in western Lake Erie is presently being investigated (pers. comm., J. CIBOROWSKI, University of Windsor, Canada and D. BERG, Miami University, Oxford, Ohio).

### *2.3. Additional Data*

Length-frequency distributions of nymphs were also obtained from nymphs collected in Ponar grab samples from one other site in Lake St. Clair (site 177 coordinates in EDSALL *et al.*, 1991) and one in western Lake Erie (near 8D–11D site coordinates in CARR and HILTUNEN, 1965) May and October 1986 and 1994, respectively (unpublished data, DWS). Density and relative size (i.e., small versus large) of length groups of nymphs found in the St. Marys River in 1974 and in western Lake Erie in 1942–1944 were obtained from SCHLOESSER and HILTUNEN (1984) and a figure constructed by D. C. CHANDLER (Fig. 2 in MANNY, 1991), respectively. These distributions were visually assessed to determine the number of distinguishable-length groups of nymphs (CHANDLER, 1963; SCHLOESSER and HILTUNEN, 1984; HEISE *et al.*, 1987; GIBERSON and ROSENBERG, 1994).

## 3. Results

Wide fluctuations in abundance of mayfly nymphs occurred within and between years in both Lake Erie and Lake St. Clair (Fig. 2). In both lakes, densities in 1997 were relatively high in spring (April and May), decreased through early and mid summer (June and July) and became relatively stable between late summer and mid fall (August through October). Densities remained about the same between fall 1997 and spring 1998. In 1998, densities remained stable or decreased slightly between spring and summer (June and July), then increased substantially in late summer through fall (August–October/November). Densities remained about the same between fall 1998 and spring 1999. In 1999, a similar pattern of high densities in spring, low densities in summer and increased densities in fall occurred in Lake Erie, but not in Lake St. Clair where densities continually declined between spring and fall. Thus, two patterns of seasonal-density changes occurred: one pattern where densities of nymphs were high in spring and gradually decreased through fall (Lake Erie and Lake St. Clair in 1997 and Lake St. Clair in 1999) and one pattern where densities were high in spring, declined abruptly in summer and then increased between summer and fall (Lake Erie and Lake St. Clair in 1998 and Lake Erie in 1999).

Mean densities of nymphs ranged between 34 and 2100 $m^{-2}$ in western Lake Erie and 7 and 1391 $m^{-2}$ in Lake St. Clair (Fig. 2). In general, smaller changes in density were associated with the seasonal pattern of gradual decline in density than in the seasonal pattern of decline to increase. In Lake Erie and Lake St. Clair in 1997 and Lake St. Clair in 1999, mean densities between spring and fall declined 65% (2100 to 740 nymphs $m^{-2}$), 72% (1391 to 393 $m^{-2}$), and 73% (882 to 234 $m^{-2}$), respectively. Whereas, in Lake Erie and Lake St. Clair in 1998 and Lake Erie in 1999 changes in density between spring and summer declined 95% (682 to 34 $m^{-2}$), 98% (289 to 7 $m^{-2}$), and 68% (599 to 193 $m^{-2}$), respectively and increases between summer and fall were 1438% (34 to 523 $m^{-2}$), 13386% (7 to 944 $m^{-2}$), and 610% (193 to 610 $m^{-2}$), respectively.

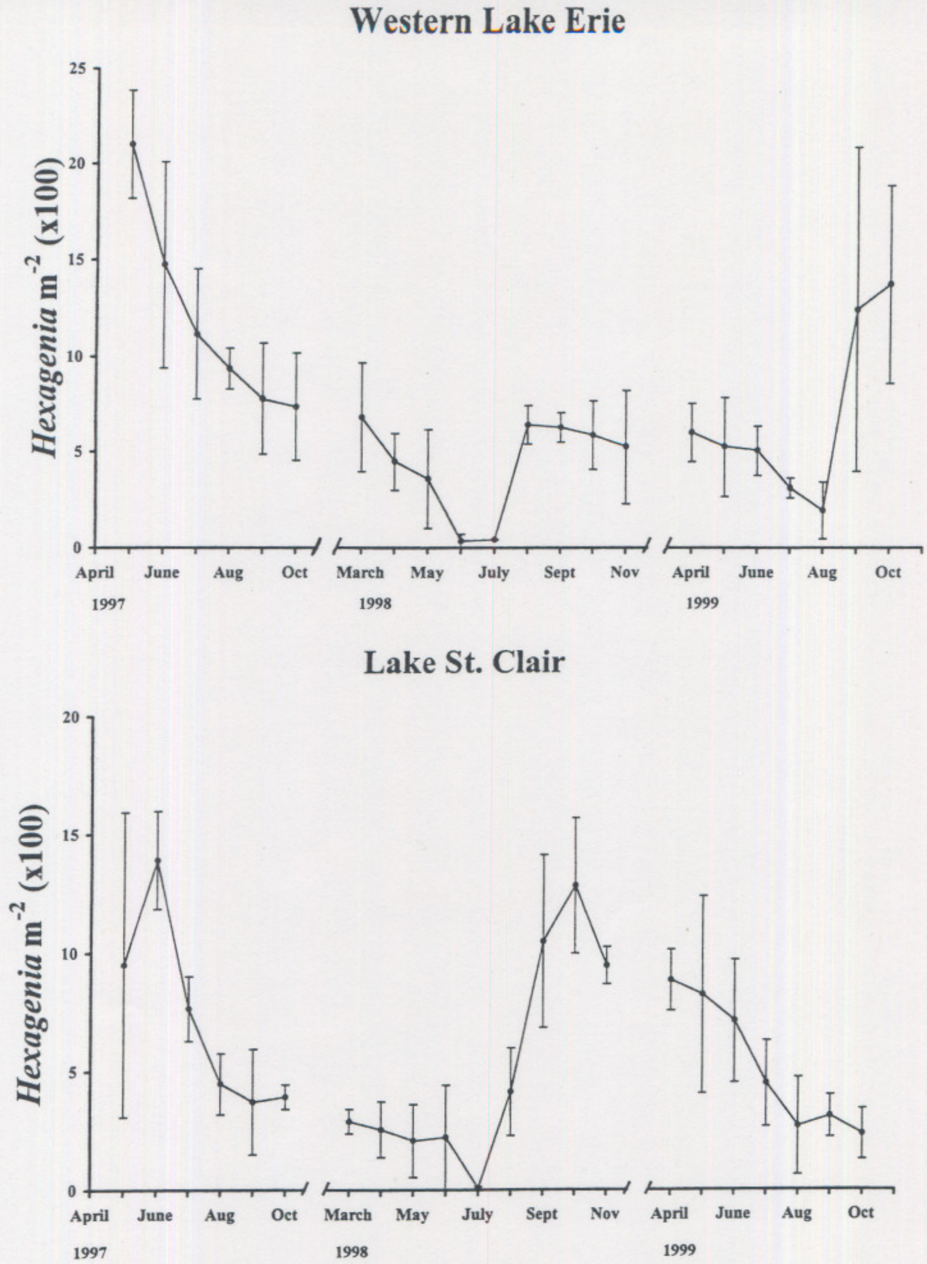


Figure 2. Mean densities (number $m^{-2} \pm 95\%$ confidence intervals) of *Hexagenia* nymphs collected at site 7M in western Lake Erie and site 1 in Lake St. Clair May 1997 to October 1999.

Length-frequency ranges and mean lengths of mayfly nymphs indicate the presence of one or two groups, with peak numbers of individuals being clustered near the middle of each size group, during each sampling period (Tables 1 and 2). One length group accounted for all or a majority of the population (i.e., >85%) each sampling period in both Lake Erie and Lake St. Clair. A second length group was distinguishable in Lake Erie, but not in Lake

Table 1. Length-frequency distributions of *Hexagenia* nymphs ($m^{-2}$) and mean lengths (mm ± 95% confidence interval [c.i.]) of all nymphs and nymphs in small and large size groups based on distinguishable size groups and interpretation of life-history characteristics (e.g., emergence) at site 7M in western Lake Erie May 1997–October 1999. Lines in columns indicate probable separation of length groups when more than one group occurred.

| Length (mm) | 1997 | | | | | | 1998 | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 5/28 | 6/24 | 7/24 | 8/28 | 9/22 | 10/23 | 3/24 | 4/20 | 5/27 | 6/23 |
| 1 | | | | | | | | | 3 | |
| 2 | | | | | | | | | | |
| 3 | | | | | | | | | | |
| 4 | 21 | | | | | | | | | |
| 5 | 72 | 41 | | | | | | | | |
| 6 | 186 | 51 | 10 | | | | | | | |
| 7 | 238 | 102 | | | | | | | 7 | |
| 8 | 279 | 102 | | | | | | | 11 | |
| 9 | 197 | 174 | 10 | 7 | | | | | | |
| 10 | 228 | 143 | 41 | | | | 7 | | 11 | |
| 11 | 155 | 82 | 21 | 7 | | | 14 | 4 | 14 | |
| 12 | 155 | 103 | 82 | 14 | 7 | | 21 | 9 | 11 | 3 |
| 13 | 134 | 113 | 123 | 49 | 14 | 14 | 21 | 13 | ___ | 3 |
| 14 | 52 | 164 | 184 | 62 | 28 | 7 | 28 | 4 | 4 | |
| 15 | 72 | 133 | 174 | 90 | 56 | 21 | 21 | 17 | 7 | |
| 16 | 31 | 72 | 154 | 83 | 49 | 35 | 35 | 26 | | 3 |
| 17 | 52 | 41 | 133 | 146 | 83 | 35 | 56 | 30 | 7 | 9 |
| 18 | 31 | 41 | 82 | 132 | 104 | 70 | 49 | 26 | 22 | |
| 19 | 31 | 41 | 51 | 132 | 97 | 126 | 56 | 64 | 29 | |
| 20 | 10 | 20 | 41 | 62 | 49 | 70 | 77 | 64 | 61 | 9 |
| 21 | 72 | 10 | | 42 | 97 | 56 | 84 | 47 | 40 | |
| 22 | ___ | 10 | 10 | 42 | 83 | 112 | 84 | 43 | 25 | |
| 23 | | | | 49 | 56 | 91 | 42 | 43 | 25 | 7 |
| 24 | 10 | ___ | | 14 | 21 | 56 | 49 | 30 | 22 | |
| 25 | 31 | | | 7 | 21 | 14 | 28 | 17 | 14 | |
| 26 | 10 | | | | | 14 | 7 | 4 | 14 | |
| 27 | 21 | 20 | | | 7 | 14 | | 8 | 18 | |
| 28 | 10 | 10 | | | | | | | 11 | |
| 29 | | | | | 7 | | | | | |
| 30 | | | | | | | | | | |
| 31 | | | | | | | | | | |
| Mean length (mm) | | | | | | | | | | |
| all | 11.0 | 12.2 | 15.0 | 17.6 | 19.2 | 20.4 | 19.3 | 19.9 | 19.6 | 18.0 |
| 95% c.i. | 0.68 | 0.72 | 0.50 | 0.51 | 0.59 | 0.57 | 0.75 | 0.65 | 1.09 | 2.42 |
| small group[a] | 10.4 | 11.9 | | | | | | | 9.4 | |
| 95% c.i. | 0.56 | 0.64 | | | | | | | 1.40 | |
| large group[a] | 25.9 | 27.3 | 15.0 | 17.6 | 19.2 | 20.4 | 19.3 | 19.9 | 21.6 | 18.0[b] |
| 95% c.i. | 1.13 | 1.43 | 0.50 | 0.51 | 0.59 | 0.57 | 0.75 | 0.65 | 0.69 | 2.42 |
| Number of nymphs examined | 203 | 144 | 109 | 135 | 112 | 105 | 97 | 105 | 99 | 11 |

[a] Underlined means follow growth of a distinguishable group.

[b] Change attributed to emergence and growth of some nymphs of one group.

| | 1998 | | | | | 1999 | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 7/16 | 8/26 | 9/23 | 10/15 | 11/18 | 4/8 | 5/20 | 6/21 | 7/26 | 8/11 | 9/1 | 10/12 |
| | | | | | 11 | 5 | | | | 2 | 23 | |
| | | | | 11 | 5 | 15 | | | | 8 | 102 | 25 |
| | | 13 | 10 | 11 | | | | | | 6 | 102 | 38 |
| | | 61 | | 16 | 5 | 10 | 7 | 5 | | 10 | 159 | 75 |
| | | 115 | 5 | 11 | 5 | 35 | 13 | 5 | | 5 | 125 | 88 |
| | | 122 | 10 | 21 | 22 | 20 | 7 | 19 | | 6 | 114 | 163 |
| | | 135 | 21 | 16 | 38 | 25 | 20 | 24 | | | 137 | 264 |
| | | 61 | 31 | 21 | 11 | 25 | 13 | 28 | | — | 91 | 189 |
| | | 34 | 16 | 21 | 22 | 40 | 13 | 33 | | | 91 | 138 |
| | 2 | 61 | 42 | 32 | 43 | 15 | 40 | 47 | | 2 | 34 | 101 |
| | 2 | 13 | 68 | 42 | 32 | 40 | 26 | 38 | | | 23 | 101 |
| | 8 | | 68 | 42 | 22 | 20 | 46 | 28 | | 5 | 23 | 50 |
| | 4 | 7 | 99 | 47 | 38 | 45 | 33 | 43 | 8 | 5 | 11 | 25 |
| | 6 | — | 26 | 69 | 22 | 65 | 53 | 28 | 34 | 2 | — | 25 |
| | 4 | | 52 | 37 | 32 | 35 | 53 | 38 | 51 | 19 | 11 | 25 |
| | | 7 | 57 | 47 | 54 | 40 | 40 | 33 | 25 | 30 | 11 | — |
| | 2 | | 47 | 53 | 70 | 50 | 66 | 28 | 56 | 32 | 46 | |
| | 4 | | 26 | 16 | 43 | 25 | 33 | 33 | 39 | 14 | | 25 |
| | 2 | 7 | 16 | 26 | 27 | 40 | 20 | 33 | 37 | 11 | 23 | 25 |
| | 2 | | 10 | 26 | 22 | 25 | 13 | 14 | 20 | 10 | 11 | 13 |
| | 4 | 7 | 10 | 5 | | 5 | 7 | 19 | 25 | 8 | 46 | 13 |
| | | | 5 | 5 | | 5 | | | 11 | 11 | 23 | |
| | | | | | | 5 | 7 | 5 | | 5 | 23 | |
| | | | 5 | 5 | | | 7 | | 3 | 3 | | |
| | | | | 5 | | 5 | | | | | 11 | |
| | | | | | | | 7 | | | | | |
| | 18.1 | 10.1 | 16.1 | 16.0 | 16.1 | 15.8 | 17.0 | 16.2 | 20.3 | 17.9 | 11.1 | 11.4 |
| | 1.60 | 0.59 | 0.70 | 0.91 | 0.94 | 0.93 | 0.98 | 0.85 | 0.46 | 1.08 | 1.12 | 0.70 |
| | | 9.7 | 16.1 | 16.0 | 16.1 | 15.8 | 17.0 | 16.2 | | 6.7 | 8.8 | 10.8 |
| | | 0.42 | 0.70 | 0.91 | 0.94 | 0.93 | 0.98 | 0.85 | | 0.65 | 0.57 | 0.53 |
| | 18.1 | 20.3 | | | | | | | 20.3 | 20.5 | 22.8 | 22.8 |
| | 1.60 | 5.60 | | | | | | | 0.46 | 0.55 | 1.39 | 1.52 |
| | 20 | 95 | 120 | 111 | 97 | 119 | 79 | 106 | 110 | 121 | 109 | 109 |

Table 2. Length-frequency distributions of *Hexagenia* spp. nymphs ($m^{-2}$) and mean lengths (mm ± 95% confidence interval [c.i.]) of all nymphs and nymphs in small and large size groups based on distinguishable size groups and interpretation of life-history characteristics (e.g., emergence) at site 1 in Lake St. Clair May 1997–October 1999. Lines in columns indicate probable separation of length groups if more than one occured.

| Length (mm) | 1997 | | | | | | 1998 | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 5/27 | 6/23 | 7/24 | 8/28 | 9/22 | 10/23 | 3/24 | 4/20 | 5/27 | 6/15 |
| 1 | | | | | | | | | | |
| 2 | | | | | | | | | 4 | |
| 3 | 10 | | | | | | | | | |
| 4 | 51 | | | 7 | | | | | | 4 |
| 5 | 41 | 41 | | | | | | | 4 | |
| 6 | 81 | 21 | | | | | | | | |
| 7 | 40 | 135 | 7 | | | | | | | |
| 8 | 101 | 62 | 7 | | | | | | | |
| 9 | 121 | 125 | 7 | | | | | | | |
| 10 | 182 | 83 | 28 | | | | | | | |
| 11 | 71 | 145 | 21 | | | | | | | |
| 12 | 71 | 197 | 28 | | 7 | | | | | |
| 13 | 71 | 176 | 28 | | | 6 | | | | |
| 14 | 81 | 135 | 69 | | | 13 | | 4 | | |
| 15 | 20 | 104 | 69 | 36 | 7 | 19 | 7 | | | |
| 16 | 10 | 52 | 96 | 36 | 7 | 26 | | 4 | 4 | |
| 17 | | 42 | 89 | 28 | 20 | 20 | 21 | 7 | | |
| 18 | | 21 | 96 | 64 | 60 | 32 | 34 | 18 | | 12 |
| 19 | | 21 | 69 | 50 | 93 | 58 | 62 | 29 | 8 | 12 |
| 20 | | 21 | 83 | 71 | 47 | 52 | 62 | 51 | 8 | 24 |
| 21 | | 10 | 21 | 78 | 13 | 58 | 48 | 40 | 11 | 39 |
| 22 | | | 48 | 43 | 40 | 52 | 28 | 33 | 19 | 24 |
| 23 | | | | 21 | 47 | 32 | 21 | 33 | 8 | 16 |
| 24 | | | | 14 | 33 | 13 | 7 | 18 | 26 | 47 |
| 25 | | | | | | 6 | | 11 | 15 | 20 |
| 26 | | | | | | 6 | | 4 | 26 | 12 |
| 27 | | | | | | | | | 34 | 4 |
| 28 | | | | | | | | | 8 | 4 |
| 29 | | | | | | | | 4 | 23 | 4 |
| 30 | | | | | | | | | 11 | |
| 31 | | | | | | | | | 4 | |
| Mean length (mm) | | | | | | | | | | |
| all | 9.5 | 11.8 | 16.5 | 19.1 | 19.9 | 19.7 | 19.9 | 21.0 | 24.4 | 22.2 |
| 95% c.i. | 0.61 | 0.58 | 0.62 | 0.77 | 0.67 | 0.73 | 0.59 | 0.59 | 1.39 | 0.95 |
| small group[a] | 9.5 | 11.8 | | 4.0 | | | | | 3.5 | 4.0 |
| 95% c.i. | 0.31 | 0.30 | | n.a.[c] | | | | | 19.06 | n.a.[c] |
| large group[a] | | | 16.5 | 19.3 | 19.9 | 19.7 | 19.9 | 21.0 | 25.1 | 22.5[b] |
| 95% c.i. | | | 0.32 | 0.61 | 0.67 | 0.73 | 0.59 | 0.59 | 0.90 | 0.69 |
| Number of nymphs examined | 94 | 134 | 111 | 63 | 56 | 61 | 42 | 70 | 55 | 56 |

[a] Underlined means follow growth of a distinguishable group.
[b] Significant decrease from previous sampling attributed to emergence of larger nymphs.
[c] Not applicable, n = 1.

| 1998 | | | | | 1999 | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 7/16 | 8/26 | 9/25 | 10/15 | 11/18 | 4/8 | 5/3 | 6/22 | 7/8 | 8/11 | 9/1 | 9/22 |
| | 14 | | | | | | | | | | |
| | 78 | 10 | | | | | | 3 | | | |
| | 107 | | | 7 | | | | | | | |
| | 142 | | | 15 | 7 | 7 | 7 | —— | | | |
| | 43 | 21 | 21 | 15 | | | 7 | | | | |
| | 21 | 73 | 41 | 22 | 28 | 22 | 7 | | | | |
| | 7 | 52 | 10 | 15 | 42 | 15 | —— | | | | |
| | | 104 | 62 | 22 | 21 | 22 | | 6 | | | |
| | | 104 | 21 | 37 | 49 | 30 | 14 | 9 | 5 | | 2 |
| | | 156 | 93 | 59 | 21 | 60 | 21 | 9 | 2 | | —— |
| | | 114 | 62 | 66 | 49 | 67 | 14 | 21 | 5 | 6 | |
| | | 114 | 83 | 125 | 49 | 75 | 41 | 18 | 9 | 12 | 5 |
| | | 145 | 186 | 125 | 112 | 60 | 34 | 24 | 11 | 9 | 2 |
| | | 62 | 176 | 148 | 112 | 97 | 83 | 41 | 18 | 6 | 7 |
| | | 41 | 134 | 118 | 77 | 97 | 55 | 47 | 25 | 24 | 21 |
| | | 21 | 114 | 103 | 119 | 90 | 62 | 50 | 34 | 53 | 21 |
| | | 21 | 145 | 15 | 70 | 105 | 83 | 59 | 41 | 29 | 25 |
| | | 10 | 83 | 30 | 56 | 90 | 89 | 53 | 27 | 50 | 25 |
| | | | 31 | 7 | 21 | 22 | 76 | 29 | 39 | 53 | 42 |
| 4 | | | 10 | 15 | 21 | 15 | 48 | 44 | 23 | 29 | 32 |
| 8 | | | 10 | | 21 | 7 | 21 | 18 | 11 | 9 | 28 |
| 4 | | | | | | | 34 | 6 | 11 | 6 | 12 |
| | | | | | 7 | | 7 | 6 | 5 | 3 | 7 |
| 4 | | | | | | | | 6 | 2 | | 2 |
| | | | | | | | | | | | 2 |
| | | | | | | | 7 | | | | |
| 22.6 | 4.6 | 11.6 | 14.6 | 13.8 | 14.8 | 14.9 | 17.1 | 17.1 | 18.0 | 18.3 | 19.4 |
| 1.88 | 0.33 | 0.59 | 0.61 | 0.57 | 0.67 | 0.63 | 0.75 | 0.57 | 0.55 | 0.50 | 0.54 |
| | 4.6 | 11.6 | 14.6 | 13.8 | 14.8 | 17.9 | 6.0 | 2.0 | | | 10.0 |
| | 0.33 | 0.59 | 0.61 | 0.57 | 0.67 | 0.63 | 2.48 | n.a. | | | n.a. |
| 22.6 | | | | | | | 17.5 | 17.2 | 18.0 | 18.3 | 19.5 |
| 1.88 | | | | | | | 0.66 | 0.53 | 0.55 | 0.50 | 0.52 |
| 5 | 58 | 101 | 124 | 128 | 126 | 118 | 103 | 152 | 118 | 98 | 101 |

Table 3. Length-frequency distributions of *Hexagenia* nymphs ($m^{-2}$) and mean lengths (mm ± 95% confidence interval [c.i.]) of all nymphs and nymphs in small and large size groups based on distinguishable size groups at sites 8D, 5B, 7L, and 5R in western Lake Erie May 1998 and 1999. Lines in columns indicate probable separation of length groups.

| Length (mm) | 1998 | | | | | 1999 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 8D | 5B | 7L | 5R | Total | 8D | 5B | 7L | 5R | Total |
| 1 | | | | | | | | | | |
| 2 | | | | | | | | | | |
| 3 | | | | | | | | | | |
| 4 | 2 | | | | 1 | | | | | |
| 5 | | | | | | 14 | 7 | 3 | | 6 |
| 6 | 4 | 2 | 2 | | 2 | 28 | | 5 | 7 | 10 |
| 7 | 8 | | | | 2 | 21 | 35 | 11 | 7 | 18 |
| 8 | 4 | | 2 | 1 | 2 | 42 | 35 | 8 | 24 | 27 |
| 9 | 8 | 4 | | 1 | 3 | 90 | 21 | 5 | 10 | 32 |
| 10 | | | | 1 | | 56 | 85 | 8 | 21 | 42 |
| 11 | | | | 3 | 1 | 63 | 63 | 8 | 14 | 37 |
| 12 | | | 2 | | 1 | 76 | 113 | 11 | 14 | 53 |
| 13 | 2 | | | 1 | 1 | 49 | 92 | 8 | 14 | 41 |
| 14 | | | | | | 56 | 92 | 5 | 24 | 44 |
| 15 | 6 | 2 | | 4 | 3 | 69 | 120 | 8 | 24 | 55 |
| 16 | 2 | 2 | | | 1 | 83 | 106 | 16 | 10 | 54 |
| 17 | 2 | | 2 | | 1 | 28 | 77 | 19 | 14 | 35 |
| 18 | 12 | 10 | 2 | 15 | 10 | 49 | 35 | 19 | 14 | 29 |
| 19 | 19 | 12 | | 22 | 13 | 35 | 14 | 16 | 17 | 21 |
| 20 | 33 | 48 | 2 | 23 | 27 | 35 | 7 | 63 | 7 | 28 |
| 21 | 33 | 37 | | 20 | 22 | 7 | 7 | 33 | 14 | 15 |
| 22 | 35 | 48 | 10 | 12 | 26 | 14 | 7 | 27 | 10 | 15 |
| 23 | 25 | 27 | 10 | 39 | 25 | | 7 | 14 | 3 | 6 |
| 24 | 17 | 31 | 12 | 24 | 21 | | | 8 | | 2 |
| 25 | 33 | 14 | 14 | 19 | 20 | | | 11 | | 3 |
| 26 | 12 | 15 | 12 | 9 | 12 | | | 8 | | 2 |
| 27 | 6 | 6 | 10 | 5 | 7 | | 7 | 3 | 3 | 3 |
| 28 | 2 | 8 | 7 | 3 | 5 | | 14 | | | 4 |
| 29 | 2 | 4 | 5 | | 3 | | | | | |
| 30 | | 2 | 5 | | 2 | | | 3 | | 1 |
| 31 | | | 5 | | 1 | | | | | |
| Mean length (mm) | | | | | | | | | | |
| all | 20.4 | 22.0 | 24.1 | 21.6 | 21.6 | 13.1 | 13.8 | 17.9 | 14.2 | 14.8 |
| 95% c.i. | 0.90 | 0.56 | 1.65 | 0.57 | 0.39 | 0.80 | 0.67 | 0.95 | 1.12 | 0.46 |
| small group | 7.8 | 8.0 | 8.7 | 10.3 | 8.5 | 13.1 | 13.5 | 18.0 | 14.1 | 14.5 |
| 95% c.i. | 1.20 | 4.30 | 7.59 | 1.84 | 0.90 | 0.80 | 0.57 | 0.96 | 1.07 | 0.43 |
| large group | 21.9 | 22.3 | 25.2 | 22.0 | 22.4 | | 27.7 | 30.0 | 27.0 | 27.2 |
| 95% c.i. | 0.52 | 0.45 | 1.05 | 0.45 | 0.27 | | 1.43 | n.a.[a] | n.a.[a] | 1.00 |
| Number/$m^2$ | 269 | 270 | 104 | 203 | 203 | 813 | 944 | 324 | 251 | 583 |
| Number of nymphs examined | 130 | 140 | 43 | 151 | 364 | 117 | 134 | 118 | 73 | 442 |

[a] Not applicable, n = 1.

St. Clair. Two groups were evident in Lake Erie in May (small group 4–21 mm, large group 24–28 mm) and June (5–22 mm and 27–28 mm) 1997, May (2–12 mm and 14–28 mm) and, possibly, August (6–16 and 19–24 mm) 1998 and August (4–9 mm and 13–27 mm), September (4–17 mm and 18–28 mm) and October (5–18 mm and 21–24 mm) 1999. In Lake St. Clair, a few small nymphs occurred in August 1997, May and June 1998 and June, July and September 1999, but the more abundant size group comprised all or greater than 95% of the total number of nymphs in each sampling period.

Mean lengths of two year-classes of nymphs were similar in corresponding sampling periods in Lake Erie and Lake St. Clair (Tables 1 and 2). One year-class was distinguishable for 12 consecutive sampling periods (small group in May 1997 through the large group in July/August 1998). This group was larger in Lake Erie than the corresponding size group in Lake St. Clair for only 2 of 12 sampling periods. A second year-class consisted of nymphs found in 11 sampling periods (small group in August 1998 through the large group September/October 1999). In this second year-class, nymphs from Lake Erie were larger than those from Lake St. Clair for 9 of 11 comparisons. However, like changes in abundance, two patterns occurred in changes of lengths of nymphs. In one pattern total mean lengths increased between spring and fall (Lake Erie and Lake St. Clair in 1997 and Lake St. Clair in 1999) and in the other pattern lengths increased between spring and summer, decreased abruptly in summer, then increased between summer and fall (Lake Erie and Lake St. Clair in 1998 and Lake Erie in 1999).

In general, length-frequency distributions and mean size of nymphs found at four sites located throughout western Lake Erie were similar to distributions found at site 7M in May 1998 and 1999, but they were not similar between the two years (Tables 1 and 3). In 1998, small nymphs accounted for a small portion of the total number of nymphs (6% and 16%) at the four sites and site 7M (respectively). Similarly, length ranges of groups at the four sites and 7M were, respectively: the small groups were 4 to 13 mm (mean = 8.5 mm) and 2 to 12 mm (9.4 mm) and the large groups were 15 to 31 mm (22.4 mm) and 14 to 28 mm (21.6 mm). In 1999, small groups made up the majority of nymph densities (98% and 100%) at the four sites and site 7M (respectively). Length ranges of all nymphs at the four sites and 7M were similar (5 to 30 mm and 7 to 29 mm, respectively), but no large length group was found at 7M. Mean length of nymphs of the large group (mean $\pm$ 95% confidence interval, 25.2 $\pm$ 1.05 mm) in 1998 and small group (17.3 $\pm$ 0.95) in 1999 were larger at site 7L than mean lengths of corresponding groups at the other three sites.

## 4. Discussion

High fluctuations in densities of *Hexagenia* nymphs occurred in western Lake Erie and Lake St. Clair over the 1997–1999 period. These changes were associated with two seasonal patterns: (1) relatively high densities of nymphs in spring with gradual decreases through fall and (2) relatively high densities in spring with gradual decreases through summer, abrupt decreases in summer and then relatively abrupt increases in late summer and fall. The primary difference between these two patterns is attributed to failed (pattern # 1) and successful (pattern # 2) recruitment of young-of-the-year nymphs. Failed recruitment occurred in Lake Erie and Lake St. Clair in 1997 and Lake St. Clair in 1999 and successful recruitment occurred in Lake Erie and Lake St. Clair in 1998 and Lake Erie in 1999. Growth, mortality and emergence of distinguishable year-classes/cohorts also contributed to seasonal and yearly differences in abundance and were similar between lakes when the same recruitment pattern occurred in each lakes. Fluctuations in densities and patterns of seasonal change are believed to have occurred throughout western Lake Erie and possibly Lake St. Clair because similar length-frequency distributions found at site 7M occurred at four sites over a broad geographic area in western Lake Erie in 1998 and 1999.

### 4.1. Density Fluctuations

Maximum densities of mayfly nymphs in western Lake Erie and Lake St. Clair (2100 and 1391 $m^{-2}$, respectively) in 1997–1999 are typical of maximum densities found in Lake St. Clair and other areas of the Great Lakes such as the St. Marys and St. Clair rivers (range 1081 to 3099 $m^{-2}$; SCHLOESSER *et al.*, 1991). Maximum densities in Lake St. Clair in 1997–99 were comparable to densities found in 1986, but densities in western Lake Erie are the highest observed in western Lake Erie in 45 years (SCHLOESSER *et al.*, 1991; reviewed in SCHLOESSER *et al.*, In review).

Seasonal fluctuations in densities of nymphs in western Lake Erie and Lake St. Clair are attributed to expected life-history characteristics previously described for populations of mayflies in the Great Lakes (CHANDLER, 1963; SCHLOESSER and HILTUNEN, 1984; MANNY, 1991), and in other north-temperate water bodies (SPEITH, 1938; RIKLIK and MOMOT, 1982; HEISE *et al.*, 1987). Typically, about 95% of the total mayfly emergence from western Lake Erie occurred the last two weeks of June and first two weeks of July. This is followed by mating and egg deposition, and by young-of-the-year nymphs being collected by routine sampling methods in mid August (CHANDLER, 1963; SCHLOESSER and HILTUNEN, 1984; MANNY, 1991; KRIEGER *et al.*, 1996; unpublished data, DWS and B. KOVALAK, Detroit Edison, Detroit, Michigan). In the present study, emergence resulted in about a 50% decrease in densities in 1997, a 90% decrease in 1998 and a 35% decrease in 1999. In other relatively cold waters (temperatures greatly affect emergence patterns), such as the St. Marys River and a reservoir in northern Manitoba, 90% of total emergence occurred within a two-to-three week period when densities of nymphs decreased about 65% (SCHLOESSER and HILTUNEN, 1984; GIBERSON and ROSENBERG, 1992, 1994).

### 4.2. Failed Recruitment

Lack of recruitment of young nymphs in the presence of other nymphs in the sediments over such a broad geographic area in western Lake Erie and Lake St. Clair in 1997 and Lake St. Clair in 1999 has not been observed before and cannot be attributed to an observed event (e.g. anoxia) (SCHLOESSER and HILTUNEN, 1984; GIBERSON and ROSENBERG, 1992, 1994; unpublished data, DWS). Recruitment is dependent on the success of emergence, mating, egg deposition and egg hatching (JOHNSON, 1969; KOVATS *et al.*, 1996). The population of nymphs emerging from western Lake Erie in 1997 was higher (ca. 1000 nymphs $m^{-2}$ based on decrease in nymph densities May–July) than in 1998 (ca. 300 $m^{-2}$). However, swarming subadult and adult mayflies were about one-third as abundant in 1997 as 1998, and egg hatching success observed in the laboratory was about 50% in 1997 and about 85% in 1998 (pers. comm., J. CIBOROWSKI, University of Windsor, Ontario and B. KOVALAK, Detroit Edison, Detroit, Michigan). Detailed information of weather indicates no unusual disruptive events occurred during the period of nymph emergence in 1997 (pers. comm., B. KOVALAK, Detroit Edison, Detroit, Michigan). Observed differences between relative emergence and egg hatchability suggest that lack of recruitment in 1997 and 1999 was a result of an unknown parameter (e.g., food supply) critical to egg hatching and/or young nymphs, but not to older nymphs, which survived in sediments during failed recruitment periods.

Total failure of recruitment of nymphs into the population after emergence as observed in this study is unusual in the Great Lakes (Table 4). In general, *Hexagenia* populations in western Lake Erie and other waters of the Great Lakes consist of two distinct size groups in spring and fall. The small-sized group found in fall is a result of summer/fall recruitment. This small-sized group generally comprised 64–100% of the population, except in western Lake Erie in 1942 and 1943 (CHANDLER, 1963), in western Lake Erie and Lake St. Clair in 1997 and Lake St. Clair in 1999. Little to no recruitment of nymphs occurred as a result of

Table 4. Percent of total numbers of nymphs in two distinguishable size groups before (May/June) and after (September/October) nymph emergence in waters of the Great Lakes.

| | | Small Group | Large Group | |
|---|---|---|---|---|
| **Present Study** | | | | |
| Western Lake Erie | May | 100 | 0 | Table 1 |
| 1999 site 7M | October | 95 | 5 | |
| 1999 4 sites | May | 100 | <1 | Table 3 |
| Lake St. Clair | May | 100 | 0 | Table 2 |
| 1999 site 1 | September | 1 | 99 | |
| Western Lake Erie | May | 16 | 84 | Table 1 |
| 1998 site 7M | October | 100 | <1 | |
| 1998 4 sites | May | 6 | 94 | Table 3 |
| Lake St. Clair | May | 3 | 97 | Table 2 |
| 1998 site 1 | October | 100 | 0 | |
| Western Lake Erie | May | 96 | 4 | Table 1 |
| 1997 site 7M | October | 0 | 100 | |
| Lake St. Clair | May | 100 | 0 | Table 2 |
| 1997 site 1 | October | 0 | 100 | |
| **Other Studies** | | | | |
| Western Lake Erie | June | 71 | 29 | Unpublished data, DWS |
| 1994 site 8D–11D | October | 87 | 13 | |
| Western Lake Erie | May | 75 | 25 | MANNY, 1991 |
| 1943 South Bass Is. | October | 26 | 74 | |
| Western Lake Erie | May | 96 | 4 | MANNY, 1991 |
| 1942 South Bass Is. | October | 19 | 81 | |
| Lake St. Clair | May | 90 | 10 | Unpublished data, DWS |
| 1986 site 177 | October | 87 | 13 | |
| St. Marys River | May | 94 | 6 | SCHLOESSER and |
| 1974 125 sites | October | 64 | 36 | HILTUNEN, 1984 |

emergence in 1942, 1997 and 1999 which led to densities of nymphs $<100$ m$^{-2}$ the following July of 1943 and 1998 (2000?). Although, a relatively low proportion of small nymphs (26%) occurred in western Lake Erie in October 1943, good recruitment (from about 50 to 300 m$^{-2}$) did result from emergence, but it did not occur until April–May 1944, presumably as a result of delayed egg hatching. Similar densities in Lake Erie and Lake St. Clair in fall 1997 and spring 1998 indicate that delayed recruitment as observed in 1943–44 did not occur in 1997–98. CHANDLER (1963) attributed the lack of recruitment of the 1942 year class to the possible presence of a 2-year life cycle, with alternating year-class abundance, and cites a similar observation based on data collected in 1928. In theory, this would result in one year-class of high densities followed by a year-class of low densities, *etc*., but no reason for this theory has been developed. However, evidence for alternating year class abundance of *Hexagenia* nymphs has been seen in several other lakes and in diets of fish where eutrophication has been suggested as a possible casual mechanism (RIKLIK and MOMOT, 1982; RITCHIE and COLBY, 1988; TOWNSEND and PERROW, 1989). To date, implications of CHANDLER's theory to the life history of mayflies in the Great Lakes have not been determined, but failed recruitment of nymphs in Lake St. Clair in 1997 and 1999 supports the theory of alternating year-class. However, strong recruitment in Lake Erie in 1998 and 1999 does not support the theory of alternating year-class strength.

### *4.3. Life-Cycle of Hexagenia*

For the past 45 years, it has been assumed that *Hexagenia* spp. nymphs have a 2-year life cycle in western Lake Erie (CHANDLER, 1963). This assumption is based only on information obtained in 1942–1944 and summarized in a presentation and abstract (CHANDLER, 1963). However, MANNY (1991) presented a figure of CHANDLER's (which partially supports the conclusion that a 2-year life cycle existed in 1942–44) and concluded that without actual lengths of nymphs (only mean lengths available), the 2-year life cycle could not be verified. Length-frequency distributions in 1997 and 1998 indicate that the population may consist of individuals with either a 1-year or 2-year life cycle. Based on changes in densities of nymphs and adult emergence patterns along the shores (i.e., more adults in 1997 than in 1996 and 1998, pers. comm., B. KOVALAK, Detroit Edison, Detroit, Michigan), it is probable that many (ca. 50%) nymphs of the small (ca. 4–21 mm) size group emerged in June-July 1997. Many others did not because large (ca. 9–25 mm) nymphs were abundant after emergence in August and did not emerge from the water until June–July 1998 (2-year life cycle). We found no evidence of distinct size groups within small-size groups in spring 1997 and speculate that the group that emerged in June–July (1-year life cycle) and the large nymphs in August (2-year life cycle) were probably both recruited in 1996.

Populations of nymphs in the latitudinal range of western Lake Erie and Lake St. Clair have been found to have both 1- and >1-year life cycles (reviewed in HEISE *et al.*, 1987; GIBERSON and ROSENBERG, 1994). Alternatively, a protracted emergence of two years for small length groups in 1997 may be due to egg diapause, which has been shown to exist in *Hexagenia* populations in the most northern portion of its range (GIBERSON and ROSENBERG, 1992). Nymphs from eggs that undergo a diapause may account for as much as 50–90% of a length group (NEAVE, 1932; GIBERSON and ROSENBERG, 1992). Occurrence of small numbers of nymphs (ca. 15% of total) in western Lake Erie in May 1998 indicates that some eggs probably did undergo a diapause, which could account for the wide variation in emergence of nymphs from what appears to be a single size group. Delayed recruitment (August to April) resulting from emergence in 1943 (discussed above) is another indication of delayed egg hatching that could affect interpretation of life-history of mayflies in western Lake Erie. Complex life-history patterns of mixed cohorts of up to 4 years have been observed for *Hexagenia*, but these populations had small nymphs throughout the year due to long emergence periods (up to 6 months) that resulted in extended egg laying and hatching and hatching of eggs that had under gone diapause (HUDSON and SWANSON, 1972; RUTTER and WISSING, 1975; HEISE *et al.*, 1987; GIBERSON and ROSENBERG, 1994). In the present study, emergence occured primarily (ca. >95%) during a six week period between mid June and late July (pers. comm., B. KOVALAK, Detroit Edison, Detroit, Michigan), small nymphs comprised a large portion of the population only in late fall and few nymphs were attributed to egg-diapause hatching. These three characteristics suggest that life-history patterns of *Hexagenia* in Lake Erie and Lake St. Clair may be simpler than some of the more complex patterns found in other waters.

### *4.4. Importance of Fluctuating Densities*

Our results indicate that management objectives for western Lake Erie that are partly based on *Hexagenia* densities must be cognizant of the wide temporal variations observed in this organism. Densities prior to emergence (May) ranged between 350 and 2100 nymphs $m^{-2}$, densities immediately after emergence (August) ranged between 190 and 925 $m^{-2}$ and densities after recruitment (October) ranged between 575 and 1375 nymphs $m^{-2}$. A mean lake-wide density of 350 nymphs $m^{-2}$ has been adopted as a management goal for "fair" substrate quality, 400 $m^{-2}$ for "good" substrate quality and 450 to 500 $m^{-2}$ for "excellent" substrate quality (OHIO LAKE ERIE COMMISSION, 1998). The management goal of 350 nymphs $m^{-2}$ for fair substrate quality occurred 13 of 15 times at 7M in 1997 and 1998, but in lake-wide surveys conducted in May only 9 of 23 sites exceeded 350 $m^{-2}$ in 1997 and only 3 of 23 sites exceeded 350 $m^{-2}$ in 1998 (SCHLOESSER *et al.*, In review). Clearly, if densities are to be used to assess the "state" of western Lake Erie relative to pollution-abatement programs, the population of mayflies needs to be sampled consistently over several years because of life-history characteristics and spatial variability.

Relatively high fluctuations in densities of nymphs would be expected based on examination of *Hexagenia* tusks contained in sediment cores from western Lake Erie (REYNOLDSON and HAMILTON, 1993). Sediment profiles containing mayfly tusks indicate that numbers of nymphs fluctuated more after European settlement (ca. 1875) with increased eutrophication than before settlement when conditions were believed to be mesotrophic (BURNS, 1985). Therefore, as the eutrophic state of western Lake Erie changes back to pre-settlement trophic conditions (if it is not there already as a result of pollution-abatement programs and impacts of zebra mussels), we expect relatively high fluctuations in densities of nymphs before a less eutrophic state is reached.

## 5. Conclusion

At present, total recruitment failure of a year class of mayfly nymphs in waters of the Great Lakes is believed to be an unusual event of unknown origin. Because larger nymphs continued to survive in sediments during periods of failed recruitment the causal mechanism was unlikely to have been one of anthropogenic origin. Changes in abundance of nymphs attributed to life-history characteristics in Lake Erie and Lake St. Clair indicate that, caution is needed in determining progress toward management goals. Based on abundance of benthic species such as *Hexagenia* spp. in the Laurentian Great Lakes and possibly other water bodies throughout the world.

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