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Recolonization and possible recovery of Burrowing Mayflies (Ephemeroptera: Ephemeridae: *Hexagenia* spp.) in Lake Erie of the Laurentian Great Lakes *

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Abstract

Burrowing mayflies of the genus *Hexagenia* spp. were widely distributed (ca. 80% of sites) and abundant (ca. 160 nymphs/m^2) in the western basin of Lake Erie of the Laurentian Great Lakes in 1929–1930, prior to a period of anoxia in the mid 1950s. Nymphs were absent or rare in the basin between 1961 and 1973–1975. In 1979–1991, nymphs were infrequently found (13–46% of sites) in low abundance (3–40 nymphs/m^2) near shore (<7.5 km from shore), but were absent or rare offshore (0–7% of sites at 0–1 nymphs/m^2). Increased abundance occurred offshore between 1991 (0% of sites) and 1993 (52% of sites at 7/m^2). Annual sampling, beginning in 1995, indicates that nymphs increased in both nearshore and offshore waters. By 1997, nymphs were found throughout the lake (88% of sites) at a mean density 40-fold greater (392/m^2) than that observed in 1993 (11/m^2). In 1998, the distribution of nymphs remained the same as 1997 (88% of sites) but density declined 3-fold (392 to 134/m^2). These data indicate that mayflies have recolonized sediments of western Lake Erie and that their abundance may be similar to levels observed before their disappearance in the mid 1950s. However, prior to the mid 1950s, densities were greater in offshore than nearshore waters, but between 1979 and 1998 greater densities occurred near shore than offshore. In addition, there were two areas in the 1990s where low densities consistently occurred. Therefore, recovery of nymphs in western Lake Erie may not have been complete in 1998. At present we do not know the cause for the sudden recolonization of nymphs in large portions of western Lake Erie. Undoubtedly, pollution-abatement programs contributed to improved conditions that would have ultimately led to mayfly recovery in the future. However, the explosive growth of the exotic zebra mussel, *Dreissena polymorpha*, undoubtedly diverted plankton foods to bottom substrates which could have increased the speed at which *Hexagenia* spp. nymphs recolonized sediments in western Lake Erie in the 1990s.

Introduction

Examination of macrobenthos in the western basin of Lake Erie indicates that one primary event determined the character of benthic communities between the mid 1950s and early 1990s (Beeton, 1961, 1969; Carr & Hiltunen, 1965; Burns, 1985). This was the sudden decline of burrowing mayfly nymphs (*Hexagenia* spp.) as a result of anoxia in bottom waters of the eastern portion of the basin in autumn 1953 (Britt, 1955a, b). Before the anoxic event, the benthic macroinvertebrate community was described as being dominated by relatively large-bodied organisms, such as burrowing mayflies and caddisflies larvae (e.g., *Oecetis* spp., Shelford & Boesel, 1942). After the 1950s, the benthos community became dominated by relatively small organisms, such as oligochaetes (70% of total, Schloesser et al., 1995; Manny & Schloesser, 1999), and mayflies and caddisflies were absent or rare (Beeton, 1961; Carr & Hiltunen, 1965; Reynoldson et al., 1989; Manny & Schloesser, 1999). Between the 1950s and 1988 there was no substantial change in macrobenthos in open waters of western Lake Erie until high densities of zebra mussels (*Dreissena polymorpha*) occurred in 1989 (Carr & Hiltunen, 1965; Nalepa & Schloesser, 1993; Manny & Schloesser, 1999). In the early 1990s, adults of burrowing mayflies began to be seen along the shores of western Lake Erie, which led to subsequent discovery of nymphs and their expansion into offshore waters in 1995 (Krieger et al., 1996).

The return of burrowing mayflies to western Lake Erie is important because they are indicators of mesotrophic conditions and their densities have been proposed as criteria for measuring the reversal of eutrophication through international pollution-abatement programs initiated in the late 1960s (Hunt, 1953; Burns, 1985; Reynoldson et al., 1989; Fremling & Johnson, 1990; Sweeney, 1993; Ohio Lake Erie Commission, 1998). Mayflies are relatively immobile, long lived, and have been shown to be sensitive to environmental stress, especially low dissolved oxygen (Fremling, 1964; Hiltunen & Schloesser, 1983; Schloesser & Hiltunen, 1984; Fremling & Johnson, 1990; Schloesser et al., 1991). Return of mayflies to formerly eutrophic waters has been interpreted as a sign of progress toward reversing eutrophication in inland waters of North America and Europe (Harris et al., 1987; Krieger et al., 1996; Fremling & Johnson, 1990; Schloesser et al., 1991; bij de Vaate et al., 1992). In the rivers Meuse and Rhine of Europe, massive numbers of the mayfly *Ephoron virgo* were found in the first few decades of the 20th century but severe water pollution resulted in low dissolved oxygen and extirpation of nymphs from large portions of these rivers in the 1930s (bij de Vaate et al., 1992). Pollution-abatement programs allowed recovery of *E. virgo* in the Netherlands' portions of the rivers Meuse and Rhine in 1991.

Recent examination of historical information of mayfly nymphs in western Lake Erie has revealed that there is little information in general and very little quantitative, site-specific information and this site-specific information is difficult to obtain and is open to interpretation (Manny, 1991; Kolar et al., 1997; Madenjian et al., 1998; Krieger et al., 1996; Schloesser & Nalepa, 2001). In addition, past studies have only sampled portions of the entire basin, which, because of its size and proximity to different anthropogenic influences, has exhibited strong regional differences of benthic communities (Carr & Hiltunen, 1965; Schloesser et al., 1995; Manny & Schloesser, 1999; Edsall et al., 1999). Consequently, determinations of mean densities based on individual studies vary widely among comparative studies and therefore probably do not reflect basin-wide comparisons.

Here, we present our interpretation of density information from specific sites for studies conducted between 1929 and 1991 and densities for recent studies conducted between 1991 and 1998 (Appendix 1). We compare all available data to assess the status of nymphs in western Lake Erie in the 1990s. A preliminary study by Krieger et al. (1996) showed the distribution of nymphs primarily in the western portion of the basin between 1930 and 1991 and early signs of increased distribution – but not densities – of nymphs into open waters in 1995. The present study includes several regional studies conducted between 1991 and 1994, expands the 1995 study by Krieger et al. (1996) to 1996–1998, and adds a second, independent study conducted in 1996–1998. The present study is the first to report the distribution and density of *Hexagenia* spp. nymphs throughout western Lake Erie.

Methods

We determined densities of mayflies found in 10 periods between 1929 and 1991 (past studies) and in 7 periods between 1991 and 1998 (present study) (Table 1, Appendix 1). Densities in past studies were compiled by examining published documents, reports, original field records, and personal communications with individuals who were knowledgeable of methods used during the period of study (e.g., personal communication, Jarl K. Hiltunen, Sault Ste. Marie, Michigan). Criteria used in selecting data were availability of quantitative density estimates at specific sites using a recommended benthic sampler, a minimum of 10 sites per sampling period over a relatively broad geographic area, and comparable seive sizes (Clesceri et al., 1998). Sample processing varied over years but followed general guidelines for benthic sampling as follows: samples were washed through a (minimum 0.6 mm-mesh) screen, preserved in formalin, and nymphs were removed and enumerated in the laboratory by visual inspection. These methods are adequate to obtain nymphs as small as 3 mm in length (Schloesser & Hiltunen, 1984; Schloesser & Nalepa, 2001; DWS, unpublished data).

In the present study, three recommended benthic samplers (Ponar, Ekman, petite Ponar) were used to determine densities of nymphs at between 9 and 47 sites in four sample collections in 1991, 1993, and 1994 (Table 1). Then beginning in 1995 and 1996, two systematic sampling programs were initiated (Figure 1). These two sampling programs were conducted independently. In one sampling program, an Ekman grab (506 cm^2) was used to collect four samples per site (primarily in the southwestern and middle portions of the basin) at between 20 and 21 sites annually 1995–1998. These are the same sites sampled by Krieger et al. (1996) in 1995. In a second sampling program, a petite Ponar grab (225 cm^2) was used to collect five samples per site (primarily in the northern and middle portions of the basin) at between 18 and 28 sites annually 1996–1998. Several sites located in the most western portion of the basin correspond to historical sites sampled in 1929–1930, 1961, 1982, and 1993 (Appendix 1). Many sites located in the northeastern, middle, and southern portions of the basin were sampled for the first time in the present study. Combined, the two sampling programs included the entire western basin with overlap of site locations in the western and middle portions of the basin. No significant differences between densities obtained during the two sampling programs within years were found. Therefore, we used total mean densities of individual sites of the two sampling programs to obtain basin-wide densities for 1996, 1997, and 1998. The present study is one of only two (Dermott, 1994) designed to sample benthos in the entire basin even though past studies have shown dramatic differences in benthic community composition based on proximity to islands, river mouths, and open water (Britt, 1955a, b; Carr & Hiltunen, 1965; Schloesser et al., 1995; Manny & Schloesser, 1999). Substrates throughout (>90%) western Lake Erie are soft muds, which are preferred substrates of burrowing mayfly nymphs (Hunt, 1953; Thomas et al., 1976). All samples were collected in May and June because this is the period of year when nymphs are relatively abundant and large and when several past studies of benthos were conducted (1961 and 1982, Carr & Hiltunen, 1965; Schloesser et al., 1995; Manny & Schloesser, 1999; Schloesser & Nalepa, 2001). Sample preservation and analysis followed recommended methods for benthic sampling and was very similar to that of past studies (Clesceri et al., 1998). Details of methods can be found in Schloesser (1988), Schloesser et al. (1991), and Schloesser et al. (1995).

Recent examination of the life history of *Hexagenia* spp. nymphs in Lake Erie revealed no discernable groups that could be attributed to the two species of nymphs (i.e., *H. limbata* and *H. rigida*) found in Lake Erie (Schloesser & Nalepa, 2001). There is no reliable method to separate these species of nymphs and past studies combined these taxa, which historically were the only species present (Krieger et al., 1996).

Statistical comparisons of densities of nymphs between studies within years and between years were tested by two-way ANOVA (Sokal & Rohlf, 1981; Zar, 1996) after $\log_{(10)}(x + 1)$ transformation of arithmetic site means. Differences in densities of nymphs found near shore (<7.5 km from shore) and offshore (>7.5 km) were tested using one-tailed student's *t*-tests (after $\log_{(10)}(x + 1)$ transformation) based on *a priori* knowledge of the trend of differences observed before and during the anoxic event in 1953–1954. Differences between densities in two areas of low density and all other sites in 1995–1998 were tested by one-way ANOVA after transformation of site densities. Areas were designated based on visual inspection of site densities. Differences in proportions of sites with nymphs present were tested using chi square of independence in 2×2 contingency tables containing number of sites with and without nymphs in successive years.

Results

In the 1990s, the distribution and density of mayfly nymphs increased dramatically over those observed in the previous 30 years (1961–1993) and by 1997–1998 were greater or similar to those found in 1929–1930 (Table 1). Nymphs were distributed at 75–98% of the sites between 1929 and 1954, except after an anoxic event in 1953 (48%). After the 1950s, nymphs were absent or rare between 1961 and 1991 when they occurred at 0 to 24% of sites. Recolonization of nymphs began between 1991 when nymphs occurred at 24% of sites and 1993 when they occurred at 54% of sites. Nymphs occurred at only 28% of sites in a north-central portion of the basin in 1994. After 1995, nymphs were found at 70% of sites in a south-

Table 1. Inventory of quantitative data of *Hexagenia* spp. nymphs (minimum 10 sites per sampling program, Appendix 1) in western Lake Erie 1929 to 1998. Values in columns preceeded by an asterisk are significantly different ($P < 0.05$) from the preceeding value (densities tested by ANOVA using $\log_{(10)}$ $(X + 1)$ transformation and proportion of sites with nymphs present tested by chi square using number of sites with and without nymphs present)

Period of collection	Mean density ± S.E.	Maximum density	Number of sites (Percent with nymphs)	General location in lake	Sampler type	Samples per site	Seive sive (mm)	Study
1929 June–September	171 ± 45.6	508	13 (85)	Western	Ekman	8–23	0.5	Wright (1955a, b)
1930 June–September	152 ± 24.5	692	67 (75)	Western	Petersen	1–16	0.5	Wright (1955a, b)
1953 September, November	*44 ± 11.0	340	*61 (48)	Eastern	Ekman	4	0.5	Britt (1955b)
1954 September, November	*827 ± 215.2	9615	*61 (98)	Eastern	Ekman	4	0.5	Britt (1955b)
1961 May–June	*1 ± 0.5	14	*40 (18)	Northwestern	Petersen	3	0.5	Carr and Hiltunen (1965)
1967 April–August	0	0	20 (0)	Northern	Ponar	3	0.6	Veal and Osmond (1968)
1973–1975 April–December	0	0	15 (70)	Southeastern	Ponar	2	0.6	Britt et al. (1980)
1979 May, August, October	2 ± 0.8	39	82 (1)	Entire	Ponar, Shipek	1–3	0.02–0.06	OME (1991), Dermott (1994)
1979 May		20	16 (13)	Northern	Ponar	3	0.6	OME (1981)
1979 August	5 ± 2.8	39	16 (19)	Northern	Ponar	3	0.6	OME (1991)
1979 October	1 ± 0.6	30	50 (2)	Entire	Shipek	1	0.2	Dermott (1994)
1982 June	7 ± 4.4	172	*40 (23)	Northwestern	Ponar	3	0.6	Manny and Schloesser (1999)

Table 1. Continued

Period of collection	Mean density ± S.E.	Maximum density	Number of sites (Percent with nymphs)	General location in lake	Sampler type	Samples per site	Seive sive (mm)	Study
1991 May–August	21 ± 14.6	705	49 (24)	Northern & central	Ponar	3	0.6	Present Study, Farrara and Burt (1993)
1991 May	10 ± 4.6	71	16 (38)	Northern	Ponar	3	0.6	Farrara and Burt (1993)
1991 August	55 ± 44.2	705	16 (25)	Northern	Ponar	3	0.6	Farrara and Burt (1993)
1991 June–July	1 ± 1.2	19	17 (12)	North-central	Ponar	3	0.6	Present Study
1993 May–June	10 ± 1.7	40	*56 (54)	Western, Southeastern	Ponar, Ekman	3	0.6	Present Study
1993 May	10 ± 1.6	38	47 (55)	Western	Ponar	3	0.6	Present Study
1993 June	12 ± 5.7	40	9 (44)	Southeastern	Ekman	3	0.6	Present Study
1994 June–July	7 ± 2.6	44	25 (28)	North-central	Petite Ponar	5	0.6	Present Study
1995 May–June	*37 ± 10.9	183	*20 (70)	Southwestern	Ekman	4	0.6	Present Study
1996 May–June	*90 ± 25.1	755	39 (77)	Entire	Ekman, Petite Ponar	4–5	0.6	Present Study
1996 May–June	104 ± 42.1	755	21 (81)	Southwestern	Ekman	4	0.6	Present Study
1996 May–June	71 ± 23.0	302	18 (72)	Northern	Petite Ponar	5	0.6	Present Study
1997 May–June	*392 ± 66.2	2064	49 (88)	Entire	Ekman, Petite Ponar	4–5	0.6	Present Study
1997 May–June	460 ± 120.0	2064	21 (90)	Southwestern	Ekman	4	0.6	Present Study
1997 May–June	352 ± 78.8	1440	28 (86)	Northern	Petite Ponar	5	0.6	Present Study
1998 May–June	*134 ± 19.4	518	49 (88)	Entire	Ekman, Petite Ponar	4–5	0.6	Present Study
1998 May–June	172 ± 35.3	518	21 (95)	Southwestern	Ekman	4	0.6	Present Study
1998 May–June	106 ± 20.3	444	28 (84)	Northern	Petite Ponar	5	0.6	Present Study

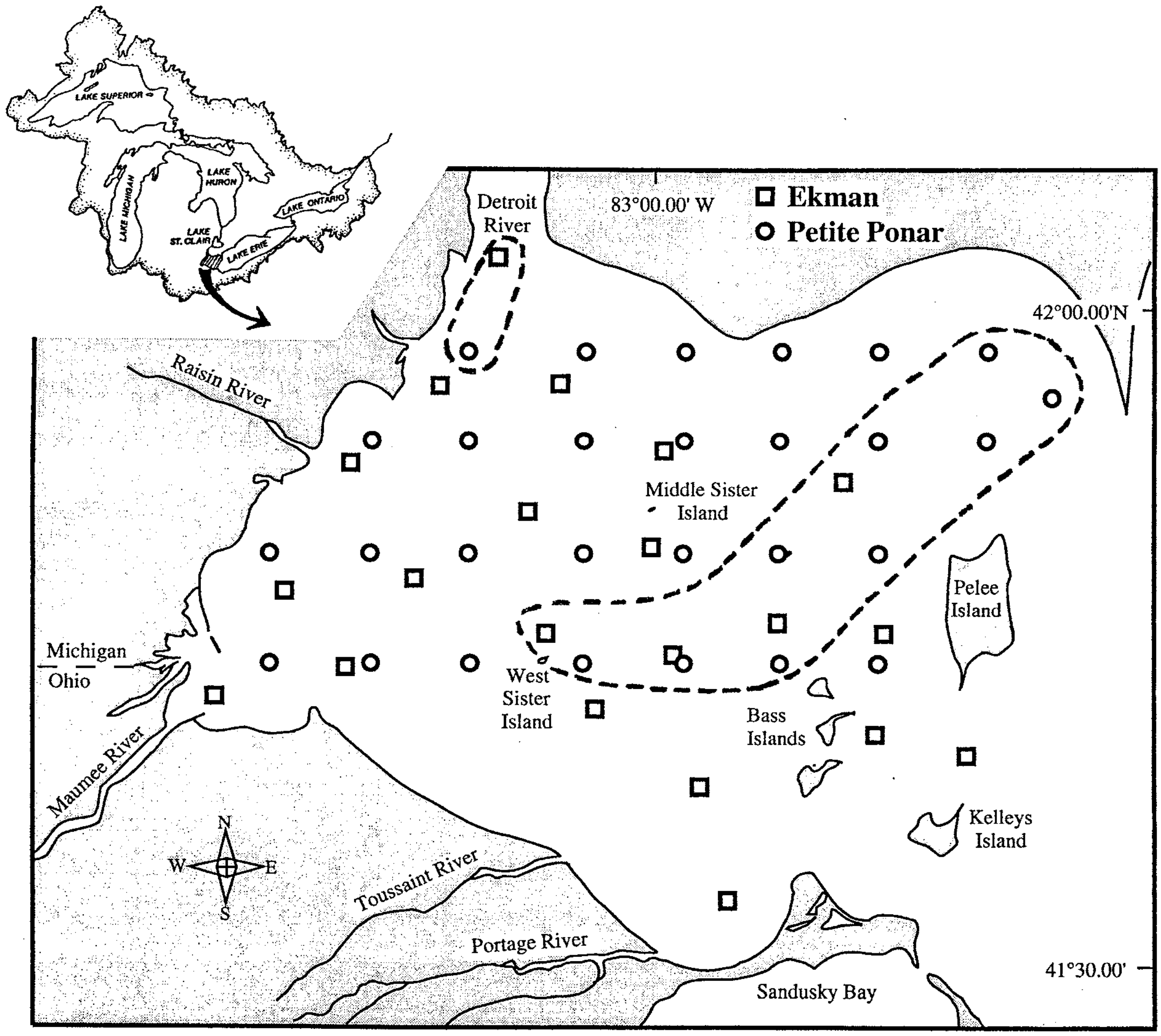

Figure 1. Location of sampling sites in two systematic studies conducted to determine the distribution and abundance of *Hexagenia* spp. mayfly nymphs in western Lake Erie 1995–1998. Samples were collected with an Ekman (squares) and petite Ponar (circles). The two areas contained within dashed lines are areas where low densities of nymphs persisted in the 1990s (see Table 2).

western portion. In 1996–1998, basin-wide sampling revealed that nymphs were found at 77% of sites in 1996 and 88% in 1997 and 1998. Increases in nymph densities over time followed the same pattern as observed for the distribution of nymphs, except between 1997 and 1998 when densities decreased 3-fold but no change was observed in the distribution of nymphs. Density changes between 1993–1994 and 1995 and successive years between 1995 and 1998 were significantly different (Table 1, $P < 0.01$).

Although regional differences in the abundance of nymphs are difficult to determine due to inconsistent sampling programs and prolonged absence of nymphs from most areas during a 30-year period, analyses of data from nearshore (<7.5 km from shore) and offshore (>7.5 km from shore) waters indicate that the abundance of nymphs in the 1990s is different than historically found in western Lake Erie (Figure 2). Between 1929 and 1954, abundance of nymphs was higher in offshore than nearshore waters, except in 1953 when an anoxic event occurred. Nymphs were absent or rare in both offshore and nearshore waters between 1961 and 1975. Although rare in occurrence, nymphs returned to nearshore waters in 1979 (13% of

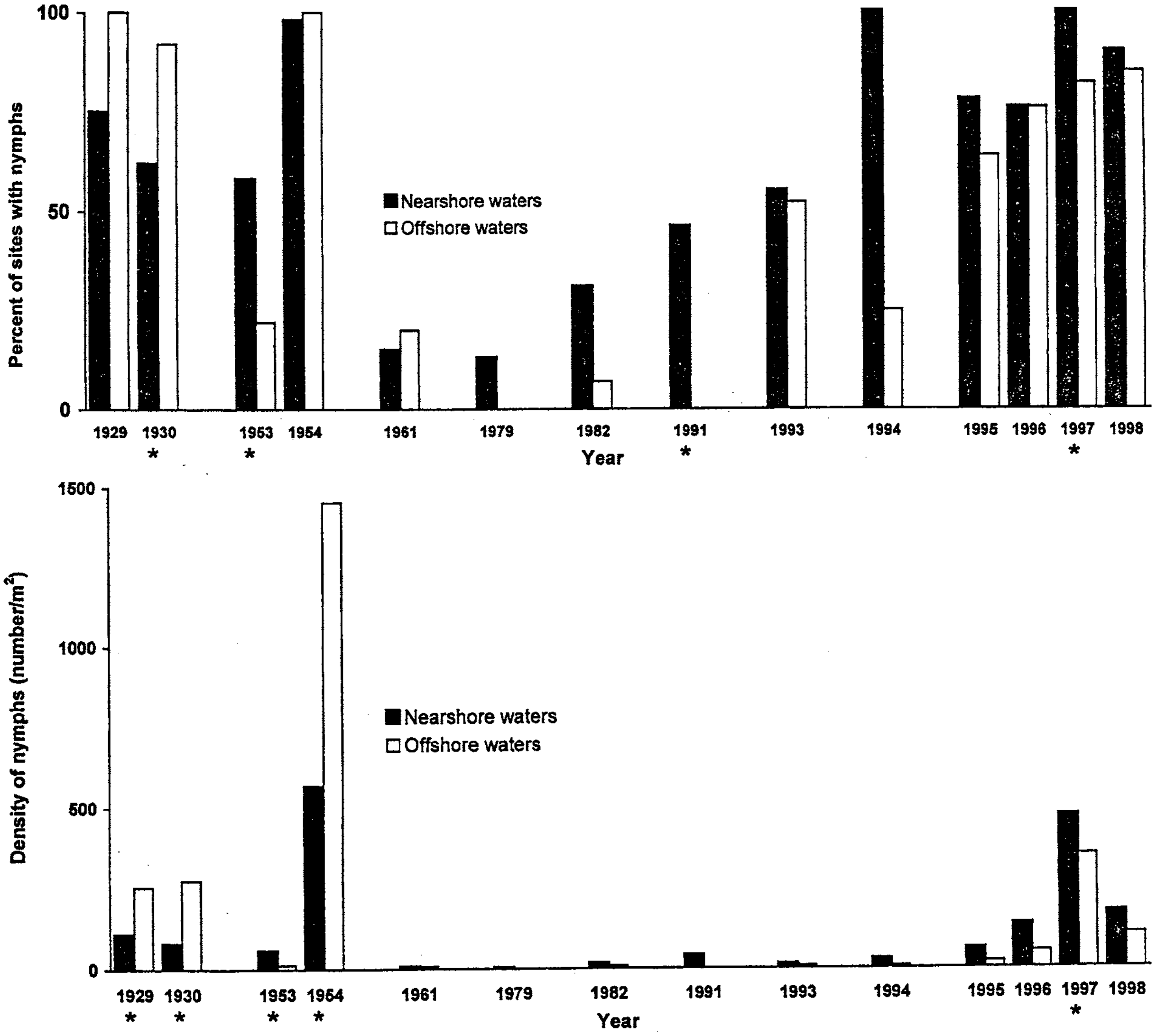

Figure 2. Percent of sites with nymphs present (top panel) and mean densities (bottom panel) of *Hexagenia* spp. nymphs in nearshore (<7.5 km from shore) and offshore (>7.5 km from shore) waters of western Lake Erie 1929–1998. Year designations with an asterisk indicate significant differences ($P < 0.05$) between nearshore and offshore areas (one-tailed Student's t-tests of $\log_{(10)}(X + 1)$ transformation and chi square of number of sites with and without nymphs present).

sites), but not to offshore waters (0%). Between 1979 and 1982, nymphs increased in distribution near shore (13 to 31% of sites, respectively) and also appeared in offshore waters (0 to 7% of sites, respectively). By 1991, nymphs had increased in distribution near shore (from 31% of sites in 1982 to 46% in 1991), but not offshore where no nymphs were found. However, by 1993 a substantial increase occurred in the distribution of nymphs offshore (from 0% in 1991 to 52% in 1993) and only a relatively small increase had occurred near shore (from 46% in 1991 to 55% in 1993). Substantial differences occurred in nymphal distribution between 1993 and 1994. In 1994, only one nearshore site was sampled and the remaining sites were located offshore in the north-central area of the basin. Between 1995 and 1997, percent of sites with nymphs increased in both nearshore and offshore waters but offshore populations of nymphs were usually found at fewer sites than those found near shore. Densities of nymphs were higher in offshore than nearshore waters between 1929 and 1954, except during an anoxic event in 1953. Nearshore waters

Table 2. Mean and, in parentheses, maximum densities of *Hexagenia* spp. nymphs at sites in two areas where relatively low densities occurred (circled on Figure 1) and at all other sites in western Lake Erie 1995–1998. Densities in rows separated by an asterisk are significantly different ($P < 0.05$; tested by ANOVA using $\log_{(10)}(X + 1)$ transformation)

	Sites in two areas with low densities		All other sites
1995	1 ± 1.0 (5)		49 ± 13.2 (183)
1996	4 ± 1.3 (10)	*	117 ± 33.0 (755)
1997	27 ± 11.0 (154)	*	568 ± 83.3 (2064)
1998	15 ± 5.0 (72)	*	187 ± 22.6 (518)

exhibited low densities and offshore waters exhibited none or very low densities between 1961 and 1994. Between 1995 and 1998, densities were consistently higher in nearshore than offshore waters. In addition, median densities in the four periods 1929–1954 were generally higher in offshore waters (247, 310, 0, and 610/m^2, respectively) than nearshore waters (40, 14, 5, and 175/m^2, respectively), whereas in 1995–1998 they were lower offshore (5, 24, 215, and 88/m^2, respectively) than near shore (43, 34, 302, and 151/m^2, respectively). Examination of abundances of nymphs in the 1990s revealed many sites within two areas that had consistently lower densities of nymphs than all other sites outside these areas (Table 2, Figure 1). These two areas of low density were located near the Detroit River mouth and in offshore waters in the central and northeastern region of the basin.

Discussion

The 17 density estimates of *Hexagenia* spp. nymphs in various portions of western Lake Erie between 1929 and 1998 indicate that dramatic increases occurred in abundances in the 1990s, and that these increases followed a two step process that may not have reached the carrying capacity or 'full recovery' in the basin by 1998. Although there is little quantitative data before the lake was impacted by pollution, it appears that basin-wide abundances of nymphs in the 1990s were similar to the earliest base-line data obtained in 1929–1930 (Wright, 1955a, b). However, densities in 1929–1930 may not represent base-line or pre-impacted conditions because paleoecological studies, covering a period of about 200 years, indicate that these densities may be relatively high and, therefore their use in measuring recovery may be limited (Carr & Hiltunen, 1965; Reynoldson et al., 1989; Reynoldson & Hamilton, 1993; Manny & Schloesser, 1999). We believe the recovery of nymphs in western Lake Erie in 1998 was not complete because the pattern of abundance in nearshore and offshore waters is opposite that found in historic records. In addition, there were large areas where nymphs were relatively low in abundance in the 1990s.

Mayfly recovery in western Lake Erie was predicted by Kolar et al. (1997), who used a simple logistic model to predict that a carrying capacity (steady state of full recovery) of 350 nymphs/m^2 would occur between the years 2000 and 2031, and a full model (including impacts of competitors, sediment toxicity, predators, etc.) to predict recovery between the years 2038 and 2071. Madenjian et al. (1998) predicted that between 300 and 1000 nymphs/m^2 would occur before the year 2002. Based on the probable carrying capacity of nymphs used in these models, recovery of nymphs in western Lake Erie occurred in 1997 (392 nymphs/m^2). Maximum densities in the 1990s also indicate possible recovery of nymphs in the 1990s because they were within range of maximum densities found in earlier studies of western Lake Erie and in other waters of the Great Lakes (Wright, 1955a; Britt, 1955b; Hiltunen & Schloesser, 1983; Schloesser, 1988; Schloesser et al., 1991). In 1997, densities in Lake Erie exceeded 1000/m^2 at five sites and 2000/m^2 at one other site (Appendix 1). The only other report of such high densities in the lake was in fall 1954 when densities exceeded 1000/m^2 at six sites and 2000/m^2 at six other sites (Britt, 1955b).

Determination of densities of nymphs during the past century has been infrequent or lacking for large areas of western Lake Erie, so the time to stability and full recovery of the *Hexagenia* spp. population cannot be confidently predicted. The large, basin-wide decrease in densities between 1997 and 1998 could be interpreted as evidence of limited recovery because the only other period when such a large change occurred was between 1953 and 1954, which was followed by decades when no to few nymphs occurred in the lake and adults were rarely found along the shore (Britt, 1955b; Krieger et al., 1996). However, the decrease in density of nymphs between 1997 and 1998 has been attributed to a failure of one year-class of nymphs in 1997 (Schloesser & Nalepa, 2001). Therefore, a failed year-class of nymphs could be a result of natural causes and probably does not indicate that recovery in western Lake Erie was not complete. For example, one other study that examined this aspect of nymphal populations in the lake also suggested a failed year-class in 1943, but nymphal populations rebounded in abundance in 1944 (Manny, 1991; Schloesser & Nalepa, 2001). At present, short-term fluctuations in densities can not be used to determine population stability and recovery because we suspect that large fluctuations occurred before anthropogenic impacts, and year-to-year fluctuations in densities may be normal for these populations (Reynoldson & Hamilton, 1993; Manny, 1991: Schloesser & Nalepa, 2001).

Our inclusion of previous studies based on selective criteria represents the most comprehensive and objective delineation of historical data of *Hexagenia* spp. in western Lake Erie. As a result, we believe that estimates of past densities presented here are closer to true abundances than some densities previously reported. For example, Reynoldson et al. (1989) included 12 of 17 estimates of mayfly densities from studies of western Lake Erie and used conversion factors for sampler efficiency and sieve size to obtain mean densities (Figure 1 in Reynoldson et al., 1989) of 2025–2045/m^2 in 1929–1930. The present study estimates these densities to be 171 and 152/m^2 from 13 and 67 sites, respectively. Similarly, Reynoldson et al. (1989) recalculated densities of 2550, 1000, and 2700 nymphs/m^2 in 1942, 1943, and 1944, respectively, while Chandler (1963) initially reported a mean density of 350/m^2 for these data. Other possible sources of error that could not be objectively determined in the present study include different sampler types and time of year samples were collected, which could also affect assessment of base-line densities and predictions of future carrying capacity of nymphs in western Lake Erie (Schloesser & Nalepa, 2001).

The factor(s) that prevented mayfly recolonization in offshore waters of western Lake Erie between about 1955 and the early 1990s is not known. It is likely a similar factor(s) operated over a large area because *Hexagenia* spp. was eliminated from many areas of the Great Lakes between 1940 and 1960, including portions of southern Lake Michigan (Mozley & LaDronka, 1988), Green Bay of Lake Michigan (Howmiller & Beeton, 1971), and Georgian Bay (Loveridge & Cook, 1976 cited in Mozley & LaDronka, 1988) and Saginaw Bay (Schneider et al., 1969) of Lake Huron, and western Lake Erie (Burks, 1953; Britt, 1955a) in about the same time period (i.e., 1940–1960).

Similarly, the cause for recolonization of nymphs in western Lake Erie in the 1990s is not known. Possible causes include: (1) attainment of high enough densities near shore that supplied sufficient numbers of recruits to offshore waters, (2) pollution abatement programs that changed environmental factors, and (3) colonization of substrates by zebra mussels (*Dreissena polymorpha*) that caused environmental changes, such as increased foods to substrates. Allee's principle (i.e., that a population's survival and growth may be limited by either low or high densities, Odum, 1971) suggests that densities of nymphs near shore may have been too low to establish a resident population throughout western Lake Erie between 1955 and early 1990s. Between 1979 and 1991 abundances increased near shore probably as a result of recruitment from nearby rivers and wetlands (Schloesser et al., 1991). By 1993, the distribution and density of nymphs increased offshore probably as a result of recruitment from nearshore populations. Allee's principle has also been suggested as a cause for slow recolonization of nymphs in Green Bay of the Great Lakes (Cochran & Kinziger, 1997).

Pollution-abatement programs initiated in the 1960s have changed environmental conditions in western Lake Erie, which may have allowed recolonization of substrates by mayfly nymphs (Burns, 1985; Makarewicz & Bertram, 1991; Nicholls & Hopkins, 1993; Schloesser et al., 1995; Manny & Schloesser, 1999). Abatement programs reduced point-source discharges of total phosphorus by 84% between 1972 and 1985, and in 1982, biological and chemical evidence suggested that the western basin had shifted from a eutrophic to a mesotrophic condition (Makarewicz & Bertram, 1991; Schloesser et al., 1995). This shift to mesotrophy would favor the recovery of mayfly nymphs because of elimination of anoxia often associated with eutrophication (Reynoldson et al., 1989; Fremling & Johnson, 1990; bij de Vaate et al., 1992). Ecological changes resulting from pollution-abatement programs have been noted in several large water bodies in North America and in smaller rivers in both North America and Europe where nymphs returned to sediments after prolonged absences (Fremling & Johnson, 1990; Edmondson, 1991; bij de Vaate et al., 1992; Lathrop, 1992). However, if conditions were favorable for mayflies in western Lake Erie, the reappearance of nymphs would have been expected to occur soon after mesotrophic conditions occurred in western Lake Erie (i.e., early 1980s). Expectation of a rapid recovery of nymphs is supported by the speed at which increased densities of nymphs occurred in Lake Erie between 1953 and 1954, at two sites in fall 1991, and at many sites between 1991 and 1997 and in the Mississippi River between 1982 and 1986 (Fremling & Johnson, 1990). Mean densities of nymphs increased 15-fold between 1953 and 1954 in offshore waters of the lake. In 1991, Farrara and Burt (1993) showed that mayfly densities increased 5-fold between May and September near shore and 10-fold at two sites (sites 321 and 323, Appendix 1) near the Detroit River. In the 1990s, a 10-fold increase in densities occurred between 1995 and 1997 throughout the basin. In a portion of the Mississippi River, *Hexagenia* spp. were eliminated in 1930 due to depletion of oxygen (Fremling & Johnson, 1990). Few mayflies were found between 1930 and the late 1960s when pollution-control programs were initiated. Pollution discharges into the river leveled off in 1982. By 1986, emerging mayflies were abundant enough to cause nuisance problems along the shores. In western Lake Erie, phosphorus loadings leveled off about 1982, but mayflies did not begin to return to sediments until 1993. At minimum, pollution-abatement programs improved environmental conditions in western Lake Erie so that once nymphs did colonize sediments they were not extirpated by harsh conditions, such as anoxia.

Colonization and explosive increase in abundance of zebra mussels in western Lake Erie in 1989 may have contributed to the speed at which nymphs recolonized sediments in the 1990s (Hebert et al., 1989; Griffiths et al., 1991; Schloesser & Kovalak, 1991; Nalepa & Schloesser, 1993; Krieger et al., 1996). Rapid changes in water characteristics and benthic fauna of western Lake Erie have been associated with and attributed to impacts of zebra mussels (Nalepa & Schloesser, 1993; Schloesser & Nalepa, 1994; Madenjian, 1995; MacIsaac, 1996; Schloesser et al., 1997). In 1989, densities of zebra mussels in western Lake Erie were the highest ever recorded (up to 350 000/m^2) and by 1995, mussels covered about 10% of all available substrates (Schloesser & Kovalak, 1991; Nalepa & Schloesser, 1993; Berkman et al., 1998). High densities, combined with the mussels' ability to remove particulates (e.g., sediments, phytoplankton, and small zooplankton) from the water column and deposit the material on substrates, delivered substantial amounts of nutrients and food energy to benthic populations within a shorter period of time (up to 35% of available plankton per day, Bunt et al., 1993; Madenjian, 1995) than would be expected if zebra mussels were not present (Wisniewski, 1990; Nicholls & Hopkins, 1993; Madenjian, 1995; MacIsaac, 1996). The ability of zebra mussels to remove suspended particulates has been used as a management tool to de-eutrophy polluted water in Europe (Reeders & bij de Vaate, 1990; Reeders et al., 1993). In North America, the invasion of zebra mussels has been accompanied by an increase in diversity of macrobenthos, especially those taxa that are relatively intolerant of organic pollution (e.g., snails, amphipods, caddisflies, and mayflies) (Dermott et al., 1993; Griffiths, 1993; Stewart & Haynes, 1994; Botts et al., 1996). In addition, Karatayev et al. (1997), who summarized 60 years of research on the impacts of zebra mussels in eastern Europe, reported that in general, benthic communities in the presence of zebra mussels are composed of larger-sized species than communities in the absence of zebra mussels. The return of one of the largest benthic forms (*Hexagenia* spp.) in western Lake Erie occurred shortly after increased abundance of zebra mussels.

There is also evidence that *Hexagenia* spp. is returning to other areas of the Great Lakes in the 1990s (e.g., Cochran, 1992). Adult mayflies have been found annually since 1991 near the lower Fox River of Green Bay, Lake Michigan (Cochran, 1992; Cochran & Kinziger, 1997). Small swarms of adult mayflies were also found along the shores of the central and eastern basins of Lake Erie in the mid 1990s (personal observations, DWS, KAK, and LDC). Exuviae (nymphal skins) were observed in the Bay of Quinte in eastern Lake Ontario in 1996 (personal communication., R. Dermott, Fisheries and Oceans, Burlington, Ontario). Swarms of adults occurred near shore in northern Saginaw Bay, Lake Huron between 1994 and 1996 (personal communication, D. Stewart, State University of New York, Syracuse, New York). Similar to western Lake Erie, we do not know what is allowing recolonization of mayflies in other areas of the Great Lakes, but it is likely that the impacts of pollution abatement and zebra mussels, which colonized waters one or more years before nymphs recolonized these areas of the Great Lakes, are contributing factors (Cochran, 1992; Cochran & Kinziger, 1997).

Conclusions

The return of nymphs to much of western Lake Erie is a historical event in the Great Lakes. The cause for recolonization in the lake is unknown but is primarily attributed to pollution-abatement programs and rapid ecological changes brought about by the exotic zebra mussel, *Dreissena polymorpha*. It is probable that the recovery of nymphs in western Lake Erie was not complete in 1995–1998 because abundances of nymphs in nearshore and offshore waters were different than that historically found in the lake, and there still existed large portions of offshore waters where nymphs were absent or low in abundance in the 1990s. Although little evidence exists, we suspect that the cause for low abundances of nymphs in some areas in the 1990s was low dissolved oxygen caused by high sediment oxygen demand of settling plankton and/or residual organic carbon in sediments as a result of anthropogenic inputs into the lake prior to the 1980s. The density of burrowing mayfly nymphs could be used to monitor large areas in the Great Lakes where nymphs potentially may recolonize sediments (Cairns, 1974; Mozley & LaDronka, 1988; Schloesser, 1988; Schloesser et al., 1991). Such an indicator organism has been used in other water bodies of the world, such as in the rivers Meuse and Rhine in The Netherlands (bij de Vaate et al., 1992), where recolonization of substrates by similar Ephemeroptera nymphs (*Ephoron virgo*) parallels that observed for *Hexagenia* spp. nymphs in western Lake Erie of the Laurentian Great Lakes.

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APPENDIX 1

Site designations, locations (latitude and longitude), and mayfly densities (number/m^2; densities separated by commas correspond to dates separated by commas) in western Lake Erie. Nearshore sites, which are less than 7.5 km from shore, are in bold type

Site	Latitude	Longitude	Year/Density
			1929
68	41 40.50	82 58.30	317
75	41 44.40	83 04.50	43
82	**41 33.25**	**82 53.40**	**230**
159	**41 31.20**	**82 56.25**	**0**
			1929, 30
8F	41 53.60	82 47.20	248,565
37A	41 36.40	82 36.30	508,458
59A	**41 32.33**	**82 41.83**	**323,692**
117(4R)	**41 52.83**	**83 17.83**	**57,8**
126(9D)	**41 58.17**	**83 09.17**	**0,0**
134(6L)	41 50.83	83 07.00	154,462
158	**41 38.67**	**82 51.00**	**312,505**
252(2M)	**41 43.67**	**83 23.33**	**9,37**
254(4M)	**41 45.33**	**83 19.17**	**22,63**
			1930
72	41 42.40	83 02.10	328
105	**41 41.00**	**83 14.50**	**203**
107(6M)	**41 42.83**	**83 16.17**	**94**
109(7M)	**41 44.00**	**83 17.83**	**270**
110	41 45.00	83 18.00	162
114(8M)	**41 47.33**	**83 21.33**	**81**
116(1R)	**41 49.00**	**83 23.67**	**40**
116F	**41 51.80**	**83 20.00**	**14**
118	**41 53.50**	**83 17.00**	**0**
119(1D)	**41 54.67**	**83 15.17**	**162**
121(2D)	**41 55.50**	**83 15.17**	**0**
125	41 57.25	83 09.83	0
127	41 57.10	83 08.75	0
128(6D)	41 56.50	83 08.67	13
130(4D)	41 54.83	83 08.17	21
132(8L)	41 53.00	83 07.83	310
200	**41 53.25**	**83 19.85**	**0**
201	**41 53.40**	**83 19.85**	**0**
202	**41 53.55**	**83 19.87**	**49**
203	**41 54.10**	**83 19.93**	**0**
204	**41 54.20**	**83 19.95**	**18**
210(3R)	**41 53.17**	**83 19.83**	**0**
211	**41 53.10**	**83 19.35**	**2**

Site	Latitude	Longitude	Year/Density
213	**41 53.00**	**83 19.00**	**74**
214	**41 53.10**	**83 19.83**	**0**
215	**41 53.00**	**83 19.75**	**32**
220	**42 03.30**	**83 07.85**	**13**
221	**42 02.00**	**83 07.75**	**101**
221B	**42 02.00**	**83 09.00**	**0**
222(13D)	**42 00.50**	**83 09.17**	**0**
226	**42 00.00**	**83 03.25**	**0**
227	**41 58.65**	**83 02.50**	**14**
228	41 56.85	83 02.50	81
229(9L)	41 55.00	83 02.33	634
230	41 55.75	83 03.75	189
231(7D)	41 56.33	83 05.33	176
232(8D)	41 57.33	83 07.17	0
235	**41 40.80**	**83 13.00**	**648**
236(1L)	41 43.17	83 12.00	94
237	**41 43.00**	**83 14.00**	**108**
240(5D)	**41 57.50**	**83 11.67**	**0**
250	**41 42.00**	**83 28.20**	**0**
251(1M)	**41 42.83**	**83 25.50**	**2**
253(3M)	**41 44.50**	**83 21.33**	**34**
255	41 46.00	83 18.25	108
256(5M)	41 46.33	83 17.17	402
257	41 47.25	83 15.50	182
258(2L)	41 47.83	83 13.83	634
259(3L)	41 49.00	83 10.83	564
260	41 50.00	83 08.75	337
261	41 51.10	83 19.25	344
262(5L)	41 51.50	83 11.00	358
263(4L)	41 51.83	83 13.17	317
264(5R)	**41 52.33**	**83 15.83**	**27**
265	**41 51.25**	**83 17.80**	**0**
266	**41 49.60**	**83 18.50**	**27**
267	41 47.50	83 19.00	68
268	41 46.40	83 19.05	40
			1953, 54
1B	**42 00.30**	**82 41.50**	**0,4600**
2B	**41 58.30**	**82 41.50**	**0,2970**
3B	**41 57.83**	**82 44.00**	**0,5425**
4B	41 55.00	82 41.50	0,1340
5B	**41 52.00**	**81 41.50**	**10,120**
6B	41 55.50	82 46.70	0,2855
7B	**41 56.00**	**82 53.25**	**5,0**
8B	41 55.00	82 58.00	0,75
9B(5B)	**41 41.50**	**82 46.00**	**0,110**
10B	41 51.90	82 50.67	0,6005
11B	**41 40.00**	**82 52.00**	**0,385**
12B	41 48.90	82 48.83	0,1435
13B	41 47.60	82 48.00	40,120
14B	41 47.30	82 59.00	0,910
15B	41 46.67	82 52.00	0,1300

Site	Latitude	Longitude	Year/Density
16B	**41 40.50**	**82 50.83**	**0,110**
17B	41 44.67	82 56.25	0,745
18B	**41 37.50**	**82 52.00**	**110,250**
19B	**41 44.00**	**82 43.50**	**15,120**
20B	**41 43.50**	**82 46.50**	**0,150**
21B	**41 41.40**	**82 44.00**	**0,105**
22B	**41 39.40**	**82 49.50**	**25,25**
23B	**41 37.35**	**82 43.85**	**280,95**
24B	**41 38.50**	**82 44.00**	**0,190**
25B	**41 38.25**	**82 46.25**	**70,110**
26B	**41 39.70**	**82 45.65**	**0,1175**
27B	**41 37.65**	**82 44.70**	**180,95**
28B	**41 38.00**	**82 45.50**	**340,265**
29B	**41 39.20**	**82 45.00**	**0,755**
30B	**41 39.50**	**82 46.50**	**0,1325**
31B	**41 38.70**	**82 47.25**	**5,490**
32B	**41 39.30**	**82 47.40**	**5, 1330**
33B	**41 39.00**	**82 48.20**	**25,510**
34B	**41 38.95**	**82 51.15**	**35,225**
35B	**41 36.50**	**82 51.85**	**225,430**
36B	**41 35.40**	**82 52.25**	**70,120**
37B	41 36.20	82 57.15	0,50
38B	41 38.35	82 56.65	0,475
39B	41 40.20	82 56.65	0,210
40B	**41 41.65**	**82 53.45**	**0,515**
41B	**41 42.20**	**82 51.20**	**0,215**
42B	**41 41.35**	**82 47.65**	**55,45**
43B	**41 41.00**	**82 50.00**	**5,155**
44B	**41 40.60**	**82 49.50**	**15,125**
45B	41 42.40	82 58.00	5,60
46B	**41 38.50**	**82 51.85**	**185,155**
47B	**41 40.00**	**82 52.65**	**0,235**
48B	**41 40.00**	**82 52.05**	**0,300**
49B	**41 40.45**	**82 51.90**	**0,150**
50B	41 51.10	83 01.75	0,10
51B	**41 40.60**	**82 51.50**	**0,120**
52B	**41 40.10**	**82 50.50**	**50,330**
53B	**41 39.50**	**82 50.25**	**40,65**
54B	**41 39.80**	**82 49.75**	**15,50**
55B	**41 39.20**	**82 51.10**	**20,35**
56B	**41 38.30**	**82 50.70**	**300,215**
57B	41 44.00	82 52.65	0,750
58B	**41 39.50**	**82 49.40**	**100,25**
59B(6B)	41 52.00	82 49.00	0,9615
60B	**41 39.40**	**82 49.30**	**280,130**
61B	**41 39.30**	**82 49.25**	**195,175**
			1961, 82, 93
119(1D)	**41 54.67**	**83 15.17**	**0,0,13**
121(2D)	**41 55.50**	**83 15.17**	**0,0,13**
3D	**41 56.33**	**83 12.17**	**0,0,32**
130(4D)	41 54.83	83 08.17	0,0,26

Site	Latitude	Longitude	Year/Density
240(5D)	**41 57.50**	**83 11.67**	**0,0,0**
128(6D)	41 56.50	83 08.67	0,14,6
231(7D)	41 56.33	83 05.33	0,0,26
232(8D)	41 57.33	83 07.17	0,0,6
126(9D)	**41 58.17**	**83 09.17**	**0,0,19**
10D	**41 59.33**	**83 09.83**	**0,7,0**
11D	**41 59.33**	**83 07.50**	**7,7,38**
12D	**41 58.83**	**83 05.50**	**10,7,13**
222(13D)	**42 00.50**	**83 09.17**	**0,14,0**
14D	**42 00.50**	**83 06.00**	**0,172,26**
15D	**42 02.00**	**83 09.17**	**0,0,6**
225(16D)	**42 01.50**	**83 04.17**	**0,14,0**
236(1L)	41 43.17	83 12.00	5,0,0
258(2L)	41 47.83	83 13.83	0,0,0
259(3L)	41 49.00	83 10.83	0,0,0
263(4L)	41 51.83	83 13.17	5,0,0
262(5L)	41 51.50	83 11.00	0,0,6
134(6L)	41 50.83	83 07.00	5,0,6
7L	**41 49.00**	**83 00.00**	**0,0,0**
132(8L)	41 53.00	83 07.83	0,0,0
229(9L)	41 55.00	83 02.33	0,0,6
10L	41 53.66	82 59.17	0,0,6
251(1M)	**41 42.83**	**83 25.50**	**0,41,13**
252(2M)	**41 43.67**	**83 23.33**	**0,0,0**
253(3M)	**41 44.50**	**83 21.33**	**0,0,0**
254(4M)	**41 45.33**	**83 19.17**	**14,0,0**
256(5M)	41 46.33	83 17.17	0,0,26
107(6M)	**41 42.83**	**83 16.17**	**0,0,26**
109(7M)	**41 44.00**	**83 17.83**	**0,0,26**
114(8M)	**41 47.33**	**83 21.33**	**0,0,26**
116(1R)	**41 49.00**	**83 23.67**	**0,7,26**
2R	**41 50.67**	**83 21.17**	**5,0,0**
210(3R)	**41 53.17**	**83 19.83**	**0,0,0**
117(4R)	**41 52.83**	**83 17.83**	**0,0,0**
264(5R)	**41 52.33**	**83 15.83**	**0,0,0**
6R	**41 54.17**	**83 18.00**	**0,0,19**
			1967
130(4D)	41 54.83	83 08.17	0
240(5D)	**41 57.50**	**83 11.67**	**0**
128(6D)	41 56.50	83 08.67	0
231(7D)	41 56.33	83 05.33	0
11D	**41 59.33**	**83 07.50**	**0**
12D	41 58.83	83 05.50	0
15D	**42 02.00**	**83 09.17**	**0**
225(16D)	**42 01.50**	**83 04.17**	**0**
236(1L)	41 43.17	83 12.00	0
263(4L)	41 51.83	83 13.17	0
262(5L)	41 51.50	83 11.00	0
134(6L)	41 50.83	83 07.00	0
7L	41 49.00	83 00.00	0
132(8L)	41 53.00	83 07.83	0

Site	Latitude	Longitude	Year/Density
229(9L)	41 55.00	83 02.33	0
10L	41 53.66	82 59.17	0
251(1M)	**41 42.83**	**83 25.50**	**0**
252(2M)	**41 43.67**	**83 23.33**	**0**
116(1R)	**41 49.00**	**83 23.67**	**0**
264(5R)	**41 52.33**	**83 15.83**	**0**
			1973, 74, 75
55	**41 44.30**	**82 44.00**	**0,0,0**
56	41 54.70	82 50.40	0,0,0
57	41 49.90	83 01.10	0,0,0
58	41 41.10	82 56.00	0,0,0
59	41 43.36	83 09.00	0,0,0
60	41 53.50	83 11.80	0,0,0
61	41 56.80	83 02.70	0,0,0
65	**41 39.00**	**82 44.00**	**0,0,0**
66	41 58.00	82 40.00	0,0,0
67	**41 40.00**	**82 52.00**	**0,0,0**
68-2	**41 45.00**	**82 51.00**	**0,0,0**
69	**41 33.00**	**82 55.00**	**0,0,0**
70	**41 46.00**	**83 20.00**	**0,0,0**
75-2	**41 54.00**	**83 18.00**	**0,0,0**
76	**41 36.50**	**83 04.00**	**ns,0,0**
			1979
b-5	**41 32.27**	**82 55.07**	**0**
b-7	**41 32.50**	**82 41.65**	**0**
c-5	**41 37.53**	**82 55.27**	**0**
c-6	**41 37.80**	**82 48.00**	**0**
c-7	**41 37.85**	**82 40.90**	**0**
d-2	**41 42.47**	**83 16.92**	**0**
d-3	41 42.75	83 09.75	0
d-4	41 42.68	83 02.55	0
d-5	41 43.10	82 55.25	0
d-6	**41 42.93**	**82 47.93**	**0**
e-2	41 47.92	83 17.20	0
e-3	41 48.12	83 09.92	0
e-4	41 48.05	83 02.85	0
e-5	41 48.33	82 55.68	0
e-6	41 48.50	82 48.32	0
e-8	41 48.77	82 33.88	0
f-2	**41 52.98**	**83 16.53**	**0**
f-3	41 53.58	83 10.15	0
f-4	41 53.80	83 03.05	0
f-5	41 53.77	82 55.68	0
f-6	41 53.92	82 48.42	0
f-7	41 54.20	82 41.33	0
g-4	**41 59.10**	**83 03.33**	**30**
g-6	**41 59.18**	**82 48.75**	**0**
g-7	**41 59.42**	**82 41.58**	**0**
g-8	**41 59.55**	**82 34.20**	**0**
s-42	**41 35.08**	**82 58.68**	**0**

Site	Latitude	Longitude	Year/Density
t-40	**41 40.48**	**83 12.22**	**0**
t-41	**41 40.40**	**83 05.80**	**0**
t-42	41 40.23	82 59.30	0
t-43	**41 40.33**	**82 51.77**	**0**
t-45	**41 40.60**	**82 37.30**	**0**
u-39	**41 44.95**	**83 20.95**	**0**
u-40	41 45.38	83 13.47	0
u-41	41 45.58	83 06.25	0
u-42	41 45.72	82 59.27	0
u-43	**41 45.68**	**82 51.77**	**0**
u-44	**41 45.85**	**82 44.57**	**0**
v-39	**41 50.25**	**83 20.08**	**0**
v-40	41 50.83	83 13.85	0
v-41	41 50.90	83 06.52	0
v-42	41 51.12	82 59.43	0
v-43	41 51.18	82 51.93	0
v-44	**41 51.28**	**82 45.00**	**0**
w-40	**41 56.12**	**83 13.68**	**0**
w-41	41 56.37	83 06.50	0
w-42	**41 56.65**	**82 59.48**	**0**
w-43	**41 56.32**	**82 52.45**	**0**
w-44	41 56.58	82 44.85	0
w-45	41 56.75	82 37.52	0
	May/August		**1979, 91**
277	41 51.35	82 36.03	0/0,0/0
284	**41 57.82**	**82 33.17**	**0/0,19/0**
294	**42 01.50**	**82 39.65**	**0/0,19/0**
308	41 55.43	82 44.13	0/0,0/0
314	**41 57.32**	**82 56.50**	**0/0,26/0**
318	**42 00.97**	**83 04.37**	**0/20,0/19**
321	**42 03.10**	**83 08.10**	20/0,13/135
323	**42 01.63**	**83 08.07**	**20/20,71/705**
327	**41 58.58**	**83 07.67**	**0/39,0/13**
333	**41 57.43**	**83 13.68**	**0/0,0/0**
346	41 52.17	82 58.40	0/0,0/0
370	41 51.37	83 05.65	0/0,0/0
374	**41 52.63**	**83 17.27**	**0/0,0/0**
386	41 45.67	83 19.65	0/0,0/0
423	**41 42.35**	**82 43.92**	**0/0,6/0**
1052	**41 59.68**	**82 48.78**	**0/0,0/0**
			1991
130(4D)	41 54.83	83 08.17	0
231(7D)	41 56.33	83 05.33	0
11D	**41 59.33**	**83 07.50**	**6**
14D	**42 00.50**	**83 06.00**	**0**
236(1L)	41 43.17	83 12.00	0
258(2L)	41 47.83	83 13.83	0
259(3L)	41 49.00	83 10.83	0
263(4L)	41 51.83	83 13.17	0
262(5L)	41 51.50	83 11.00	0

Site	Latitude	Longitude	Year/Density
134(6L)	41 50.83	83 07.00	0
7L	41 49.00	83 00.00	0
132(8L)	41 53.00	83 07.83	0
229(9L)	41 55.00	83 02.33	0
10L	41 53.67	82 59.17	0
256(5M)	41 46.33	83 17.17	0
117(4R)	**41 52.83**	**83 17.83**	**0**
264(5R)	**41 52.33**	**83 15.83**	**19**
			1993
1P	**41 32.92**	**82 55.00**	**13**
2P	**41 36.00**	83 02.50	**0**
3P	**41 39.00**	**83 09.00**	**19**
4P	41 45.00	83 06.25	0
5P	41 44.00	82 58.25	0
6P	41 38.42	82 56.67	0
7P	41 41.25	83 02.42	6
2B	41 58.30	82 41.50	7
3B	41 57.83	82 44.00	0
4B	41 55.00	82 41.50	40
9B(5B)	**41 41.50**	**82 46.00**	40
59B(6B)	41 52.00	82 49.00	0
1K	**41 45.00**	**82 45.00**	**0**
2K	41 46.00	82 52.00	0
3K	41 43.00	83 04.00	0
4K	41 37.00	82 56.00	20
			1994
103C	**41 55.80**	**82 56.80**	**27**
104C	41 52.60	82 57.70	18
105C	41 50.70	82 59.50	9
106C	41 51.00	82 59.70	0
107C	41 51.50	83 00.00	0
108C	41 51.00	83 00.40	0
110C	41 50.50	82 59.40	0
115C	41 52.80	83 00.20	0
117C	**41 55.50**	**82 55.10**	**0**
118C	41 52.30	82 52.80	0
119C	41 49.20	82 51.60	0
120C	41 49.10	82 52.40	0
121C	41 48.20	82 52.70	9
122C	41 47.90	82 50.30	0
123C	41 48.20	82 49.80	0
124C	41 47.20	82 53.60	0
125C	**41 50.50**	**82 40.00**	**0**
126C	41 53.65	82 52.00	0
127C	41 57.00	83 03.00	44
129C	41 49.60	82 58.20	0
132C	**41 44.50**	**82 44.00**	**0**
133C	**41 42.00**	**82 38.00**	**0**
134C	41 52.00	83 12.00	44
135C	**41 47.50**	**83 20.00**	**15**

Site	Latitude	Longitude	Year/Density
136C	41 36.50	82 55.50	0
			1995, 96, 97, 98
9B(5B)	**41 41.50**	**82 46.00**	**43,34,624,240**
59B(6B)	41 52.00	82 49.00	0,10,154,72
3D	**41 56.33**	**83 12.17**	**183,120,302,298**
232(8D)	41 57.33	83 07.17	38,82,1680,250
15D	**42 02.00**	**83 09.17**	**0,5,10,5**
1K	**41 45.00**	**82 45.00**	**29,48,216,302**
2K	41 46.00	82 52.00	0,0,0,14
258(2L)	41 47.83	83 13.83	87,14,283,259
134(6L)	41 50.83	83 07.00	34,159,149,34
7L	41 49.00	83 00.00	5,67,619,110
10L	41 53.67	82 59.17	14,24,216,38
251(1M)	**41 42.83**	**83 25.50**	**58,125,499,494**
109(7M)	**41 44.00**	**83 17.83**	**115, 755, 2064,518**
114(8M)	**41 47.33**	**83 21.33**	**96, 553, 1109,394**
1P	**41 32.92**	**82 55.00**	**0, 0, 384,115**
4P	41 45.00	83 06.25	5, 0, 10,5
5P	41 44.00	82 58.25	0,0,0,0
6P	41 38.42	82 56.67	0,154,250,86
7P	41 41.25	83 02.42	29,5,763,173
117(4R)	**41 52.83**	**83 17.83**	**10,24,418,5**
			1996, 97, 98
6K	**41 40.00**	**82 40.00**	**5,115,202**
7K	**41 34.00**	**82 40.00**	**0,5,19**
1C	**41 58.04**	**83 11.00**	**9,27,0**
2C	**41 58.04**	**83 04.08**	**302,240,53**
3C	**41 58.04**	**82 58.04**	**338,578,169**
4C	**41 58.04**	**82 52.02**	**27,676,249**
5C	**41 58.04**	**82 46.00**	**0,71,151**
6C	**41 58.04**	**82 39.08**	**0,18,18**
7C	**41 54.00**	**83 17.00**	**80,862,71**
8C	41 54.00	83 11.00	98,498,258
9C	41 54.00	83 04.08	160,240,89
10C	41 54.00	82 58.04	53,213,116
11C	41 54.00	82 52.02	44,107,124
12C	41 54.00	82 46.00	0,0,36
13C	41 54.00	82 39.08	9,44,27
17C	41 49.02	83 04.08	142,284,98
18C	41 49.03	82 58.04	36,551,151
19C	41 49.02	82 52.02	0,89,18
20C	41 49.02	82 46.00	9,36,0
34C	**41 56.06**	**82 35.06**	**0,18,27**
			1997, 98
14C	**41 49.02**	**83 23.01**	**1378,133**
15C	41 49.02	83 17.00	782,444
16C	41 49.02	83 11.00	382,98
21C	**41 44.02**	**83 23.01**	116,0
22C	41 44.02	83 17.00	1440,276

Site	Latitude	Longitude	Year/Density
136C	41 36.50	82 55.50	0
23C	41 44.02	83 11.00	1013,204
24C	41 44.02	83 04.08	0,0
25C	41 44.02	82 58.04	0,0
26C	**41 44.02**	**82 52.02**	**0,9**
27C	**41 44.02**	**82 46.00**	**196,160**

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