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RECRUITMENT OF *HEXAGENIA* MAYFLY NYMPHS IN WESTERN LAKE ERIE LINKED TO ENVIRONMENTAL VARIABILITY

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Abstract. After a 40-year absence caused by pollution and eutrophication, burrowing mayflies (*Hexagenia* spp.) recolonized western Lake Erie in the mid 1990s as water quality improved. Mayflies are an important food resource for the economically valuable yellow perch fishery and are considered to be major indicator species of the ecological condition of the lake. Since their reappearance, however, mayfly populations have suffered occasional unexplained recruitment failures. In 2002, a failure of fall recruitment followed an unusually warm summer in which western Lake Erie became temporarily stratified, resulting in low dissolved oxygen levels near the lake floor. In the present study, we examined a possible link between *Hexagenia* recruitment and periods of intermittent stratification for the years 1997–2002. A simple model was developed using surface temperature, wind speed, and water column data from 2003 to predict stratification. The model was then used to detect episodes of stratification in past years for which water column data are unavailable. Low or undetectable mayfly recruitment occurred in 1997 and 2002, years in which there was frequent or extended stratification between June and September. Highest mayfly reproduction in 2000 corresponded to the fewest stratified periods. These results suggest that even relatively brief periods of stratification can result in loss of larval mayfly recruitment, probably through the effects of hypoxia. A trend toward increasing frequency of hot summers in the Great Lakes region could result in recurrent loss of mayfly larvae in western Lake Erie and other shallow areas in the Great Lakes.

Key words: benthos; dead zone; eutrophication; Hexagenia; *hypoxia; Lake Erie; Laurentian Great Lakes; mayfly; oxygen; recruitment; stratification.*

INTRODUCTION

Until the middle of the last century, western Lake Erie provided extensive habitat for nymphs of burrowing mayflies (*Hexagenia* spp). Warm water temperatures, soft sediments, and plentiful organic inputs from the Detroit and Maumee Rivers sustained what was possibly the world's largest *Hexagenia* population, estimated to be at least 17 660 tonnes (1 tonne = 1 Mg) (Manny 1991). In the early 1950s, mayflies were considered to be an annoyance and often a hazard. Swarming adults collected by the millions under streetlights and were crushed by automobiles, creating slick road conditions (Langlois 1951). Despite their nuisance, *Hexagenia* were an important component of the Lake Erie ecosystem and economy, supporting large populations of rapidly growing yellow perch (*Perca flavescens*), a valuable sport and commercial fishery (Hayward and Margraf 1987).

In 1953, the cumulative effects of cultural eutrophication and an extended period of sultry weather combined to produce extensive anoxia across much of western Lake Erie (Britt 1955) and *Hexagenia*, which is intolerant of low dissolved oxygen concentrations (Nebeker 1972, Winter et al. 1996), was nearly extirpated from the basin (Britt 1955). In the following years, the usefulness of mayfly populations as indicators of environmental health became widely recognized in North America and Europe (Bauernfeind and Moog 2000), and the reestablishment of *Hexagenia* to pre-1953 densities became a management goal for pollution-abatement programs. (Reynoldson et al. 1989, Ohio Lake Erie Commission 1998). Despite steady improvements in water quality in the 1980s, however, mayflies continued to be rare for nearly 40 years (Krieger et al. 1996).

In the late 1980s, western Lake Erie was colonized by zebra mussels (*Dreissena polymorpha*) and subsequently returned to mesotrophic conditions (Leach 1993). Soon afterward, *Hexagenia* nymphs began to reappear in substantial numbers (Krieger et al. 1996). Although the relative importance of the various factors influencing the return of *Hexagenia* is not known, between 1991 and 1997 *Hexagenia* populations increased exponentially (Madenjian et al. 1998), and by 1999 the basin-wide mean density in western Lake Erie approached pre-extirpation levels (Schloesser et al. 2000, Schloesser and

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Nalepa 2001). Yellow perch responded to the return of *Hexagenia* by increasing the annual percentage of mayflies in their diet from 0% in 1990 to about 20% by weight by 1997 and this change may account for the corresponding rebound of yellow perch population size and growth rates in western Lake Erie (Tyson and Knight 2001).

Despite the apparent success of the mayfly recovery, *Hexagenia* population size and yearly reproduction remain highly variable with no young-of-year recruitment in 1997 (Schloesser and Nalepa 2001). To date, there has been no explanation for this variability, but oxygen conditions near the sediments are likely to play an important role. For profundal benthic invertebrates in dimictic lakes, survival depends on whether dissolved oxygen trapped in the hypolimnion at the onset of stratification will persist until fall turnover, whereupon the entire water column is recharged with oxygen. The central basin of Lake Erie is prone to summer hypoxia in part because its morphometry dictates stratification for several months each summer with a relatively thin hypolimnion (Charlton et al. 1993). Consequently, the offshore areas of the central basin have probably never been suitable habitat for mayflies (Reynoldson and Hamilton 1993). In contrast, shallow western Lake Erie (where average depth is 7.4 m) provides good mayfly habitat because it does not form a true summer hypolimnion. Instead, the waters of western Lake Erie follow a diel pattern, typically becoming stratified in early afternoon and mixing during the night (Ackerman et al. 2001). Extended periods of calm conditions, however, can result in complete stratification for several days at a time (Bartish 1984).

Two separate observations prompted our investigation. First, we noted that large benthic areas of western Lake Erie were subjected to at least one episode of severe oxygen depletion following temporary thermal stratification in the summer of 2002. Second, almost no *Hexagenia* young-of-year nymphs were found in this region in the fall of the same year. These observations gave rise to an obvious question: were low densities of young-of-year *Hexagenia* the result of transient summer hypoxia? Although we could not address this question directly, we attempted to gain insight by relating the recent history of *Hexagenia* reproductive success (1997–2002) to the probable occurrences of low oxygen in those years.

In this research, we show that relatively short periods of stratification can result in low dissolved oxygen near the floor of western Lake Erie. Then, using historical records of daily surface water temperature and wind speed, we devised a simple method of quantifying the relative frequency of summer stratification for all years for which mayfly recruitment data is available (1997–2002). Finally, we related stratification to *Hexagenia* recruitment over the same period.

MATERIALS AND METHODS

In order to investigate *Hexagenia* recruitment and stratification patterns, we first analyzed spatial and temporal stratification and dissolved oxygen patterns using data we collected in 2002. We then predicted thermal stratification using surface weather data and stratification data from 2003, and used the resulting model to hind cast stratification. Finally, we determined mayfly recruitment for 1997–2002 and related this to past stratification.

Environmental data

Monitoring of the physical, chemical, and biological characteristics of the southwest portion of western Lake Erie, including Maumee Bay began in April and continued through September in 2002 and 2003. Sampling was conducted about once per week and data were collected at 12 to 20 locations on each trip (Fig. 1). At each location, a Hydrolab multiprobe (Datasonde 4a, Hach Environmental, Loveland, Colorado, USA) equipped with a stirrer was used to record water column measurements of temperature, turbidity, and dissolved oxygen concentration (DO). On most occasions, the water column was not thermally stratified, and multiprobe readings were recorded at 2-m intervals between the surface and lake bottom. On 24 June 2002 however, we detected the presence of a thermocline located 1–2 m above the sediments at many of our sampling locations. To record the duration of this event, we conducted sampling trips on 25 June, 2 July, 3 July, and 16 July, recording multiprobe measurements at 0.5–1 m depth intervals. In each vertical profile, the final "bottom" or epibenthic DO measurement was taken with the probe just above the sediments. Turbidity readings were used to verify that sediments were not disturbed when DO measurements were recorded. The spatial dimensions of the hypoxic area were mapped using spatial analyst in ArcView GIS (ESRI, Redlands, California, USA). In June 2003, water temperature loggers (HOBO Water Temp Pro, Onset Computer Corporation, Bourne, Massachusetts, USA) were deployed at a western Lake Erie location with an historical record (Carr and Hiltunen 1965) of benthic sampling (Station 4P: 41°45′00″ N, 83°06′14″ W; depth = 9.5 m) and recovered in September. Loggers were placed at depths of 1, 3.75, 6.5, 8.5, 9.0, and 9.3 m, and set to record temperature at 20-min intervals.

Because the same detailed data on stratification were not available for years in which *Hexagenia* recruitment data were collected, we identified periods between 1997 and 2002 in which western Lake Erie may have become stratified during summer months using historical data on wind speed (m/s) and water temperature (°C) collected by National Data Buoy Station 45005 (41°40′37″ N, 82°23′53″ W), a floating meteorological station maintained by the National Oceanic and Atmospheric Administration and the National Weather Service. Wind speed sensors were located 5 m above the

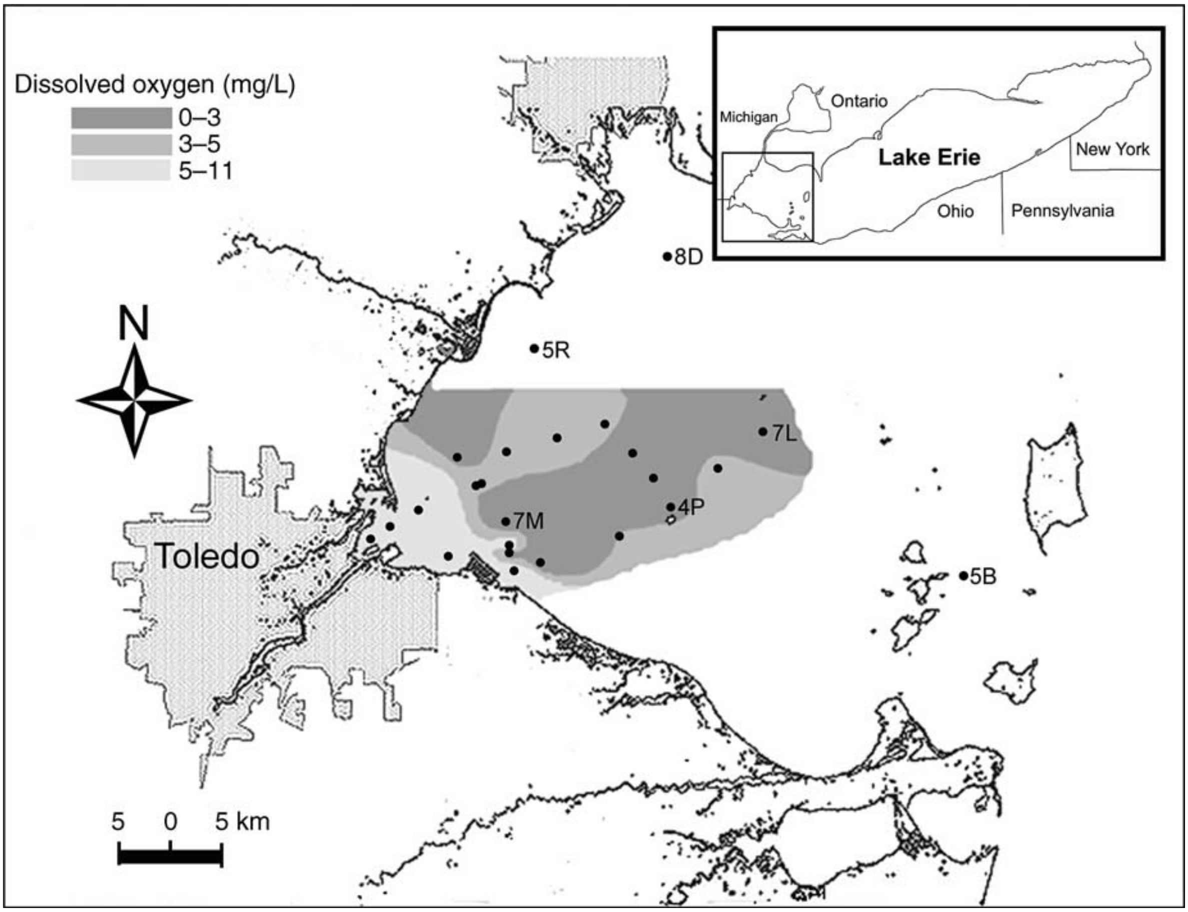

FIG. 1. Dissolved oxygen concentrations based on measurements at locations (black dots) in western Lake Erie, USA, 2–3 July 2002. Measurements were made ~10 cm above substrates. Samples for estimating mayfly recruitment were collected at site 7M. Sites 7M, 5B, 7L, 8D, and 5R were used to compare mayfly abundance from a previously published study. Temperature loggers were located at site 4P.

lake surface and water temperatures were recorded 0.6 m below the surface. Although Station 45005 is located about 60 km east of the research area and averaged 1.5°C cooler than our loggers recorded in 2003, daily variation in surface temperatures between locations were highly correlated ($r = 0.987$, $P < 0.001$).

Prediction of thermal stratification

From 2003 buoy data (from Databuoy 45005) on surface temperature and wind speed, we developed a model to predict stratification from the detailed stratification data we collected in 2003 with temperature loggers. This model was then applied to 1997–2002 data from Databuoy 45005 to identify biologically significant stratified periods between 1997 and 2002 for which no water column data exists. Stratification (S) was defined as the difference in temperature between the lake surface and bottom, where we had 94 observations for S in 2003. Databuoy 45005 data were used as follows: hourly wind speeds and water temperatures were averaged to obtain daily means; daily mean temperatures were subtracted from the following day's mean temperature to obtain a daily surface temperature change (ΔT). Epibenthic oxygen depletion begins within several hours after stratification and increases the longer stratification is maintained, therefore we examined cumulative development of stratification over periods of 1, 2, 3, 4, 5, 6, and 7 d. Surface temperatures tend to spike upward during stratification while bottom temperatures remain constant, therefore we tested the ability of 1–7 d running sums of ΔT ($\Sigma\,\Delta T$) to predict S on the final day of each period. In addition, stratification tends to develop during calm periods, therefore we tested the ability of average wind speed ($\mathrm{WS}_{\mathrm{avg}}$, defined as the average wind speed over the same period of 1–7 d used to calculate $\Sigma\,\Delta T$) to predict S. Because high winds tend to cause mixing, the relationship of wind speed and stratification was expected to be inversely correlated rather than simply negatively correlated, thus we also tested models where we substituted $\mathrm{WS}_{\mathrm{avg}}$ with the inverse of $\mathrm{WS}_{\mathrm{avg}}$ ($\mathrm{WS}_{\mathrm{avg}}^{-1}$). Wind influences lake mixing at the square of its velocity (Imberger and Hamblin

TABLE 1. Models used to predict thermal stratification.

Model	Equation
1	$Y = \beta_0 + \beta_1(\Sigma\ \Delta T) + \varepsilon$
2	$Y = \beta_0 + \beta_1(\mathrm{WS_{avg}}) + \varepsilon$
3	$Y = \beta_0 + \beta_1(\mathrm{WS_{avg}}) + \beta_2(\mathrm{WS^2_{avg}}) + \varepsilon$
4	$Y = \beta_0 + \beta_1(\mathrm{WS^{-1}_{avg}}) + \varepsilon$
5	$Y = \beta_0 + \beta_1(\mathrm{WS^{-1}_{avg}}) + \beta_2(\mathrm{WS^{-2}_{avg}}) + \varepsilon$
6	$Y = \beta_0 + \beta_1(\Sigma\ \Delta T) + \beta_2(\mathrm{WS_{avg}}) + \varepsilon$
7	$Y = \beta_0 + \beta_1(\Sigma\ \Delta T) + \beta_2(\mathrm{WS_{avg}}) + \beta_3(\Sigma\ \Delta T \times \mathrm{WS_{avg}}) + \varepsilon$
8	$Y = \beta_0 + \beta_1(\Sigma\ \Delta T) + \beta_2(\mathrm{WS_{avg}}) + \beta_3(\mathrm{WS^2_{avg}}) + \varepsilon$
9	$Y = \beta_0 + \beta_1(\Sigma\ \Delta T) + \beta_2(\mathrm{WS_{avg}}) + \beta_3(\mathrm{WS^2_{avg}}) + \beta_4(\Sigma\ \Delta T \times \mathrm{WS_{avg}})$
10	$Y = \beta_0 + \beta_1(\Sigma\ \Delta T) + \beta_2(\mathrm{WS_{avg}}) + \beta_3(\mathrm{WS^2_{avg}}) + \beta_4(\Sigma\ \Delta T \times \mathrm{WS_{avg}}) + \beta_5(\Sigma\ \Delta T \times \mathrm{WS^2_{avg}}) + \varepsilon$
11	$Y = \beta_0 + \beta_1(\Sigma\ \Delta T) + \beta_2(\mathrm{WS^{-1}_{avg}}) + \varepsilon$
12	$Y = \beta_0 + \beta_1(\Sigma\ \Delta T) + \beta_2(\mathrm{WS^{-1}_{avg}}) + \beta_3(\mathrm{WS^{-2}_{avg}}) + \varepsilon$
13	$Y = \beta_0 + \beta_1(\Sigma\ \Delta T) + \beta_2(\mathrm{WS^{-1}_{avg}}) + \beta_3(\Sigma\ \Delta T \times \mathrm{WS^{-1}_{avg}}) + \varepsilon$
14	$Y = \beta_0 + \beta_1(\Sigma\ \Delta T) + \beta_2(\mathrm{WS^{-1}_{avg}}) + \beta_3(\mathrm{WS^{-2}_{avg}}) + \beta_4(\Sigma\ \Delta T \times \mathrm{WS^{-1}_{avg}})$
15	$\boldsymbol{Y = \beta_0 + \beta_1(\Sigma\ \Delta T) + \beta_2(\mathrm{WS^{-1}_{avg}}) + \beta_3(\mathrm{WS^{-2}_{avg}}) + \beta_4(\Sigma\ \Delta T \times \mathrm{WS^{-1}_{avg}}) + \beta_5(\Sigma\ \Delta T \times \mathrm{WS^{-2}_{avg}}) + \varepsilon}$

Notes: Y, stratification; β_0, intercept; β_1, β_2, β_3, β_4, β_5, slopes associated with x variables; $\Sigma\ \Delta T$, running sum of daily change in surface temperature (1–7 d); $\mathrm{WS_{avg}}$ = wind speed average (1–7 d); ε, residual error. Boldface type for Model 15 indicates that it was the best model as identified by the $\mathrm{AIC_c}$.

1982), therefore we included a quadratic term for wind speed ($\mathrm{WS^2_{avg}}$ or $\mathrm{WS^{-2}_{avg}}$). Overall, we developed a set of 15 regression equations building from simple linear regressions with one factor to multifactor regressions to response surface regressions (Table 1). These models were then tested across the seven time periods. The model equations were estimated in SAS (SAS Institute 2002–2003). Because of our mix of factors, model results were compared using the lowest corrected Akaike Information Criteria ($\mathrm{AIC_c}$) value to select the best approximating model for S. The parameter estimates from the best model were then used with buoy data to calculate predicted thermal stratification (PTS) for each summer day during 1997–2002, beginning on the first date that surface waters attained 18°C through 25 September (1997–2002). May and early-June dates prior to the attainment of 18°C were excluded to prevent the normal seasonal increase in water temperature from being confused with mid-summer temperature peaks associated with stratification. Dates after 25 September were not used in order to exclude severe autumn storms that sometimes occur in late September. The 635 PTS values calculated for 1997–2002 were sorted in descending order, with the highest values representing unusually rapid surface heating and likely stratification. Because there is no discreet value of PTS that distinguishes between stratified and non-stratified conditions, a range of cutoff points between the 85th and 96th percentile of PTS values were used to obtain an average estimate of the relative severity of stratification among years. For example, values above the 96th percentile ($N = 25$) were sorted by year and then the stratification frequency was calculated as the number of individual PTS values in each year that were above the cutoff, divided by N (for 1997, $6/25 = 0.24$; for 1998, $5/25 = 0.20$). This procedure was repeated using the 85th through 95th percentiles as cutoffs, resulting in 12 estimates of stratification frequency for each year. These estimates were then averaged, resulting in an estimate that is independent of any arbitrary cutoff. Because it is based on the sum of high PTS values for each year, the stratification frequency metric takes into account both the number of stratified periods in a given summer and their duration.

Prediction of bottom dissolved oxygen

To determine, in part, the relationship between the onset of stratification and epibenthic oxygen depletion, we used PTS to predict epibenthic DO concentration. This was determined by simple linear regression of 2002 and 2003 summer dates for which DO measurements were collected ($n = 17$). Since DO is also dependent on the amount of time spent under stratified conditions and on primary production, data collected late in stratified periods (beyond day 4) and data indicating high levels of primary production (DO > 8.5 mg/L) were excluded from the analysis.

Hexagenia recruitment

Sampling and laboratory procedures for *Hexagenia* are detailed in Schloesser and Nalepa (2001). In summary, ponar grabs were collected monthly at one location chosen for historically high density of mayfly nymphs (Station 7M; 41°00′0″ N, 83°17′49″ W), August through November 1997–2002 to determine young-of-year densities (individuals/m^2). A minimum of three replicate ponar grabs were collected on each date. Sediments were rinsed through a 0.6-mm mesh and nymphs retained on the sieve were enumerated, measured, sexed, and then preserved in 10% buffered formalin. Although a mesh of 0.6 mm may not retain all first instars, nymphs increase in size within a few weeks of hatching so that they are adequately retained by the sieve. Young-of-year nymphs were determined by tracking *Hexagenia* size-frequency distributions over time, with young-of-year appearing in August–September as a separate smaller-sized distribution. Maximum density of young-of-year in the fall of each year was operationally defined as recruitment for the present study. Nymphs of *H. rigida* cannot reliably be distinguished from co-occurring *H. limbata*, in western Lake Erie (Nalepa and Schloesser 2001). Therefore, reference to *Hexagenia* throughout this work includes both species.

Although fall benthic samples for the determination of recruitment were collected at only one location (7M), spatial information on mayfly distribution is provided by annual spring surveys at 50 locations across western Lake Erie (Schloesser et al. 2000) including stations 4P and 7M. To determine whether site 7M was representative of a broader area, we used cohort abundance data from Schloesser and Nalepa (2001) to compare nymph distributions for May of 1998 and 1999 at 5 western basin locations (including 7M) ranging from near the mouth of the Detroit River to the Bass Islands (Fig. 1). Other site locations were 5B (41°41′31″ N, 82°49′01″ W), 7L (41°49′01″ N, 83°00′00″ W), 8D (41°57′22″ N, 83°07′12″ W), and 5R (41°52′19″ N, 83°15′50″ W). Analyses were performed using three-way ANOVA in SAS where we tested a full model with interactions effects to predict overall abundance with the class effects of year (1998, 1999), cohort (YOY, year 2), and site (7M, 5B, 7L, 8D, 5R). A three-way interaction term was not considered because there were not enough degrees of freedom. *Hexagenia* young-of-year recruitment was plotted against stratification frequency. An illustrative line was fitted to the data using a four-parameter Gompertz sigmoidal function in Sigmaplot (SPSS, Inc. Chicago, Illinois, USA). This relationship could not be statistically tested because there were only six data points and there was error associated with both the x and y variables.

RESULTS

Observed stratification and hypoxia

Thermal stratification (Fig. 2a) and near-substrate oxygen depletion (Fig. 2b) in western Lake Erie were observed on four of 21 dates sampled April through October 2002 (25 June, 2 July, 3 July, and 16 July). During the stratified period in early July, near-substrate oxygen depletion was observed at all locations with water depths greater than about 4 m (16 of 21 locations; Fig. 1). In these deeper waters, DO concentrations were lower above soft sediments than above firm sediments. Stratification and oxygen depletion were not observed in the shallow waters of Maumee Bay and shoreline locations with depth less than 4 m. At stratified locations, major changes in temperature and DO concentration occurred about 1 m above the sediments (Fig. 2). The thermocline and oxycline followed the gradual slope of the lake bottom, remaining 1 m above the bottom in waters ranging in depth from 5.5 m (Site 7M, Fig. 2) to 10 m (Site 4P) at sites 16 km apart. Stratification developed in late June during a period of rapidly increasing air and surface water temperature, and relatively low wind speeds which persisted until at least 4 July. Although our sampling area covered only the southwest quadrant of the western basin, concurrent measurements by the Ohio Department of Natural Resources confirmed that the low-oxygen zone continued at least another 17 km east of our sampling area (J. Tyson, *personal communication*). Thermal profiles collected on 16 July indicate that mixing occurred at some point between 3 July and 16 July, probably with the arrival of cool weather on 4 July. By 16 July,

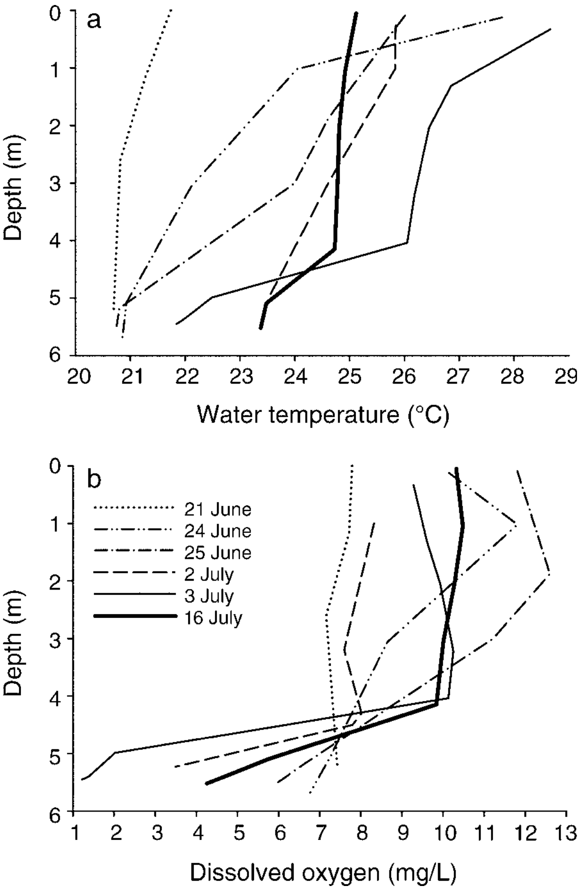

FIG. 2. Progressive development of (a) thermal stratification and (b) low epibenthic dissolved oxygen at a medium-depth station (7M) in western Lake Erie 24 June–16 July 2002.

TABLE 2. Summary of the Δ_i in the AIC$_c$ values of the 105 candidate models to predict thermal stratification.

	Time period (d)						
Model	1	2	3	4	5	6	7
1	142.83	115.45	81.23	49.10	42.77	60.18	86.81
2	137.36	118.05	102.90	100.90	106.55	117.10	127.46
3	138.15	112.56	89.40	74.51	77.55	102.83	122.90
4	140.40	108.92	88.65	77.88	85.16	106.75	123.55
5	137.64	110.99	90.60	73.46	68.22	97.03	123.49
6	138.41	109.31	71.78	41.50	40.15	60.53	87.95
7	128.44	90.22	49.01	19.13	21.18	50.14	84.12
8	139.74	107.51	68.91	36.65	34.20	58.89	88.28
9	124.35	89.19	49.95	21.21	23.39	52.05	86.33
10	126.61	90.62	51.98	19.76	25.52	54.32	88.61
11	140.16	104.52	67.88	36.39	35.81	59.09	87.38
12	139.45	106.47	70.07	37.46	31.66	57.68	88.37
13	138.85	93.18	57.77	28.24	24.56	50.81	84.73
14	134.17	87.86	48.94	26.21	26.47	52.39	86.71
15	131.81	89.82	41.58	0.00	18.66	54.55	85.61

however, the surface temperatures were increasing rapidly again and stratification was becoming reestablished (Fig. 2a).

Prediction of thermal stratification

Of the 105 models which used varying factors and time periods to predict observed stratification from surface temperature and wind speed buoy data in 2003, we found that the model with the lowest AIC$_c$ value (Table 2) was a response surface regression for time period 4 with the squared inverse term for wind speed:

$$S = \beta_0 + \beta_1\left(\sum \Delta T\right) + \beta_2\left(\mathrm{WS}_{\mathrm{avg}}^{-1}\right) + \beta_3\left(\mathrm{WS}_{\mathrm{avg}}^{-2}\right) + \beta_4\left[\sum \Delta T\left(\mathrm{WS}_{\mathrm{avg}}^{-1}\right)\right] + \beta_5\left[\sum \Delta T\left(\mathrm{WS}_{\mathrm{avg}}^{-2}\right)\right] + \varepsilon$$

where $\beta_0 = -1.5992$, $\beta_1 = -2.9561$, $\beta_2 = 14.7676$, $\beta_3 = -21.0686$, $\beta_4 = 21.9626$, $\beta_5 = -32.7260$ ($F = 71.50$, df = 5, 88, $R^2 = 0.803$, $P < 0.001$; for all parameters, $P < 0.05$). High peaks of stratification were observed when there were "spikes" in surface temperature and bottom temperatures remained relatively constant during the rapid surface heating phase (Fig. 3a). The predicted stratification did well at tracking peaks of observed stratification during the summer of 2003 (Fig. 3b). The parameter estimates from the model were then used along with temperature and wind speed buoy data to calculate daily PTS values for the summers of 1997–2002. PTS values were closely associated with changes in surface temperature and varied considerably between mild summers and summers that had several "heat waves" (Fig. 4). For 635 summer dates from 1997 to 2002, the mean PTS was 0.851, with scores ranging from 4.503 (23 June 2002) indicating low wind speeds and rapid surface heating to −1.625, indicating rapid cooling. PTS values at the 96th percentile and above were associated with 25 dates with PTS greater than 2.59°C. PTS values at the 85th percentile and above were associated with 95 dates with PTS greater than 1.46°C (Fig. 5).

Several high PTS values on consecutive dates indicated periods of stratification sustained longer than three or four days. For example, six consecutive high

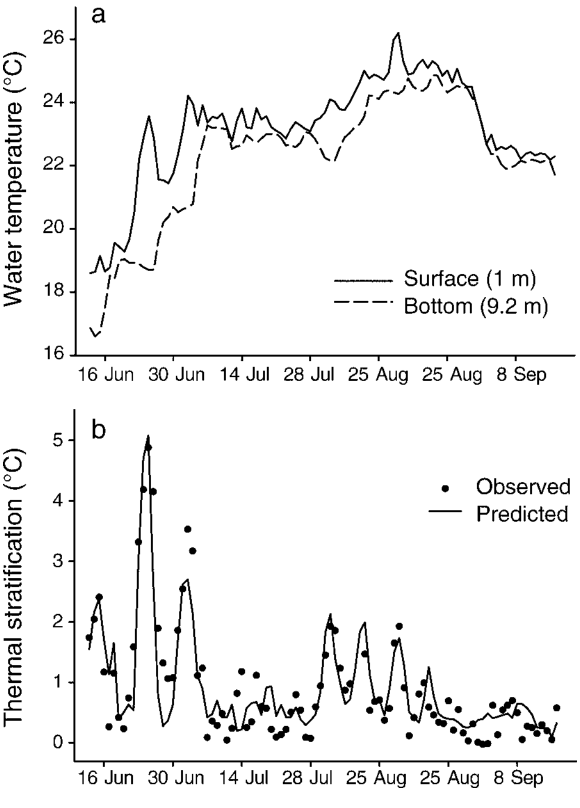

FIG. 3. (a) The 2003 surface (1.0 m) and epibenthic (9.2 m) daily mean water temperatures at site 4P in western Lake Erie. (b) Thermal stratification (temperature at surface, T_s, minus temperature at bottom, T_b) observed at site 4P and predicted thermal stratification based on ΔT_s and 1/average wind speed ($R^2 = 0.803$).

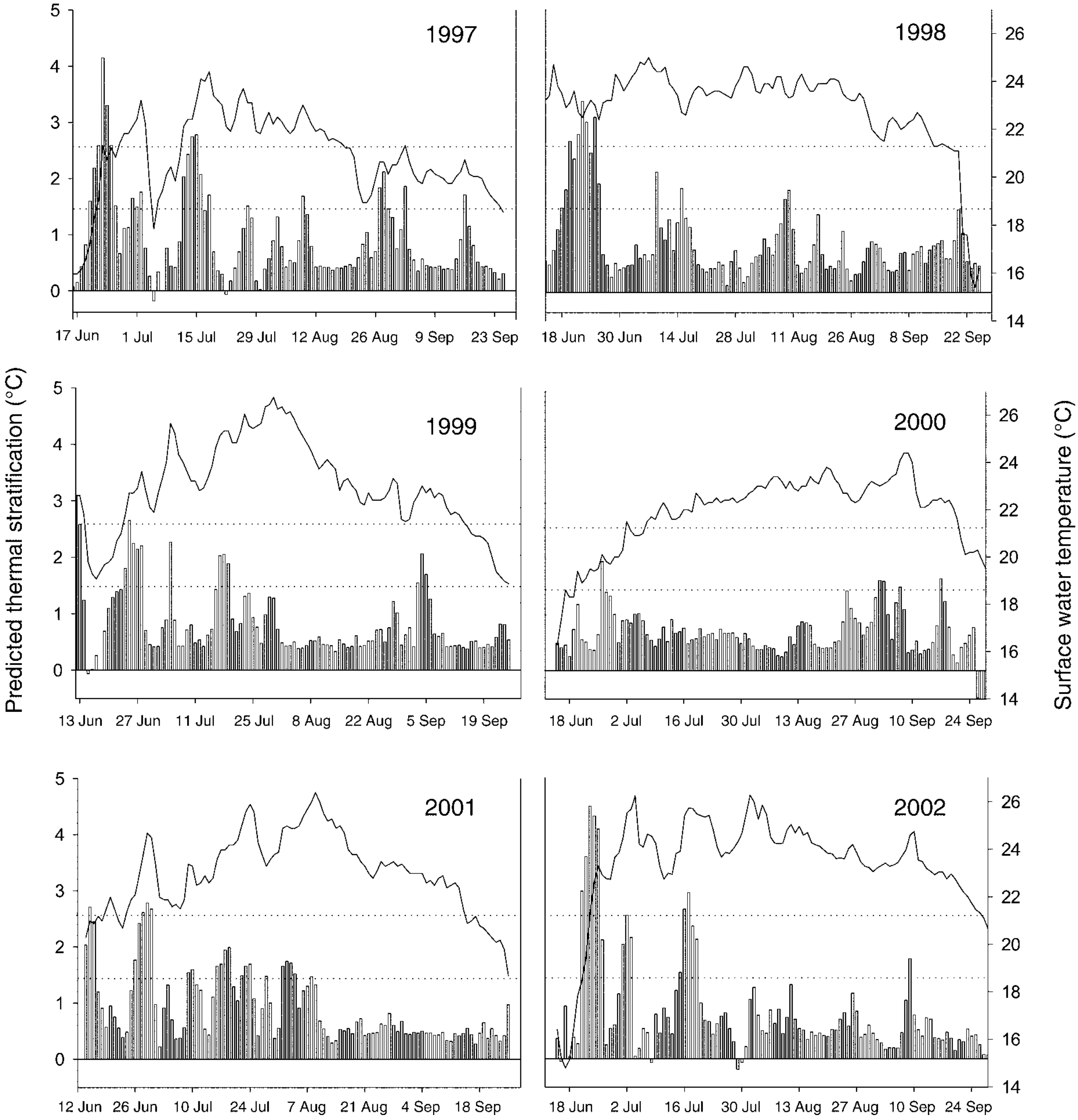

FIG. 4. Surface water temperature (line) and predicted thermal stratification (PTS; bars) for years 1997–2002. We used a range of cutoffs between the 85th and 96th percentiles (dotted lines) to determine the distribution of the highest PTS values between years. See *Results: Prediction of thermal stratification* for calculation of thermal stratification.

values in late June 2002 (Fig. 4) indicated a stratified period that probably lasted about nine days (including the four days needed to obtain the first high value). In most years, there were between one and three periods of significant stratification lasting between four and eight days each. The summer of 2002 had the greatest stratification and 2000 was the least stratified summer, with no PTS values greater than 1.95°C. The remaining four years fell between these two extremes with 1997 as another high-stratification summer and 1998, 1999, and 2001 as moderately stratified.

Prediction of bottom dissolved oxygen

As expected, epibenthic DO concentration was negatively related to the degree of thermal stratification ($F = 20.91$, df = 1, 16, $R^2 = 0.58$, $P < 0.001$; Fig. 6). This relationship, however, is limited in scope because DO continues to decline over time as long as stratification is maintained. To reduce the effect of time, data from beyond four consecutive days of stratification was excluded from the analysis. Therefore, Fig. 6 represents the effect of thermal stratification on epi-

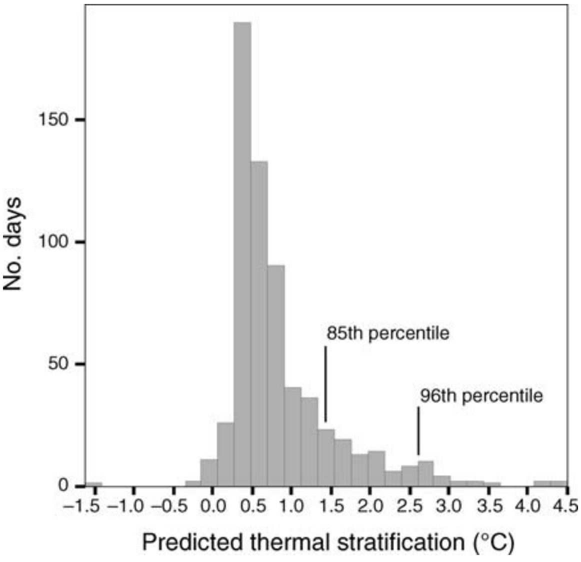

FIG. 5. Distribution of predicted thermal stratification values ($n = 635$) June–September 1997–2002.

benthic DO only during the setup phase of stratification. From this figure, a PTS value of 2.67°C, representing the cutoff for the 96th percentile, would result in an initial near-benthic DO concentration of 5.1 mg/L.

Hexagenia nymph density and recruitment

Our results from the analysis of previously published *Hexagenia* nymph abundance help support an earlier study in which a broad survey of 50 western Lake Erie sites (1995–2002) showed basin-wide trends of nymphs increasing steadily during 1995–1997, declining two- to fourfold in 1998, and then rebounding in 1999 (Schloesser et al. 2000; J. Ciborowski, K. Krieger, and D. Schloesser, *unpublished data*). In our analysis of five of the 50 sites, we found with an ANOVA that both interactions with site had large P values (year × site, $P = 0.6921$, and site × cohort, $P = 0.7088$; overall $F = 2.76$; df = 15, 4; $P = 0.1683$). After reducing the model by removing those two interactions effects, we found that site was not a significant factor in predicting overall abundance ($P = 0.2593$), whereas year ($P = 0.0268$), cohort ($P = 0.0203$), and year × cohort ($P = 0.0001$) were significant ($F = 7.39$; df = 7, 12; $P = 0.0014$). The difference in cohort abundance across years was most likely a result of recruitment failure in 1998 where sites had fewer year-1 cohort nymphs in May of 1998 (21.6 ± 23.9 individuals/m^2 [mean ± SE]) than in 1999, as documented by Schloesser and Nalepa (2001) the previous fall. In May of 1999, all five sites had many year-1 nymphs (559 ± 300.7 individuals/m^2), probably indicating a recruitment success. These results are similar to the basin-wide trends observed in the larger study. Because of this similarity of the five representative sites (including site 7M) to the broader basin-wide trends, we concluded that it is reasonable to use fall data collected at station 7M to represent young-of-year recruitment across a large geographical area.

Relationship between Hexagenia recruitment and stratification frequency

In general, a high frequency of stratification during the summer corresponded to low densities of young-of-year nymphs in fall for the years 1997–2002 (Fig. 7). Fall densities of young-of-year *Hexagenia* nymphs at site 7M were lowest following the summers with the most frequent or prolonged periods of stratification (2002, 1997) and highest following the mild summers of 1999 and 2000. The recruitment densities for 1997 (0 individuals/m^2) and 2002 (10 individuals/m^2) represent complete or near-complete recruitment failures. The best fit to these data was an asymmetric sigmoidal curve indicating that the relationship between *Hexagenia* recruitment and stratification frequency was potentially nonlinear. The sharp decline in recruitment between a stratification frequency of 0.15 and 0.20 suggests the existence of a threshold of summer stratification beyond which mayfly young-of-year nymphs cannot survive in western Lake Erie.

DISCUSSION

In this research, we have attempted to demonstrate a relationship between summer weather phenomenon and the recruitment of *Hexagenia* mayfly larvae by establishing intermediate links between weather and thermal stratification, stratification and hypoxia, and hypoxia and mayfly recruitment. The first link, the relationship between surface weather and thermal stratification is demonstrated by our model in which surface temperature and wind speed predicted thermal stratification. The second link, the relationship between stratification and hypoxia is demonstrated by the hypoxic episode we

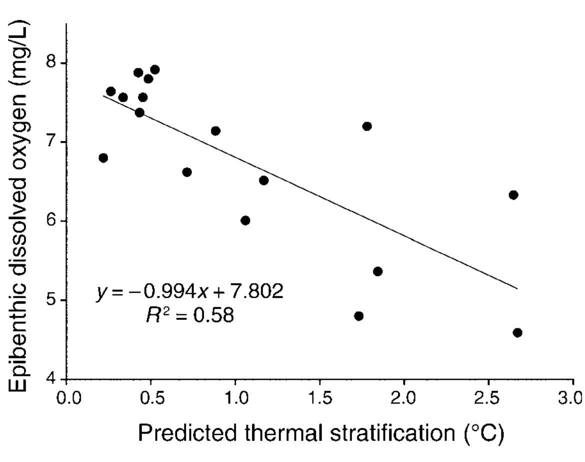

FIG. 6. Relationship between epibenthic dissolved oxygen concentrations and predicted thermal stratification during the setup phase of stratification. Data are from summer dates 2002–2003.

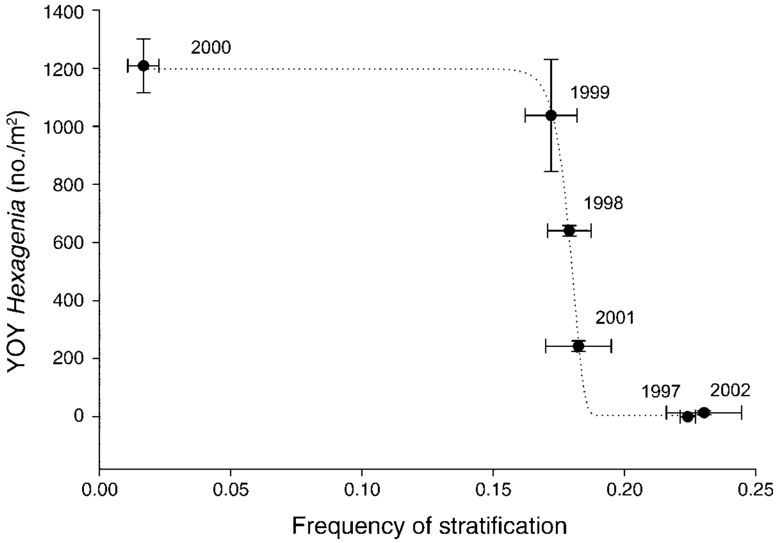

FIG. 7. The relationship between young-of-year (YOY) *Hexagenia* recruitment and stratification frequency, the proportion of high PTS values (based on the 85th and greater percentile through the 96th and greater percentile) attributed to each year (1997–2002). The line is a Gompertz sigmoidal equation fitted to the data. Vertical and horizontal bars represent ±SE associated with young-of-year estimates and stratification frequency.

documented in 2002 and other measurements that indicate a decline in epibenthic DO as stratification increases. The third link, between hypoxia and mayfly recruitment is inferred from our understanding of the known intolerance of mayflies of hypoxic conditions. These links culminate in an apparent negative relationship between summer heat waves and mayfly recruitment in western Lake Erie.

In the past, direct measurement of stratification and accompanying low epibenthic dissolved oxygen in western Lake Erie has been difficult because stratified periods typically last for less than a week. In recent years, biweekly or monthly monitoring has detected only a few, geographically isolated instances of low dissolved oxygen (Krieger et al. 1996, Madenjian et al. 1998). Our results indicate that in the absence of continuous water column temperature data, continuous surface water temperature and wind speed data can be used to identify likely periods of stratification in western Lake Erie. Under stratifying conditions, solar energy absorbed at the surface causes surface temperatures to rise quickly. The end of a stratified period may be indicated by a decline in surface temperature. If wind energy is great enough to overcome stratification, the surface temperature may decline as the surface waters mix with cooler epibenthic water layers. We found that the running averages across four days of change in surface temperature and the quadratic inverse of wind speed were predictors of stratification. This final best model was similar to our preliminary model developed on first principles, a simple ratio of $\Delta T(\mathrm{WS}_{\mathrm{avg}}^{-1})$ based on a four-day time period. We also investigated whether brief periods of high winds potentially disrupted stratification by testing whether the maximum average wind speed for the period could predict stratification, but we found that it was not as good a predictor as average wind speed (top model ranked 19th in $\mathrm{AIC_c}$), and its inclusion would have nearly doubled the number of models under consideration.

Models using a four-day period provided the best fit with stratification, probably reflecting the tendency for hot, calm periods in the Great Lakes region to last no more that four or five days before passing weather systems bring cooler temperatures and higher winds. A four-day period is also probably biologically relevant for mayflies, because unlike the hypolimnion of the central basin of Lake Erie which requires about two months of stratification to become anoxic (Charlton et al. 1993), the epibenthic waters of western Lake Erie can become anoxic within a few days. In the 1970s, epibenthic waters of the western basin became anoxic three to four days after stratification (Rathke 1984). The relationship we show between stratification and epibenthic DO demonstrates that hypoxia begins even with small differences between surface and bottom temperature. In order to further understand the relationship between stratification and epibenthic DO, continuous measurements of epibenthic DO will be required. Because the pumping action of *Hexagenia* mayflies typically maintains their burrows at 75–100% of the DO concentration found in the overlying water (Wang et al. 2001), DO concentrations encountered by mayflies are probably equal to or only slightly lower than measured by our probe.

The model developed for this study is not as sophisticated as physical mixing models (McCormick and Meadows 1988) and cannot be considered as a substitute for these models. Rather, it is intended to compare relative stratification between years using only readily available surface data. With adjustment, our approach could potentially be useful in other shallow, productive areas such as Saginaw Bay in Lake Huron and Oneida Lake, but not in any water body that forms a true summer hypolimnion, such as the central and eastern basins of Lake Erie. The installation of observation buoys and benthic monitoring devices in western Lake Erie currently underway will undoubtedly increase our understanding of the relationship between weather, stratification, and hypoxia and may eventually replace the need for models with direct observation. As in our study, models may continue to be useful to examine historical relationships between weather and benthic populations.

Stratification and hypoxia appear to have an adverse effect on the density of *Hexagenia* young-of-year larvae in western Lake Erie, but the exact mechanism of how this occurs is not known. Most *Hexagenia* nymphs die when DO concentrations drop below about 1.0 mg/L for one to two days (Hunt 1953, Eriksen 1963, Nebeker 1972). Mortality also increases rapidly if DO concentrations less than about 4.5 mg/L are maintained for 21 days (Winter et al. 1996). Although there are few available data on the effect of hypoxia on newly hatched nymphs, Winter et al. (1996) reported that small nymphs are less likely to survive hypoxia than larger nymphs. Our study also suggests that small nymphs may be more vulnerable. Size–frequency data from the relatively highly stratified summer of 1997 (Schloesser and Nalepa 2001) do not indicate any unusual disruption to nymph populations other than the failure of the young-of-year cohort to appear in late summer. *Hexagenia* are mainly semivoltine in western Lake Erie and the large-sized cohort from the previous year appeared relatively unaffected by stratification. Also, the two years in the study in which recruitment failed (1997, 2002) are also the years with the latest stratified periods (mid-July). At summer temperatures, *Hexagenia* eggs hatch in one to two weeks (Hunt 1953, Winter et al. 1996), therefore it is likely that many of the eggs laid after the major June emergence had hatched by the time of the mid-July stratification episode. *Hexagenia* eggs are dormant under anoxic conditions and can be induced to hatch after aeration (Hunt 1951, Gerlofsma and Ciborowski 1998), therefore a potential hazard of intermittent hypoxia is that periods of mixing and aeration could induce many eggs to hatch only for the young nymphs to be suffocated by the next hypoxic episode. Larger larvae may be at greater risk of fish predation as low oxygen drives them from the substrate into the water column in search of higher oxygen concentrations (Hunt 1953, Kolar and Rahel 1993). Mayfly populations may be able to compensate somewhat for the adverse effects of hypoxia in that their eggs may remain viable in the sediments for a number of years. Overlapping generations, delayed emergence of some individuals and varying egg development times (Corkum et al. 1997) may also ensure survival of the population even in years in which the major fall recruitment of young-of-year nymphs fails. In order to completely understand the relationship between hypoxia and larval survival more research is needed on the effects of varying degrees of hypoxia over various time periods on all early life stages of mayflies.

Other factors, such as summer lake level and overall water temperature, may be expected to affect the oxygen content of epibenthic waters, and therefore the success of mayfly recruitment. Years in which lake levels are low are associated with higher depletion rates of dissolved oxygen in the central basin of Lake Erie (El-Shaarawi 1984). However, neither fall density of young-of-year mayflies nor frequency of high PTS were correlated with the summer water levels in western Lake Erie. Summer lake levels in 1997 and 1998 were high compared to the years 1999–2002, yet recruitment failed in both high-water years (1997) and low-water years (2002). Similarly, mayfly recruitment and frequency of high PTS were not correlated with average water temperatures. The year 1998, the hottest year on record (according to NOAA/NASA), had the highest average western Lake Erie water temperature (11 June–25 September) in our study and average mayfly young-of-year recruitment. Cooler summers had both recruitment successes and failures.

Our results suggest that in about half of the years from 1997–2002, *Hexagenia* recruitment was poised on a narrow threshold between success and failure, an observation that raises concerns about the continued success of mayflies in western Lake Erie. Mayfly populations may be able to withstand isolated recruitment failures, but western Lake Erie has warmed significantly over the past 85 years (McCormick and Fahnenstiel 1999, Shuter et al. 2002). If a warming climate brings more frequent summer heat waves and increasing periods of stratification, mayfly recruitment failure may occur in most years, likely resulting in a decline in western Lake Erie *Hexagenia* populations.

In spite of its importance, stratification is only one-half of the hypoxia equation, with benthic and sediment oxygen demand playing an equally important part. From a management perspective, it may be possible to reduce the negative consequences of future increases in stratification by reducing the loading of nitrogen, phosphorus, and organic material from tributaries that cause high rates of sediment oxygen demand. Reductions in loadings could potentially slow oxygen depletion rates enough so that epibenthic DO concentrations do not plunge to dangerous levels during intermittently stratified periods. Among other benefits, these actions would help ensure the continued success of *Hexagenia* in Lake Erie and the valuable sport fisheries which rely on this important resource.

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