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POPULATION MODELS OF BURROWING MAYFLY RECOLONIZATION IN WESTERN LAKE ERIE

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Abstract. Burrowing mayflies, *Hexagenia* spp. (*H. limbata* and *H. rigida*), began recolonizing western Lake Erie during the 1990s. Survey data for mayfly nymph densities indicated that the population experienced exponential growth between 1991 and 1997. To predict the time to full recovery of the mayfly population, we fitted logistic models, ranging in carrying capacity from 600 to 2000 nymphs/m^2, to these survey data. Based on the fitted logistic curves, we forecast that the mayfly population in western Lake Erie would achieve full recovery between years 1998 and 2000, depending on the carrying capacity of the western basin. Additionally, we estimated the mortality rate of nymphs in western Lake Erie during 1994 and then applied an age-based matrix model to the mayfly population. The results of the matrix population modeling corroborated the exponential growth model application in that both methods yielded an estimate of the population growth rate, r, in excess of 0.8 yr^{-1}. This was the first evidence that mayfly populations are capable of recolonizing large aquatic ecosystems at rates comparable with those observed in much smaller lentic ecosystems. Our model predictions should prove valuable to managers of power plant facilities along the western basin in planning for mayfly emergences and to managers of the yellow perch (*Perca flavescens*) fishery in western Lake Erie.

Key words: carrying capacity; exponential growth; Hexagenia; *lake restoration; logistic equation; matrix population model; mayflies; population growth rate; recolonization; recovery.*

INTRODUCTION

Burrowing mayflies of the genus *Hexagenia* inhabit many lakes and rivers of North America (Riklik and Momot 1982, Giberson and Rosenberg 1994), and are of economic importance for three main reasons. First, they are a preferred food item of several species of fish of recreational and commercial value (Hunt 1953, Hayward and Margraf 1987, Schaeffer 1994, Synnestvedt 1996). Second, mayfly emergences are a hazard to the operation of power plant facilities because large swarms of subadults and adults may cause short-circuiting of power plants and the temporary shutdown of power to consumers (W. Kovalak, Detroit Edison Company, Detroit, Michigan, USA, *personal communication*). Third, the swarms present a hazard and nuisance to the public by greasing roadways (Fremling and Johnson 1990).

Prior to 1950, burrowing mayflies (*H. limbata* and *H. rigida*) dominated the biomass of the benthic invertebrate community in western Lake Erie (Wright and Tidd 1933). The population of burrowing mayflies in western Lake Erie was nearly extirpated from the basin by 1960, presumably due to recurring anoxia associated with organic pollution and eutrophication (Britt 1955, Beeton 1961, Krieger et al. 1996). Although water quality improved in western Lake Erie during the 1970s and 1980s in response to a reduction in phosphorus loadings (Makarewicz and Bertram 1991), densities of mayfly nymphs remained very low throughout most of the basin. However, between 1991 and 1995, the population quickly spread throughout western Lake Erie (Krieger et al. 1996).

The yellow perch (*Perca flavescens*) fishery in western Lake Erie is economically important from both recreational and commercial perspectives (Knight et al. 1984, Henderson and Nepszy 1989). Growth rates of yellow perch are controlled in large measure by the abundance of *Hexagenia* (Hayward and Margraf 1987, Schaeffer 1994, Synnestvedt 1996). Indeed, growth was substantially slower during the 1970s and 1980s when *Hexagenia* was virtually absent from the western basin (Hayward and Margraf 1987). Therefore, understanding the population dynamics of *Hexagenia* is important in managing the yellow perch fishery in western Lake Erie.

When organisms invade or recolonize an ecosystem, their population growth typically follows an S-shaped or sigmoid curve that can be described by the logistic equation (Emlen 1984):

$$N_t = N_0 \frac{K}{(K - N_0)e^{-r_0 t} + N_0}$$

where N_t = population size at time t, N_0 = population size at time 0, r_0 = the maximum population growth rate (when population size is close to zero), and K =

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carrying capacity. During the early phases of recolonization or invasion, the population size increases exponentially, but then population growth rate decreases as the population size slowly approaches an asymptote, K. The carrying capacity represents the maximum population size that can be maintained by the ecosystem when the population is at equilibrium.

Kolar et al. (1997), using a computer simulation model based on a system of differential equations, forecasted that full recovery of the mayfly population in western Lake Erie would not be attained until the year 2038. We report herein, based on regression modeling and on matrix population modeling, that by the year 2000 the mayfly population in western Lake Erie will approach densities not observed for over 50 yr.

Our intent was to: (1) determine whether the mayfly population growth in western Lake Erie between 1991 and 1997 can be characterized as exponential, (2) fit logistic curves to observed mayfly nymph densities between 1991 and 1997 for various scenarios of ecosystem carrying capacity, (3) use the fitted logistic curves to predict population growth, (4) compare our forecasts for mayfly population growth with those of Kolar et al. (1997), (5) apply an age-based matrix population model to the *Hexagenia* population in western Lake Erie using mortality rates calculated from 1994 data, and (6) compare the population growth rate, r, estimated from the exponential growth model with that estimated from the matrix population model.

METHODS

We estimated the population growth rate, r, of *Hexagenia* in western Lake Erie during the 1990s using two different modeling approaches. In our first approach, we applied the exponential growth model to mayfly survey data for years 1991–1997; r was estimated via linear regression. In our second approach, we applied a matrix population model to mortality and fecundity data for the 1990s to estimate r. We then compared the two estimates of r. Additionally, we used nonlinear regression to fit the logistic model to the survey data, and then we projected the recovery trajectory for the mayfly population in western Lake Erie from the fitted logistic model.

Regression population models

Routine annual monitoring of the mayfly population density in western Lake Erie did not begin until 1995, however survey data were available for years 1991 and 1993 (Krieger et al. 1996). In 1991, 17 stations were sampled using a Ponar grab (~0.05 m^2/sample). Most of these stations were in the western half of the western basin (Krieger et al. 1996). In 1993, a Ponar grab was used to sample 47 stations, and again emphasis was placed on the western half of the basin. Beginning in 1995, an Eckman grab (0.052 m^2/sample) was used to sample 20 stations, which were scattered evenly across the western basin (Krieger et al. 1996). To continue monitoring the average mayfly density in western Lake Erie in 1996 and 1997, we sampled the same 20 stations and used the same gear as in 1995. All sampling in all five sampling years was done in May and early June. Refer to Krieger et al. (1996) for more details on the sampling procedures.

We fitted an exponential curve of the form $N_t = N_0 e^{rt}$ to the mayfly nymph survey data for years 1991–1997 to determine whether population growth could be characterized as exponential during that time period. The curve was fitted to annual mean density data. We used linear regression to estimate the population growth rate, r, and N_0. The estimate of N_0 was adjusted by converting from a geometric mean value to an arithmetic mean value (Ricker 1975).

To investigate the effect of changing gear and sampling stations in the surveys conducted between 1991 and 1995 on the estimate of r, we used analysis of covariance. We tested for a significant difference between the value of r from the fit of the exponential growth model to mean density data for years 1991–1997 and the value of r from the exponential growth model fit to data for just years 1991–1995. If there was no significant difference in these two estimates of r, we would conclude that the changing of gear and sampling stations had a nondetectable effect on our estimate of the population growth rate of *Hexagenia* in western Lake Erie during the 1990s.

Next, we used nonlinear regression, more specifically the DUD (Doesn't Use Derivatives) method (Ralston and Jennrich 1978, SAS 1990), to fit the logistic equation to the mean density data for years 1991–1997 so that we could predict the time of *Hexagenia* recovery in western Lake Erie. The logistic equation was fitted to the data for values of $K = 600$, 800, 1000, and 2000 nymphs/m^2. Britt (1955) reported that mayfly densities in the eastern half of western Lake Erie averaged between 300 and 500 nymphs/m^2 during 1930 and the early 1950s, whereas Reynoldson et al. (1989) estimated that historical *Hexagenia* densities in Lake Erie may have been substantially higher than 500 nymphs/m^2. It is plausible that early in this century, the average density for mayfly nymphs in western Lake Erie was ~2000 nymphs/m^2 (Reynoldson et al. 1989). Because we observed an average density of nearly 500 nymphs/m^2 in western Lake Erie in 1997, we entertained values of K from 600 to 2000 nymphs/m^2. We defined year of recovery as the year in which the mayfly population first attained a population size equal to at least 90% of its carrying capacity.

Matrix population model

To estimate mayfly nymph mortality, we performed some additional sampling. We used a Ponar grab to obtain 24 sediment samples from an area ~10 km south of the Detroit River mouth (41°59′20″ N latitude, 83°07′30″ W longitude) in western Lake Erie on both 2 June and 13 October 1994. Samples were washed through a 0.60-mm mesh screen and were preserved with a 10% formalin solution following Carr and Hiltunen (1965). In the laboratory, mayfly nymphs were sorted from sediments and counted. Each nymph was measured to the nearest millimeter, sexed (if possible), and assigned a wing pad developmental stage. Refer to Heise et al. (1987) for details on categorizing mayfly nymphs according to wing pad development.

Based on the length–frequency distributions of mayfly nymphs from western Lake Erie, *Hexagenia* in the western Lake Erie emerge after one or two years in nymphal stages; the 2-yr life history is most common (Britt 1955, Manny 1991). Therefore, we used a 2-yr life cycle in the model. We estimated the annual survivorship of 2nd-yr nymphs using the densities of stage-2 and stage-3 nymphs on 2 June 1994 and the densities of stage-4 and stage-5 nymphs from 13 October 1994. We assumed that stage-2 and stage-3 nymphs from June would not emerge from the lake as adults during the summer of 1994, rather they would emerge during the summer of 1995. Further, we assumed that the stage-4 and stage-5 nymphs in October 1994 were the survivors from the stage-2 and stage-3 population in June 1994. These were reasonable assumptions based on the findings of Heise et al. (1987), who observed a drastic decline in the abundance of larger nymphs in Dauphin Lake (Manitoba) between June and July, due to emergence, but no such decline in the abundance of smaller nymphs during that time. In our study, the instantaneous mortality rate, Z, for 2nd-yr nymphs was calculated by subtracting the logarithm of the pooled density of stage-4 and stage-5 nymphs in October from the logarithm of the pooled density of stage-2 and stage-3 nymphs in June, and then dividing the difference by the number of years between the June and October sampling. The October sampling occurred 133 d after the June sampling, so the difference was divided by 133/365 or 0.36 yr. Annual survivorship of the 2nd-yr nymphs was estimated by taking the exponential of $-Z$ (Ricker 1975). An additional source of mortality during the 2nd yr of life was that associated with the transition from the largest nymph stage to adult; this transition normally takes place within a matter of one or two days (Horst 1976). Horst (1976) estimated the survival from the largest nymph stage to adult to be 30.8% for *Hexagenia* in Tuttle Creek Reservoir, Kansas; so, in our study, we multiplied the annual survivorship of the 2nd-yr nymphs by 0.308 to arrive at the survivorship for the second year of life.

The average length of the stage-2 and stage-3 pool of nymphs in June 1994 was 11 mm, whereas the stage-4 and stage-5 pool of nymphs averaged 17 mm in October 1994. Horst (1976) estimated that survival of mayfly nymphs from hatching to 11-mm nymphs was roughly equal to survival from 11-mm nymphs to the largest nymph stage in Tuttle Creek Reservoir. Additionally, Horst (1976) estimated mayfly egg survival to be 10.5%. Thus, we estimated 1st-yr survivorship, which included survival from egg to end of the 1st yr, by multiplying our estimate of 2nd-yr nymph survivorship by 0.105. Mayfly fecundity in western Lake Erie was estimated via the relationship of number of eggs per female as a function of female imago length described by Hunt (1951), given that female imago body length for mayflies from the western Lake Erie-Detroit River area averaged 19.0 mm (Corkum and Ciborowski 1995). The ratio of males to females among the stage-4 and stage-5 nymphs from June 1994 did not significantly differ from 1:1 ($\chi^2 = 1.39$, df = 1, $P = 0.24$). Therefore, average fecundity of an adult mayfly in the western Lake Erie population was set equal to female fecundity divided by 2.

Using these estimates of mayfly life history characteristics for the *Hexagenia* population in western Lake Erie during 1994, we formed an age-class projection matrix, as described by Emlen (1984) and Caswell (1989). The natural logarithm of the largest real eigenvalue of the matrix yields the population growth rate (Horst 1976, Emlen 1984, Crouse et al. 1987). We calculated the population growth rate from the projection matrix, and compared it with the estimate of r from regression analysis of the monitoring data.

Sensitivity of the population growth rate to 1st-yr survivorship, 2nd-yr survivorship, and fecundity was investigated using the individual parameter perturbation method (Bartell et al. 1986). We perturbed one life history parameter at a time and then calculated r from the projection matrix. The perturbation was effected by either increasing the parameter 10% from its nominal value or decreasing the parameter 10% from its nominal value. Thus, six different projection matrices were evaluated.

Results

Regression population models

The *Hexagenia* population in western Lake Erie exhibited exponential growth between 1991 and 1997 (Fig. 1), reaching 488 nymphs/m^2 in 1997. Variation about the mean density increased as mean density increased. Very high densities were observed at a few locations during 1996 and especially during 1997, when mayfly density at one station located in the southwestern portion of the basin exceeded 2000 nymphs/m^2. The fitted curve (solid line in Fig. 1) was: $N_t = 1.42e^{0.92t}$, where N_t = density of nymphs (number per square meter) at year t, and t = time, in years, accrued since 1991. Thus, the population growth rate was estimated at 0.92 yr^{-1}. The 95% confidence interval half width for this estimate was 0.22 yr^{-1}.

The estimate of the population growth rate using all five survey years was 0.92 yr^{-1}, whereas the estimate of the population growth rate based on just years 1991–1995 was 0.81 yr^{-1}. These estimates were not significantly different from one another (analysis of covari-

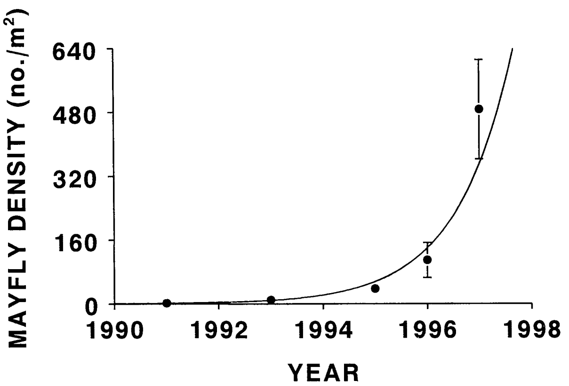

FIG. 1. Average *Hexagenia* density in western Lake Erie, 1991–1997. Error bars represent ±1 SE. Standard errors for mean mayfly density in 1991, 1993, and 1995 were <11 nymphs/m^2. The plotted curve represented the exponential growth model fitted to the data. Our fitted model explained 98% of the variation in the natural logarithm of mean *Hexagenia* density.

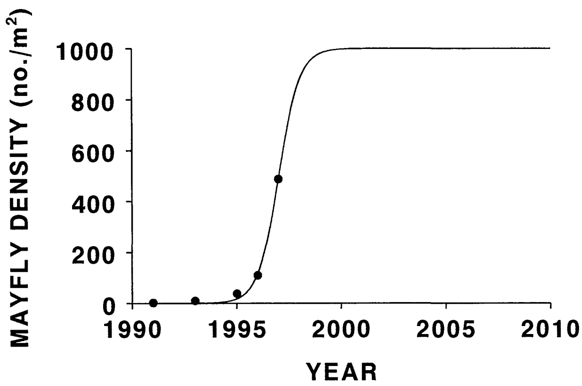

FIG. 2. Logistic curve, with carrying capacity K equal to 1000 nymphs/m^2, fitted to average *Hexagenia* densities observed in western Lake Erie, 1991–1997. The logistic curve was extrapolated to year 2010. Our fitted model explained over 99% of the variation in mean *Hexagenia* density.

ance, $P = 0.43$), and therefore we concluded that the changes in gear and sampling stations between 1991 and 1995 had only a minor effect on the estimate of r.

The estimated values of r_0 from the logistic curve fits ranged from 1.66 to 2.89 (Table 1). The fitted logistic curve for carrying capacity (K) equal to 1000 nymphs/m^2 indicated that *Hexagenia* density in western Lake Erie would substantially increase in 1998, and the recovery would be complete by 1999 (Fig. 2). The mayfly population was predicted to achieve recovery in western Lake Erie by year 2000 if K is equal to 2000 nymphs/m^2 (Table 1).

Matrix population model

Density of pooled stage-2 and stage-3 nymphs in June 1994 was 44.8 nymphs/m^2, and pooled density of stage-4 and stage-5 nymphs in October 1994 was 31.8 nymphs/m^2 (Fig. 3). Thus, the annual survivorship of 2nd-yr nymphs was estimated to be 0.393, and survivorship during the 2nd-yr of life was estimated to be 0.121 (see *Methods* for details on this calculation). Survivorship during the first year of life was estimated to be 0.041 (see *Methods*). We estimated an average of 1000 eggs per adult per year (assuming equal numbers of males and females). From the age projection matrix, we calculated the population growth rate to be 0.80 yr^{-1} (see *Methods*). This estimate of r was within the 95% confidence interval for the value of r (0.92 yr^{-1}) from the exponential growth model fit to field data for 1991–1997. Sensitivity analysis of the population matrix model showed that population growth rate was equally affected by 1st-yr survivorship, 2nd-yr survivorship, and fecundity. A 10% increase in any three of these model parameters yielded a 5.9% increase in the value of r, and a 10% decrease in any of the these three model parameters yielded a 6.6% decrease in the value of r.

TABLE 1. Expected year at which the *Hexagenia* population in western Lake Erie will be recovered, based on extrapolations of the logistic model fitted to survey data for years 1991–1997. The population is considered recovered once it has attained a density equal to at least 90% of its carrying capacity. Also included are nonlinear least-squares estimates of the maximum population growth rate, r_0, and the initial *Hexagenia* density in 1991, N_0.

Carrying capacity (K) (no./m^2)	Estimate of N_0 (no./m^2)	Estimate of r_0 (yr^{-1})	Year of recovery
600	0.00007	2.89	1998
800	0.00210	2.21	1998
1000	0.00664	1.98	1999
2000	0.03038	1.66	2000

DISCUSSION

We observed good agreement between the results of our exponential growth model analysis of the survey data and our matrix population modeling. Both approaches showed that the *Hexagenia* population in western Lake Erie was increasing at an exponential rate

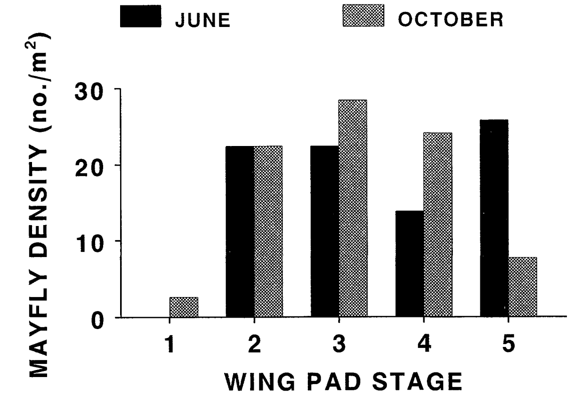

FIG 3. Frequency distributions for *Hexagenia* nymphs, according to wing pad stage, collected from western Lake Erie on 2 June and 13 October 1994. The sampling station was situated ~10 km south of the Detroit River mouth.

between 1991 and 1997, with $r > 0.8$ yr^{-1}. The corroboration between these two different modeling applications strongly supported the contention that the mayfly recovery was occurring at a rapid rate during the 1990s in western Lake Erie. Kolar et al. (1997) estimated $r = 0.8$ yr^{-1} for *Hexagenia* during colonization of Lewis and Clark Lake, a new reservoir in South Dakota. Lewis and Clark Lake has a surface area of 113 km^2 (Hudson and Swanson 1972), whereas the surface area of western Lake Erie was 3276 km^2 (Hartman 1973). Thus, it appears that *Hexagenia* recolonization rate in a large aquatic ecosystem is similar to the rate observed in a much smaller lentic ecosystem.

We conclude that the size of the *Hexagenia* population in western Lake Erie should approach its carrying capacity by the year 2000. For a carrying capacity of 1000 nymphs/m^2, Kolar et al. (1997) predicted an average density of only 75 nymphs/m^2 in 1997, whereas we observed 488 $\pm$ 260 nymphs/m^2. Thus, their prediction was well outside the 95% confidence interval for the observed mean density. The Kolar et al. (1997) model apparently was not calibrated with the observed densities in western Lake Erie during the 1990s. Moreover, Kolar et al. (1997) assumed that contaminated sediments in western Lake Erie would cause a substantial reduction in the population growth rate of *Hexagenia* in western Lake Erie, and they postulated that low dissolved oxygen (DO) conditions would slow down the recovery rate of the *Hexagenia* population. In contrast to the Kolar et al. (1997) model, our model fitted the observed mean densities between 1991 and 1997 reasonably well. For $K = 1000$ nymphs/m^2, our model predicted a mean *Hexagenia* density of 486 nymphs/m^2 in 1997, and the observed mean density was 488 nymphs/m^2 (Fig. 2).

DO conditions and contaminated sediments were probably not major impediments to mayfly population growth in western Lake Erie during the 1990s. The Ohio Department of Natural Resources and the Ontario Ministry of Natural Resources have measured DO near lake bottom at stations chosen randomly throughout the western basin proper (excluding the western basin-central basin border) of Lake Erie during August from 1987 through 1995. Only four observations of DO concentration lower than 4.0 mg O_2/L were made during those 9 yr: 1 of 39 readings was below 4.0 mg O_2/L during 1993, and 3 of 32 readings were below 4.0 mg O_2/L during 1995. Although Krieger et al. (1996) observed incidences of low DO during 1993–1995, these events occurred on the western basin–central basin border where anoxic central basin hypolimnial water may protrude into the eastern margin of the western basin. Furthermore, one of the sites was within a depression (>14 m deep), which was considerably deeper than neighboring water. Therefore, there was no indication that low DO conditions occurred over a large area of the basin from 1987 to the present time. Additionally, we are not aware of any direct evidence that the contaminant levels present in western Lake Erie sediments during the 1990s could slow down the population growth rate of *Hexagenia.* Presently, scientists are unsure as to which factor, or set of factors, triggered the mayfly recovery in western Lake Erie (Krieger et al. 1996). The improvement in water quality brought about by decreased loadings of phosphorus and organic materials, as well as a decrease in contaminant loadings, was probably necessary, but may not have been sufficient to cause the mayfly recovery. Krieger et al. (1996) suggested that the zebra mussel invasion during the late 1980s may have served as an additional catalyst for the mayfly recolonization during the early 1990s, but no specific mechanisms were proposed by these researchers.

Variability about the mean *Hexagenia* density in western Lake Erie increased from 1991 through 1997, as mean *Hexagenia* density increased exponentially (Fig. 1). Such an increase in variability in *Hexagenia* density among sampling stations was expected, based on previous studies. Schloesser et al. (1991) sampled between 6 and 50 different stations in 18 different bodies of water in the connecting channels of the upper Great Lakes, and they clearly showed that variability in *Hexagenia* density among sampling stations located in the same body of water increased as mean *Hexagenia* density increased. The high degree of spatial variability that we observed in *Hexagenia* densities in western Lake Erie during 1997 has been documented during the early 1950s in western Lake Erie, as well as in other lakes. We observed a mean density of 488 nymphs/m^2, with a standard error of 124 nymphs/m^2, from 20 stations in western Lake Erie during 1997. Similarly, the mean *Hexagenia* density from 12 stations in western Lake Erie during the early 1950s was 327 nymphs/m^2, with a standard error of 109 nymphs/m^2 (Britt 1955), and the mean density of *Hexagenia* from 18 stations in Lake St. Clair during spring 1985 was 528 nymphs/m^2, with a standard error of 171 nymphs/m^2. A high degree of spatial variability was expected, and observed, for the *Hexagenia* density in western Lake Erie when the population reached a level comparable to that measured prior to 1953.

While mayfly density should reach 600 nymphs/m^2 or more by the year 2000, we may also expect fluctuations in the population size in western Lake Erie beyond year 2000. These fluctuations could arise from: (1) an overshooting of the carrying capacity, K, and then dampened cycles about K with time (May 1976), and/or (2) fluctuations in the value of K with time (Pielou 1977). In any case, unless K exhibits a drastic upward trend following the year 2000, the mayfly population size in western Lake Erie should approach or exceed the long-term average of K by the year 2000.

Mayfly-induced threats to power plant operation need immediate attention because the swarms are likely to increase in size and frequency between 1998 and 2000. Managers should plan on the increased likelihood of potential power outages caused by mayfly swarms in June and July during the next three years. Additionally, the expected rapid increase in the size of the mayfly population between 1995 and 2000 will likely influence the yellow perch fishery in western Lake Erie. During certain times of the year, mayflies comprised up to 50%, on a volume basis, of both the adult and juvenile perch diet between 1994 and 1996 (M. Bur, U.S. Geological Survey, Great Lakes Science Center, Lake Erie Biological Station, Sandusky, Ohio, USA, *unpublished data*); growth rate of perch should increase as mayfly density increases. Accurate data on yellow perch growth are important inputs to models used to estimate the recommended allowable catch of the Lake Erie perch fishery (Madenjian and Ryan 1995). Therefore, fishery managers should monitor yellow perch growth closely during the next three years.

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