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CONDITIONS FOR THE RETURN AND SIMULATION OF THE RECOVERY OF BURROWING MAYFLIES IN WESTERN LAKE ERIE

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Abstract. In the 1950s, burrowing mayflies, *Hexagenia* spp. (*H. limbata* and *H. rigida*), were virtually eliminated from the western basin of Lake Erie (a 3300 km² area) because of eutrophication and pollution. We develop and present a deterministic model for the recolonization of the western basin by *Hexagenia* to pre-1953 densities. The model was based on the logistic equation describing the population growth of *Hexagenia* and a presumed competitor, *Chironomus* (dipteran larvae). Other parameters (immigration, low oxygen, toxic sediments, competition with *Chironomus*, and fish predation) were then individually added to the logistic model to determine their effect at different growth rates.

The logistic model alone predicts 10–41 yr for *Hexagenia* to recolonize western Lake Erie. Immigration reduced the recolonization time by 2–17 yr. One low-oxygen event during the first 20 yr increased recovery time by 5–17 yr. Contaminated sediments added 5–11 yr to the recolonization time. Competition with *Chironomus* added 8–19 yr to recovery. Fish predators added 4–47 yr to the time required for recolonization.

The full model predicted 48–81 yr for *Hexagenia* to reach a carrying capacity of ≈350 nymphs/m², or not until around the year 2038 if the model is started in 1990. The model was verified by changing model parameters to those present in 1970, beginning the model in 1970 and running it through 1990. Predicted densities overlapped almost completely with actual estimated densities of *Hexagenia* nymphs present in the western basin in Lake Erie in 1990. The model suggests that recovery of large aquatic ecosystems may lag substantially behind remediation efforts.

Key words: Chironomus; competition; contaminants; dissolved oxygen; ecosystem recovery; Hexagenia; Lake Erie; macroinvertebrates; predation; recolonization; simulation model.

INTRODUCTION

The emergence of burrowing mayflies (mainly *Hexagenia*) en masse from the bottom muds of large rivers and lakes in eastern North America prior to the 1950s was a phenomenon that could not be ignored. Mayflies, attracted by street lights, would collect in great piles, and in extreme cases snowplows were required to re-open highway bridges that had become impassable due to their accumulation (Fremling 1960).

Whether due to eutrophication, contamination of sediments, or a combination of these and other factors, *Hexagenia* was eliminated from many of these locations. The earliest documented loss of *Hexagenia* was from a polluted 97-km stretch of the Mississippi River through and downstream of Minneapolis and St. Paul in 1928 (Fremling 1973), followed by Green Bay 1939–1955 (Howmiller and Beeton 1971), western Lake Erie 1955–1961 (Carr and Hiltunen 1965), Saginaw Bay 1955–1965 (Schneider et al. 1969), Oneida Lake 1958–1961 (Jacobsen 1966), and Lake Winnipeg

1963–1967 (Flannagan 1979). Population losses have generally been associated with low dissolved oxygen (Britt 1955*a, b*, Jacobsen 1966) coincident with periods of calm weather and increased phosphorus loading during the 1950s. In fact, Britt (1955*a, b*) estimated a 90% loss of *Hexagenia* from most of the western Lake Erie basin from a single anoxic event.

Hexagenia has been able to recolonize some of these areas, particularly in riverine situations. In 1980, *Hexagenia* nymphs were collected in regions of the Detroit River void of them in 1968 (Thornley and Hamdy 1984), including areas near the mouth (Thornley 1985). It is also making a comeback in the upper Mississippi River (Fremling and Johnson 1990), and in the lower Fox River, which drains into Green Bay, Lake Michigan (Cochran 1992). Lotic habitat recolonization would be expected first as rivers and streams receive drift from upstream while washing contaminants downstream (Elliott 1971), and they are generally more oxygenated. *Hexagenia* are still not found in larger former habitats such as Green Bay, Saginaw Bay, or western Lake Erie. However, since about 1982, small emergences of adults have been observed on South Bass Island, Lake Erie (Krieger et al. 1996). While recolonization of larger areas will probably occur, the time frame required for recolonization remains undetermined.

Management plans for rehabilitation of fish stocks

and remedial action plans for restoring water and habitat quality in polluted regions of the Great Lakes (i.e., the 43 "Areas of Concern" in the Great Lakes specified by the International Joint Commission's Great Lakes Water Quality Board) have set specific goals to restore environmental quality and beneficial uses of resources. However, in most cases the achievability and timelines of rehabilitation and restoration are unknown. Water quality standards are based on specific numerical criteria and have been useful in environmental cleanup and regulatory actions for decades. Restoration of habitat and biological resources is usually discussed in qualitative terms, and therefore its success is difficult to monitor. Simulation modeling can provide a quantitative basis to assess whether a species, community, habitat, or Area of Concern has been sufficiently restored to a specific level of biological composition, diversity, and production.

We have developed a model for the recolonization of the western basin of Lake Erie by *Hexagenia* (*H. limbata occulta* Walker and *H. rigida* McDunnough) based on population growth characteristics, behavior, presumed competition with midge larvae, possible lingering toxic effects after remediation, intermittent low dissolved oxygen conditions, and fish predation. We defined successful remediation of *Hexagenia* in western Lake Erie as recolonizing to the pre-1950s density of 350 nymphs/m² (developed from the population estimates of Wright and Tidd 1933 and Britt 1955a). The model suggests that recovery of biological systems, such as the recolonization of western Lake Erie by *Hexagenia,* may lag substantially behind remediation efforts.

METHODS

The model uses equations of mass balance (inputs minus outputs) translated from differential equations (Table 1), solving them iteratively. The state variables (densities) are reported as number per square meter and rates affecting the state variables as number per square meter per year. The model is a point model and does not take into account spatial considerations directly. We first developed a logistic model describing the population growth of *Hexagenia* and its presumed competitor, *Chironomus.* We then added various parameters including immigration, low oxygen, toxic sediments, competition, and predation to see how each affected the logistic model. We then ran the full model including all parameters. The model was constructed using SAS (SAS Institute 1990).

MODEL PARAMETER DEVELOPMENT

Population growth rate

The cornerstone of the model is the logistic equation describing the population growth of *Hexagenia* and its presumed competitor *Chironomus,* which currently inhabits substrate suitable for *Hexagenia* recolonization.

TABLE 1. Equations for the *Hexagenia* and chironomid model.

Hexagenia population:
$$dN_h/dt = r_h N_h (1 - a_t T) - (r_h/k_h \times N_h^2) + I - a_h N_h N_c - N_h F_h - a_O N_h$$

Chironomid population:
$$dN_c/dt = r_c N_c - (r_c/k_c \times N_c^2) - a_c N_h N_c - N_c F_c$$

Fish predation on *Hexagenia*:
$$dF_h/dt = r_f F_h - (r_f/p_f) \times F_h^2$$

Fish predation on chironomids:
$$dF_c/dt = p_f - F_h$$

Low-oxygen effect (O):
if $t = j$, $a_O = 0.1$, otherwise $a_O = 1$
t = years
j = random number < 20 yr

Variables for equations are:
F_c = fish predation on chironomids
F_h = fish predation on *Hexagenia*
I = immigration of *Hexagenia*
N_c = chironomid population
N_h = *Hexagenia* population
T = toxicity

Coefficients for equations are:
a_c = chironomid competition rate
a_h = *Hexagenia* competition rate
a_O = dissolved oxygen effect
a_t = toxic effect rate
k_c = carrying capacity for chironomids
k_h = carrying capacity for *Hexagenia*
p_f = total predation rate
r_h = annual population growth for *Hexagenia*
r_c = annual population growth for chironomids
r_f = increase in predation on *Hexagenia*

The sigmoid growth curve is generated by the quadratic equation $N_{t+1} = N_t + (rN - rN^2/K)$. Three parameters were estimated: N (initial *Hexagenia* and *Chironomus* densities), r (population growth rates), and K (carrying capacities).

Three initial densities for *Hexagenia* were used in the logistic model: 1, 10, and 20 nymphs/m². In May of 1991, Farara and Burt (1993a) collected 6–64 nymphs/m² at the mouth of the Detroit River and along the Canadian shoreline, with a single specimen near Pelee Island. In September they found nymphs only at the mouth of the Detroit River at densities ranging from 13–705 nymphs/m². However, most of the stations sampled in western Lake Erie in 1991 (≈90%) were still devoid of *Hexagenia*. Given that benthic invertebrates are often present in a patchy distribution and that benthic samplers typically sample a small area, confident population estimates of rare taxa are difficult to determine. For example, the probability of finding a *Hexagenia* at a density of 1 nymph/m² using three replicates and a 0.052-m² dredge is 15%, but is 50% at 10 nymphs/m². To account for this variability, we chose to run the logistic model with initial densities of 1, 10, or 20 *Hexagenia* nymphs/m²; we used 1 nymph/m² in a standard run of the full model.

We set initial *Chironomus* densities at 1000 nymphs/

m², which is conservative compared to other systems (Jonasson 1965, Hilsenhoff 1966), but is higher than 803 nymphs/m² measured in western Lake Erie in 1981 (McCall and Soster 1990) and represents an intermediate value between reported estimates.

Population growth rates (*r*) for *Hexagenia* have been estimated for only one population—in Tuttle Creek Reservoir, Kansas (Horst 1976). They ranged from 0.12 to 0.30 and were negatively correlated with nymphal densities. Colonization to an equilibrium level in this reservoir and in a newly impounded reservoir in South Dakota, Lewis and Clark Lake (Hudson and Swanson 1972) by *Hexagenia* took ≈10 yr, suggesting that growth rates in early successional stages may be more rapid. We calculated population growth rates of *Hexagenia* during colonization periods (Nelson 1970, Hudson and Swanson 1972) to be 0.8 for the Lewis and Clark Lake population and 0.6 for the Tuttle Creek population.

The above results suggest that the population growth rate can vary due to the unique conditions each system presents to the colonizer. Because of this potential variation in response, we used 0.3, 0.6, 0.9, and 1.2 to represent the range of possible *r* values. The lower *r* values may include implicitly many of the parameters (competition, predation, low oxygen) we used to slow down the logistic growth model. The two higher values could reflect colonization of a completely empty niche during ideal conditions. Lake Erie also poses special problems for the returning nymphs: episodic low oxygen and contaminated sediments, factors not implicitly included in *r* values from other systems. The range of values provides the reader with options from which to draw their own conclusions.

Prior to 1953, *Hexagenia* was the most abundant benthic organism in the western basin of Lake Erie. Densities reported from 1929 to 1953 range from 235–510 nymphs/m² (Wright and Tidd 1933, Britt 1955*a*, Chandler 1963, Wood 1963). Reynoldson et al. (1989) estimated historical *Hexagenia* densities in Lake Erie as high as 2600 nymphs/m² based on undocumented dredge and sieve efficiency adjustments. Their estimated sieve losses are probably exaggerated (see Mason et al. 1975). However, the effect of dredge efficiency on estimated *Hexagenia* densities may be significant since densities obtained, using a more modern dredge and sieve of 650-μm mesh opening, at nearby habitats similar to the western basin of Lake Erie (Lake St. Clair, St. Marys River) range from 360 to 1210 nymphs/m² (Hiltunen and Schloesser 1983, Thornley 1985, Hudson et al. 1986). In addition to sieve and dredge biases, samples collected over a short period of the life cycle (during recruitment or emergence) could also seriously overestimate or underestimate abundance (Barton 1989). To provide for this variability, we set the *Hexagenia* carrying capacity of western Lake Erie at two levels, 350 nymphs/m², slightly lower than the average reported pre-1953 densities, and 1000

nymphs/m², a reasonable estimate based on assumed sieve losses in the past and on densities estimated in recent times in habitats similar to western Lake Erie.

The carrying capacity of *Chironomus* coexisting with *Hexagenia* was set at 100 nymphs/m² based on reported densities of sympatric populations in western Lake Erie (Reynoldson et al. 1989) and reservoirs (Cowell and Hudson 1968), and similar to reported pre-1953 density (119 nymphs/m²; Wood 1963) in the western basin of Lake Erie.

Immigration

The small, localized population of *Hexagenia* at the mouth of the Detroit River (≈200 km²) indicates possible immigration of nymphs into Lake Erie from upstream. These nymphs are probably from the upper Detroit River and Lake St. Clair, where densities range from 200–1000 nymphs/m² (Hudson et al. 1986). *Hexagenia* are capable of redistribution through migration of nymphs (Swanson 1967, Riklik and Momot 1982) and drift densities from 0.5 to 4.8 nymphs/m³ have been measured in outflows from impoundments and lakes (Swanson 1967, Industrial Bio-Test Laboratories 1973). Migration of *Hexagenia* is known to be limited temporally and dielly (Swanson 1967, Riklik and Momot 1982). We used a drift density of 0.5 nymphs/m³ for an 8-wk nighttime discharge volume of the Detroit River divided by the area of the western basin suitable for habitation (70% of 3300 km² based on substrate type, Hartman 1973) to provide an immigration estimate of 2.6 *Hexagenia*·m⁻²·yr⁻¹. Lower immigration rates of 1.3 and 0.6 *Hexagenia*·m⁻²·yr⁻¹ were also simulated.

Dissolved oxygen

The dissolved oxygen concentration of water at the sediment–water interface is critical for survival of *Hexagenia*. Though resistant to low oxygen compared to other stream-dwellers (Gaufin et al. 1974), *Hexagenia* can survive only 30–48 h at 1.0 mg/L dissolved oxygen (Hunt 1953). Reported 96-h LC 50 values (lethal concentration at which 50% of mayflies died) for *Hexagenia* exposed to low oxygen include 1.4 mg/L at 18.5°C (Nebeker 1972) and 1.8 mg/L at 10°C (Gaufin et al. 1974).

In 1953, a 28-d calm period produced hypolimnetic hypoxia and a catastrophic loss of *Hexagenia* in western Lake Erie (Britt 1955*a*). Although *Hexagenia* recovered slightly from the 1953 catastrophe in 1954 (Britt 1955*b*), *Hexagenia* was virtually eliminated from the western basin by 1965 (Britt et al. 1973). Since that time, oxygen concentrations in the central and western basins of Lake Erie have improved (Makarewicz and Bertram 1993), due, in large part, to restrictions on phosphorus discharge and nonpoint source reductions begun both in the United States and in Canada in 1972 (International Joint Commission 1973).

Charlton (1987) predicted modestly improved oxy-

gen conditions with continued reductions in nutrient loading, but also warned that low dissolved oxygen concentrations may yet occur periodically (because of changing lake levels and unusual weather conditions). Phosphorus loadings have remained below target levels (Makarewicz and Bertram 1993), but oxygen conditions predicted to improve (Phosphorus Management Strategies Task Force 1980), have not (Rathke and McRae 1989). Charlton (1987), however, anticipated a 10–15 yr lag time in the response of oxygen depletion rates to further phosphorus loading reductions.

To simulate the frequency of a low-oxygen event, we generated several random numbers to represent weather events (1–3) occurring during the first 20 yr as dissolved oxygen was assumed to improve (1–5 and 1–10 yr intervals to nonlethal dissolved oxygen concentrations was also simulated). Each random low-oxygen event reduced the *Hexagenia* population by 90%, based on Britt 1955*a*.

Toxic sediments

Hexagenia has been described as pollution intolerant (Fremling 1970) and environmentally sensitive (Thornley 1985), but is less sensitive to acute toxicity than other species (e.g., *Daphnia*; Malueg et al. 1983). In fact, in 1979, *Hexagenia* was present at the site highest in DDT, PCBs, and lead, of those sampled in western Lake Erie in 1979 near the mouth of the Detroit River (OME 1981). Even though *Hexagenia* can be fairly tolerant of toxic substances, both significant (>50%) and total mortality have been induced in *Hexagenia* exposed to contaminated sediment from Duluth and Superior Harbor basins (Prater and Anderson 1977). Production of *Hexagenia* is also affected by sediment contaminants. *Hexagenia* production was higher (980–9231 mg dry mass/m²) where oil, cyanide, and six metals were below threshold criteria of the U.S. Environmental Protection Agency and the Ontario Ministry of Environment and Energy, than at sites where sediments were polluted (359–872 mg dry mass/m²; Edsall et al. 1991). Further, *Hexagenia* has been absent at sites severely impacted by contaminants (Thornley 1985) and has been eliminated from areas of the St. Marys River due to toxic sediments (Hiltunen and Schloesser 1983).

Historically productive sites in the Detroit River were found devoid of *Hexagenia* in 1968 (Thornley 1985). Since that time, *Hexagenia* populations have been rebounding in the Detroit River: lower reaches of the river where *Hexagenia* was absent in 1968 supported 1–50 *Hexagenia*/m² in 1980 (Thornley 1985), and since 1979 a modest population has been re-established in Lake Erie at the mouth of the Detroit and Maumee Rivers (K. Kreiger, Heidelberg College, Tiffin, Ohio, *personal communication*). Thus, rebounding populations of *Hexagenia* in the Detroit River indicate that once-contaminated sediments are becoming habitable for the mayfly.

The physiological costs these mayflies endure, how-ever, are not known. Diverse invertebrate taxa experience slowed growth when exposed to contaminated sediments (e.g., amphipods, Arthur and Leonard 1970; midges, Giesy et al. 1990). Malueg et al. (1984) found that sediments with high copper level in the Keewenaw Waterway, Lake Superior, were not acutely toxic to *Hexagenia* but had a subtle, long-term negative impact on *Hexagenia* populations. A recent survey found that most of the western basin is still moderately contaminated with heavy metals, nutrients, and PCBs (Farara and Burt 1993*a*), yet *Hexagenia* is present. Thus, conditions in the western basin are suitable for survival, but nymphs may endure substantially slower growth compared to others on cleaner sediments.

Toxicity was modeled by a reduction in *Hexagenia* growth rates. The reduction in growth was started at 50% and was improved by 2.5%/yr for 20 yr, assuming continued improvement in water quality over time. The 2.5% improvement per year is similar to the declining trend in PCBs (2.9%) and dieldrin (2.0%) found in Herring Gull (*Larus arsentatus*) eggs from the western basin of Lake Erie (Edwards and Ryder 1990). We concede that the pre-exposure of *Hexagenia* in western Lake Erie to contaminants will likely increase their resistance to them, as is true for other taxa (Grant and Brown 1967, Malueg et al. 1984). We believe that our prediction of an initial 50% decrease in growth, therefore, may be high, but was used to ensure conservative model parameters. We did not include a toxicity term for *Chironomus,* since midges have a high resistance to contaminants and are likely only minimally impacted by current sediment contaminant loads.

Competition

High densities of both *Hexagenia* and chironomid larvae do not typically occur together spatially and temporally. Rather, when *Hexagenia* densities are high, chironomid densities are typically low (Hergenrader and Lessig 1980); the reverse relationship is also true (Schneider et al. 1969, Cooper and Knight 1985). Given their pattern of occurrence, potential competition between *Hexagenia* and chironomid larvae has been acknowledged (Clady and Hutchinson 1976) though not quantified.

Competition for food is likely not limiting, as the diets of *Hexagenia* and *Chironomus* are generally different: *Hexagenia* are thought to nondiscriminately ingest mud and detritus (Hunt 1953, Fremling 1967), while many chironomids select for algae (Kajak and Warda 1968) and may use a combination of filter- and deposit-feeding strategies (Rasmussen 1985). Competition for space, however, may occur since both *Hexagenia* and *Chironomus* inhabit muddy sediments with similar particle sizes (Fremling 1960, Topping 1971) and are often collected together (Schneider et al. 1969).

Data to estimate presumed competition between *Hexagenia* and *Chironomus* are unavailable in the literature. Studies on newly created reservoirs reveal *Chi-*

ronomus to be the initial colonizer (Cantrell and McLachlan 1977), later replaced by *Hexagenia* after sediments suitable for construction of their burrows become available (Hudson and Swanson 1972). Because of *Hexagenia*'s large size and armor, we chose to represent competition as a negative interaction for space. The probability of permanent displacement is the product of the probability of contact between the species, probability of displacement, and the probability of survival after the displacement. We set the probability of confrontation at 10%, the probability of *Chironomus* larvae losing this battle at 10%, the probability of *Hexagenia* losing at 1%, and the probability of mortality after displacement at 1% for both species. The first two values are similar to those observed in situ in stream-dwelling insects (black fly larvae, mayfly nymphs, and caddisfly larvae; Wiley and Kohler 1981). While these estimates are based on lotic organisms, no similar work has been done on lentic invertebrates. The estimate of 1% for mortality of both species after displacement is an estimate based on the resilience of the two taxa. The products of these percentages were the competition coefficients used; 0.001 for *Chironomus* and 0.0001 for *Hexagenia*. We also varied the coefficients ±10% for a sensitivity analysis.

Fish predation

Fish adapt quickly as prey abundances change. Price (1963) noted that as *Hexagenia* abundance declined in Lake Erie, chironomids began replacing *Hexagenia* in the diets of fish. As *Hexagenia* begins to return to former densities in Lake Erie, we speculate that fish predation will delay its recovery. In 1958, channel catfish (*Ictalurus puntatus* Rafinesque), freshwater drum (*Aplodinutus grunniens* Rafinesque), and yellow perch (*Perca flavescens* Mitchell) consumed the most *Hexagenia* in western Lake Erie (Daiber 1952, Price 1963). Since that time, walleye (*Stizostedion vitreum* Mitchell) have become a larger proportion of the fish community (Wolfert and Bur 1992) and are known to eat large numbers of *Hexagenia*; walleye year-class strength has even been attributed to *Hexagenia* abundance in Savanne Lake, Ontario (Ritchie and Colby 1988).

To determine consumption rates, we first estimated fish abundance and the rate at which fish consumed *Hexagenia*. The only fish species with available biomass estimates was freshwater drum, with an estimated abundance in western Lake Erie of 9545 Mg in 1977 and 2330 Mg in 1978 (Bur 1984). The most abundant age group is 3–4 yr (Bur 1984), and these fish average 241 g (Edsall 1967). Biomass estimates divided by mean fish mass divided by the area of the western basin (3300 km^2) equals 29 and 120 freshwater drum/ha in 1977 and 1978, respectively. Adult drum can consume ≈6 *Hexagenia* a day over a 6-mo period (May–October) with *Hexagenia* comprising ≈70% of the diet (Swedberg 1968). *Hexagenia* consumption by freshwater drum, therefore, is ≈3–13 $nymphs \cdot m^{-2} \cdot yr^{-1}$.
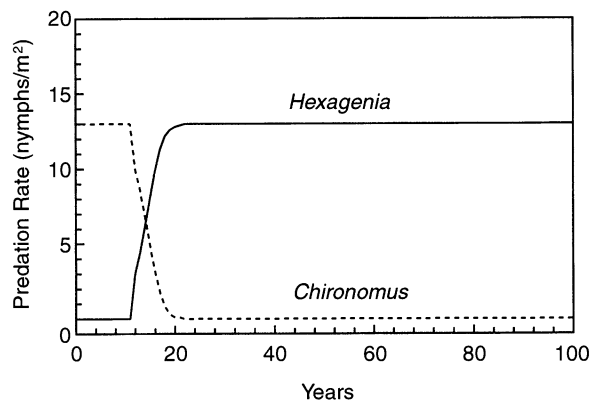

FIG. 1. *Chironomus* and *Hexagenia* fish-predation diet-switching curves used in model development. After *Hexagenia* density was >100 nymphs/m^2, fish quickly switched from *Chironomus* to *Hexagenia*.

While biomass estimates are not available for other potential predators, we can infer consumption based on biology and what is known. Yellow perch densities are about twice those of freshwater drum (M. Bur, Sandusky Biological Station, Sandusky, Ohio, *personal communication*) and they feed on *Hexagenia* during spring and summer (Price 1963) while young walleye can rely heavily on *Hexagenia* for a 3–6 mo period (Ritchie and Colby 1988). Channel catfish are currently a minor component of the Lake Erie fish community. To account for fish consumption, we doubled the estimated consumption of *Hexagenia* by freshwater drum (at 13 $nymphs \cdot m^{-2} \cdot yr^{-1}$). To determine sensitivity of the model to variation in predation rate, we also used the removal of 3 and 26 $nymphs \cdot m^{-2} \cdot yr^{-1}$ by fish predators.

We kept a constant predation rate on total invertebrates eaten. Fish ate 100% *Chironomus* initially. Once *Hexagenia* densities were >100 nymphs/m^2, fish began to eat *Hexagenia* and quickly switched to eating 100% *Hexagenia*. Switching curves were modeled using the logistic model with a population growth rate of 0.6 and carrying capacity equal to the predation rate (Fig. 1).

RESULTS

To establish standard values for the logistic equation, we determined how the model reacted to simple changes in the *r* values and initial densities for *Hexagenia* with the carrying capacity set at 350 nymphs/m^2. The number of years necessary to reach carrying capacity increased slightly from *r* = 1.2 to ≈0.5, but accelerated as *r* decreased to 0.1 (Fig. 2). Decreasing the initial density of *Hexagenia* generally slows recovery by ≈5 yr, except when *r* = 0.1, when recovery lags ≈30 yr. For comparison purposes, we established a baseline model projection using an initial *Hexagenia* density of 1 nymph/m^2 and *r* values of 1.2, 0.9, 0.6, and 0.3, which results in 10, 13, 20, and 41 yr to recovery.
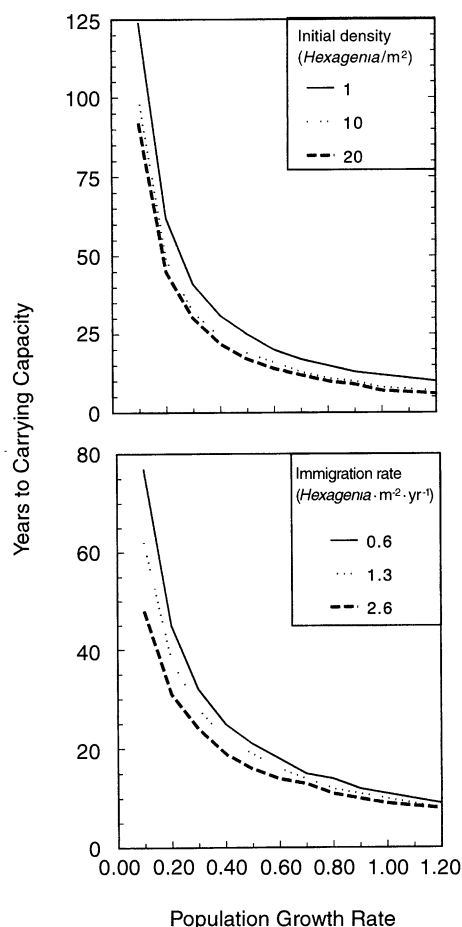
FIG. 2. The top panel shows the logistic model of years to reach carrying capacity at different *Hexagenia* population growth rates and initial condition of 1, 10, and 20 nymphs/m². The bottom panel shows the logistic model of years to reach carrying capacity at different *Hexagenia* population growth rates and immigration rates of 0.6, 1.3, and 2.6 nymphs·m⁻²·yr⁻¹, using 1 nymph/m² as the initial density.

high r values the reproducing resident population swamped the small addition from upstream. However, at low r values, these migratory nymphs became important. As migratory nymphs are the basis for establishing the initial density used in the logistic equation, immigration is important regardless of r. Using 2.6 nymphs·m⁻²·yr⁻¹ as a standard run, these additional nymphs reduced the recolonization time by 2, 3, 6, and 17 yr at r values of 1.2, 0.9, 0.6, and 0.3.

A random low-oxygen event was incorporated in the model that would lower the densities of *Hexagenia* by 10, 50, and 90% over the initial 20-yr period. The additional years to reach carrying capacity is given in Table 2 (mean and range based on 100 iterations). For a standard run of 90% mortality, occurring once over the first 20 yr, an additional 3–17, 5–15, 6–13, and 10–11 yr to recovery was needed at r values of 1.2, 0.9, 0.6, and 0.3, respectively. Decreasing the initial time intervals (5 or 10 yr) in which random low-oxygen events occurred had little effect on additional years to reaching carrying capacity ($\pm$1–2 yr). When we ran simulations with $r = 0.6$, mortality at 50%, and increased the number of events to more than one per 20-yr interval, each additional event increased the recovery by 2 yr; when we used 90% mortality, recovery took an extra 6 yr per event.

Toxicity effects on *Hexagenia* population growth added 2–22 yr on the time to recovery based on several scenarios (Table 3). Impact was greatest at higher r values over the longer cleanup period regardless of the initial reduction in population growth rate. A standard run with an initial 50% reduction in growth decreasing over 20 yr resulted in an additional 5, 6, 9, and 11 yr to the recovery of *Hexagenia* at r values of 0.3, 0.6 0.9, and 1.2.

Competition with *Chironomus* increased the recovery time of *Hexagenia* by 6–24 yr with the greatest impact at lower r values (Table 4). A standard run with a *Hexagenia* to *Chironomus* coefficient of 0.0001 to 0.001 increased the years to recovery of *Hexagenia* by 8, 8, 9, and 19 yr at r values of 1.2, 0.9, 0.6, and 0.3. Varying either coefficient ($\pm$10%) did not change results substantially, although *Chironomus* appears more sensitive than *Hexagenia*.

Fish predation substantially increased recovery time

Next, we built the full model by adding one variable at a time to the logistic model to determine subsequent changes in the time to recovery of *Hexagenia*. Changes in immigration (2.6, 1.3, and 0.6 *Hexagenia*·m⁻²·yr⁻¹) had little effect on recovery if $r > 0.5$ (Fig. 2), but greatly affected recovery at low values of $r < 0.3$. At

TABLE 2. Average number (range) of years a single, random, low-oxygen event within the first 20 yr of population growth would add to the recovery of *Hexagenia* in western Lake Erie, using several mortality rates associated with low dissolved oxygen and population growth rates of *Hexagenia* ($N = 100$ iterations).

| Mortality (%) | Population growth rate | | | | | | | |
| | 0.3 | | 0.6 | | 0.9 | | 1.2 | |
	Time (yr)	Range (yr)	Time (yr)	Range (yr)	Time (yr)	Range (yr)	Time (yr)	Range (yr)
10	2	2–2	2	2–5	3	1–10	4	1–13
50	4	4–5	4	3–9	4	2–12	4	1–13
90	10	10–11	7	6–13	7	5–15	8	3–17

TABLE 3. Number of years toxic sediments would add to the recovery of *Hexagenia* in western Lake Erie (assuming several reductions in population growth rate) given 10, 20, and 30 yr to achieve clean sediments (no toxicity) and four population growth rates of *Hexagenia*.

Population growth rate	Initial reduction in growth rate (%)	Time to clean sediments (yr)		
		10	20	30
0.3	25	2	3	4
	50	3	5	8
	75	4	8	12
0.6	25	2	4	13
	50	3	6	14
	75	4	8	15
0.9	25	1	9	19
	50	3	9	19
	75	4	9	19
1.2	25	1	11	21
	50	2	11	21
	75	3	11	22

TABLE 4. Number of years that competition between *Hexagenia* and *Chironomus* would add to the recovery of *Hexagenia* in the western basin of Lake Erie.

	Hexagenia/Chironomus competition coefficient		
Population growth rate	$0.0001H \div 0.001C$	$0.0001H \pm 10\% \div 0.001C$	$0.001H \div 0.001C \pm 10\%$
0.3	19	17–21	16–24
0.6	9	9–9	7–12
0.9	8	8–9	7–11
1.2	8	8–8	6–11

Note: For a sensitivity analysis, the initial *Hexagenia* competition coefficient was varied ±10% while the *Chironomus* competition coefficient was held constant. Then the *Chironomus* coefficient was varied ±10% while the *Hexagenia* coefficient was held constant.

and also prevented *Hexagenia* densities from reaching our carrying-capacity goal of 350 nymphs/m² (Table 5). The reduction in carrying capacity was most profound at high predation rates and low population growth rates. The standard run was set at a predation rate of 13 nymphs·m⁻²·yr⁻¹ and added 4, 12, 20 and 47 yr at *r* values of 1.2, 0.9, 0.6, and 0.3. We could achieve a carrying capacity *K* of 350 nymphs/m² by setting *K* at 400 nymphs/m² and using a predation rate of 13 nymphs·m⁻²·yr⁻¹. This higher carrying capacity did not reduce recovery time at *r* = 1.2, but did by 1 yr at *r* = 0.9, by 4 yr at *r* = 0.6, and added 10 yr to recovery time at *r* = 0.3, when compared to the lower carrying capacity.

Full model

A full model run produced a recolonization period of 48–87 yr, depending on the *r* value and the timing of the low-oxygen event (Table 6). The effects of each variable independent of the logistic equation are also given. These individual effects are not always additive; the full model produces recolonization values at the lower population growth rates.

To use the model as a predictive tool, we need to determine a starting date for the model. Although nymphs have been at and around the mouth of the Detroit River since at least 1979 (OME 1981), no nymphs from the lake proper have been reported until the early 1990s (Farara and Burt 1993a; K. Krieger, *personal communication*). We chose to start the model in 1990 using *r* = 0.9 (Fig. 3). If model conditions are reasonable, then *Hexagenia* densities will approach those that were present in the early 1950s by about the year 2020. *Hexagenia* densities slowly increase from that point until about the year 2040, after which they plateau. Using this same level of *r* with the higher carrying capacity of *Hexagenia* (1000 nymphs/m²) produces similar results; *Hexagenia* growth slows sub-

stantially at about the year 2020 and levels out at about the year 2040 (Fig. 3). Starting the model at a higher initial density (10 nymphs/m²) had no effect in the full model.

Model verification

We cannot use the parameters used in development of the model for its verification, since they are specific to the conditions present in the western basin of Lake Erie in 1990. We did, however, attempt to verify the model by choosing parameter values present in the basin in 1970, beginning the model in 1970 and running it through 1990. To this end, specifying model parameters, calculating *Hexagenia* present in the western basin in 1991, and running the model were done independently by different coauthors.

We used the estimates of *Hexagenia* made in localized areas in the western basin in 1991 from Farara and Burt (1993a) and extrapolated these findings to estimate nymph density over the entire western basin. There were on average 32 nymphs/m² at the Detroit River mouth and Point Pelee, an area that represents 10% of the western basin. Farara and Burt (1993a) sampled stations over the rest of the basin and found only one station with nymphs (6 nymphs/m²). Given the variability of sampling rare taxa, discussed earlier, a range of nymph densities is possible with this estimate. If we assume that there was 1 nymph/m² over

TABLE 5. Number of years varying rates of fish predation would add to the recovery of *Hexagenia* in western Lake Erie using several different population growth rates of *Hexagenia*. *K* = carrying capacity.

Population growth rate	Predation rate (nymphs·m⁻²·yr⁻¹)					
	3		13		26	
	Time (yr)	*K* (nymphs/ m²)	Time (yr)	*K* (nymphs/ m²)	Time (yr)	*K* (nymphs/ m²)
0.3	46	340	47	299	24	193
0.6	21	345	20	326	16	299
0.9	14	347	12	335	11	318
1.2	0	348	4	339	7	327

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TABLE 6. The number of years to reach carrying capacity at different population growth rates with logistic model and additional years each parameter adds to logistic model. Carrying capacity other than 350 nymphs/m² is noted in parentheses.

Parameter	Population growth rate			
	0.3	0.6	0.9	1.2
Original years				
Logistic	41	20	13	10
Additional years				
Immigration (2.6 nymphs·m⁻²·yr⁻¹)	−17	−6	−3	−2
Low-oxygen event (within first 20 yr, 90% mortality)	10–11	6–13	5–15	3–17
Toxicity (50% reduction during 20 yr)	5	6	9	11
Competition (*Hexagenia* = 0.0001, *Chironomus* = 0.001)	19	9	8	8
Predation (13 nymphs·m⁻²·yr⁻¹)	47	20	12	4
(new carrying capacity; nymphs/m²)	(299)	(326)	(335)	(339)
Total	105–106	55–62	44–54	34–48
Full model (yr)				
Mean	84	50	49	48
Range	82–87	50–52	49–49	48–48
(New carrying capacity; nymphs/m²)	(310)	(330)	(337)	(342)

the remaining 90% of the basin, the weighted average for the basin would be 4 nymphs/m²; if we assume 6 nymphs/m², the weighted average would be 9 nymphs/m²; and if we assume 20 nymphs/m² in this area, the weighted average would be 21 *Hexagenia* nymphs/m².
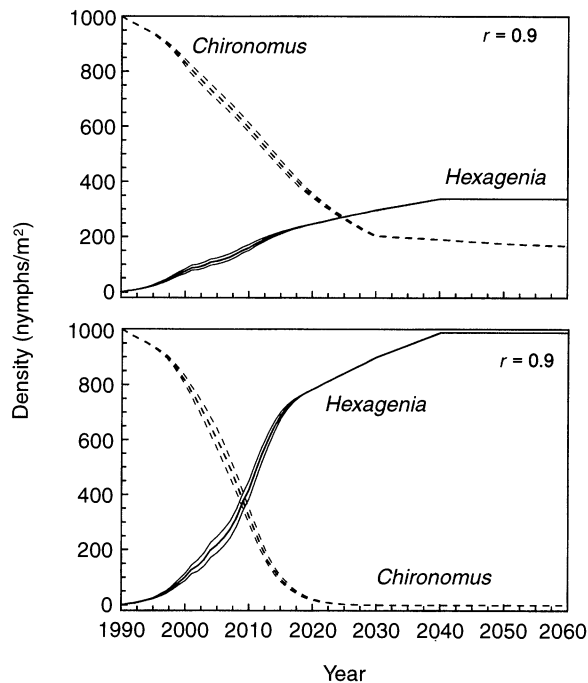

FIG. 3. The top panel shows the *Hexagenia* and *Chironomus* densities in western Lake Erie as predicted by the full model, using a carrying capacity of 350 nymphs/m² and a *Hexagenia* population growth rate of 0.9. The bottom panel shows the *Hexagenia* and *Chironomus* densities in western Lake Erie as predicted by the full model, using a carrying capacity of 1000 nymphs/m² and a *Hexagenia* population growth rate of 0.9. The outer lines represent 95% confidence intervals.

Thus, the actual density of *Hexagenia* nymphs present over the entire basin in 1991 probably ranged from ≈4–21 nymphs/m².

The following parameter values were selected for beginning the model in 1970: initial *Hexagenia* density was set at 0 nymphs/m², contaminated sediments slowed growth of nymphs from 90 to 50% over the 20-yr period, and low-oxygen events occurred randomly 5, 10, and 15 times over the period. Running the full model with these parameters resulted in predicted *Hexagenia* densities in 1990 of 3–23 nymphs/m² (Table 7). The predicted densities overlap almost completely with the actual estimated densities. We feel this quasi-independent procedure (of determining a priori densities in 1991, choosing model parameters, and running the model) gives credence to the adequacy of the model.

DISCUSSION

Reynoldson et al. (1989) posed the question "Recovery—can *Hexagenia* return to the western basin of Lake Erie?" Similarly, we ask: (1) If conditions appropriate for the return of the species could develop, and do develop, could *Hexagenia* return?, and (2) Could they return to pre-1953 densities? Recent surveys (Farara and Burt 1993*a* and K. Krieger, *personal communication*) indicate that some *Hexagenia* are present in the western basin, and 1994 emergences of *Hexagenia* have been reported in local newspapers (Askari 1994). However, environmental conditions still may be tenuous (K. Krieger, *personal communication*). The question then remains, how long will it take to achieve a full recovery? Our model predicts 10–41 yr based on the logistic equation alone. Reynoldson et al. (1989) noted that the storage of sediment contaminants and oxygen-demanding materials would delay the recovery of *Hexagenia*. After adding parameters for immigra-

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TABLE 7. Mean predicted densities of *Hexagenia* (with 95% confidence intervals in parentheses) achieved by 1990 when the full model was started in 1970 with an initial *Hexagenia* density of 0 nymph/m², an immigration rate of 2.6 nymphs/m², and 5, 10, or 15 low-oxygen events.

Low-oxygen events (number)	Population growth rate			
	0.3	0.6	0.9	1.2
5	10.4 (8.9–11.9)	14.2 (11.6–16.6)	19.1 (15.3–22.9)	25.2 (19.9–30.5)
10	5.8 (4.7–7.0)	7.1 (5.5–8.8)	8.8 (6.4–11.1)	10.6 (7.5–13.8)
15	3.3 (2.6–4.0)	3.7 (2.8–4.6)	4.2 (3.1–5.3)	4.8 (3.4–6.2)

Note: Each low-oxygen event reduced *Hexagenia* densities by 90%. Toxicity initially decreased growth rates 90%, steadily improving to a 50% reduction by 1990.

tion, low oxygen, toxic sediments, presumed competition, and predation, our model suggests an additional delay of 38–43 yr.

Is this an unreasonable estimate of recovery? Benthic recolonization studies have been conducted mainly on streams, the recolonized area usually <1 m², and the areal source of recolonizers at least 1000 times the area to be recolonized. Recolonization rates in these situations are measured in days (Williams and Hynes 1977, Sheldon 1977). Larger areas in lotic environments may require up to 3.5 yr for recolonization after physical disturbances (Minshall et al. 1983) and up to 10 yr for contaminated sites (Chadwick et al. 1986). Niemi et al. (1990) noted that for small streams, 85% of macroinvertebrate recovery endpoints to predisturbance density after pulse disturbances occurred in <1.5 yr. Due to highly altered physical habitat and polluted sediments, Fuchs and Statzner (1990) concluded that a large Central European river ecosystem like the River Rhine would take >12 yr to recover to a state significantly different from the present one. The recolonization of western Lake Erie by *Hexagenia* is unique in that the area to be recolonized is at least three times larger than any nearby source (Lake St. Clair). Since Lake St. Clair is too far from the western basin of Lake Erie to be reached by adult mayflies, *Hexagenia* nymphs would have to migrate through the Detroit River. The recolonization of western Lake Erie by *Hexagenia* may be similar to disturbances such as mining activity, channelization, and watershed disturbances reviewed by Niemi et al. (1990), which measured the recovery rates for mayflies exceeding 18 yr.

Two approaches can be used to include spatial structure in simple ecological models: modeling movement by diffusion, and modeling movement through patches (Hastings 1990). For simplicity, we have assumed movement by diffusion, i.e., immigration and eggs were assumed to be distributed uniformly across the western basin. In fact, the population will probably develop from patches in the vicinity of the major river systems (Detroit, Maumee, Sandusky) and the Bass Island region and will spread outward by adults or drift-

ing eggs and nymphs. The majority of *Hexagenia* females typically deposit their eggs in the nearshore zone with a mean dispersal distance measured in Lake St. Clair of 2600 m (Kovats and Ciborowski 1989), but have been monitored flying up to 13 000 m in a stream environment (Russev 1973). Movement of nymphs to the middle of the lake may involve random daily movements of only several meters, but seasonal movements may involve tens of kilometers based on currents moving them throughout the western basin (small but steady flow of 2 cm/s, Rathke and Edwards 1985). Additionally, *Hexagenia* nymphs have been known to migrate when densities become >100 nymphs/m² from the shallow nearshore areas to deeper water with greater silt deposition (Hudson and Swanson 1972). We also realize that nymphs would preferentially colonize the best sites nearest shore until densities become high enough to reduce the marginal suitability for subsequent colonists to zero. Inferior sites or those farther from shore would then offer higher returns and be colonized (Sheldon 1984). We also acknowledge that there is a temporal mosaic of suitable habitat due to the uneven intensity of bottom disturbances as they relate to geology and geography, but we examined a lake-wide response on an area basis. Our diffusion model is conservative and probably underestimates the time needed for recolonization.

One obvious factor affecting the recovery of *Hexagenia* in western Lake Erie that our model does not consider is the presence of vast numbers of the exotic zebra mussel (*Dreissena polymorpha*) present in the western basin of Lake Erie since 1986 (Hebert et al. 1989). Zebra mussels have a number of potential effects on the recolonization of *Hexagenia*; some effects may quicken the mayfly's return, others may dampen it. The standing crop and productivity of *Hexagenia* have been found to be higher at locations in the same system with lower chlorophyll *a* concentrations (Welch and Vodopich 1989). Therefore, reduced chlorophyll *a* in the western basin caused by zebra mussels (chlorophyll *a* dropped from 4 μg/L in 1988 to 1–2 μg/L in 1991, OME 1992) may expedite the recovery of *Hexagenia*.

As chironomids select for algae (Kajak and Warda 1968), zebra mussels may benefit *Hexagenia* by reducing competition with *Chironomus*. Also, the zebra mussel population produces large amounts of nutrient-rich pseudofaeces which may enrich the diet of *Hexagenia*.

Many contaminants in the Detroit River were higher in 1991 (Farara and Burt 1993*b*) than in 1980 (Thornley and Hamdy 1984). This increase may be related to the deposition of water-borne contaminants via faeces and pseudofaeces of zebra mussels (Farara and Burt 1993*a*). Since contaminants reduce the growth rate and production of *Hexagenia* (Edsall et al. 1991), the concentration of contaminants into sediments by zebra mussels may lengthen the time necessary for recovery of *Hexagenia*. Though zebra mussels mainly colonize hard substrates, they do form vast, dense beds on silty, muddy substrates, which remain until a storm large enough to break apart the mussel mat occurs (D. W. Schloesser, United States Geological Survey, Ann Arbor, Michigan, *personal communication*). *Hexagenia*, therefore, may have to compete for space on muddy substrate with zebra mussels or may be killed as mussel beds are destroyed by wave action—both of which will lengthen the time for *Hexagenia* to reach carrying capacity. We acknowledge the impact of zebra mussels on the recolonization of *Hexagenia* in western Lake Erie. However, in a 1991 survey, Farara and Burt (1993*a*) found that zebra mussels exerted no obvious negative impact on benthic fauna, and found no relationship between *Hexagenia* nor chironomid density and that of zebra mussels. As the effects of zebra mussels are largely unpredictable at this point, we did not include them in our model.

We have described the conditions present in Lake Erie, those necessary to sustain *Hexagenia*, and developed a model for their return. We have inventoried the available information about a system and have used a deterministic model for making predictions about how that system might change over time. Though Schindler (1987) states that deterministic models based on coefficients from the literature or measured in single ecosystems contribute little to ecosystem management, he believes that simple models grounded in empirical science have merit. Our goal was to develop a macroscopic minimodel that presents an overview of a complex system while keeping detail at a minimum (Odum 1976). This model has been useful in examining the effects of assumptions and communicating overall behavior of the benthic system of western Lake Erie as it continues to improve. The model also indicates that the qualitative goals of fish stock rehabilitation plans and remedial action plans to achieve prestress densities of given taxa may take longer than anticipated.

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