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Development of an Age-structured Metapopulation Model of Zebra Mussels

BACKGROUND AND PURPOSE: Since current water quality models do not adequately portray population dynamics (Waide and Kennedy 1998), understanding the interactions between zebra mussels and water quality will require linking water quality models and models of zebra mussel population dynamics (Kennedy, Bridges, and O'Neill 1998). This technical note describes the development of a population model for zebra mussels. The model predicts probable population trajectories (changes in abundance over time) based on current abundances and information describing vital rates.

MODELING AGE-STRUCTURED POPULATIONS: A *population* is a group of individuals of the same species who, because they are located in the same geographic space, are able to locate each other and reproduce (Açkakaya, Burgman, and Ginzburg 1997). Population ecology is the study of the dynamics of populations while providing an information base upon which to discuss and evaluate many important natural resource management challenges (e.g., invasion of nuisance species, extinction of rare species). Population models account for changes in the number of individuals over time by considering factors that increase (i.e., birth and immigration) and decrease (i.e., death and emigration) abundance.

For many species, marked differences in body form, physiology, behavior or trophic function are apparent throughout their life history. Because of this, populations are often viewed as having an age (e.g., first year, second year, etc.) or stage (e.g., larva, adult, etc.) structure. Age- or stage-structured populations can be described by a number set composed of the abundance values (number of individuals) associated with each age or stage class, the sum of which equals the total number of individuals in the population. Since individuals in each age class may exhibit different vital rates (e.g., survival rate, fecundity), a second set of descriptive numbers can be established by identifying the rates associated with each age or stage class. Taken together, these two sets of numbers represent a matrix-based population model, the solution of which predicts changes in each age or stage class over time.

Populations are often composed of several local populations or subpopulations located in different parts of a habitat (e.g., mussels in beds located along a river or in an interconnected chain of lakes, Neotropical birds in a fragmented forest habitat). Each subpopulation exhibits its own abundance distribution and a unique set of vital rates, and despite their disparate locations, may exchange individuals through dispersal. Taken together, these subpopulations represent a *metapopulation*, the characteristics of which are approximated by the sum of those for each of the subpopulations. Metapopulation models are similar to those used to describe changes in single populations with the exception that dispersal is considered.

ZEBRA MUSSEL POPULATION DYNAMICS: The zebra mussel population of the Mississippi River drainage can be viewed as a metapopulation. Although initially established in the Great Lakes, dispersal through the Illinois River led to the establishment of populations throughout the upper and middle Mississippi River and portions of the Ohio River (Miller and Payne 1997). While located discontinuously throughout this regional waterway, dispersal of juveniles (e.g., by hydraulic transport of veligers in streams) and adults (e.g., by transport associated with vessel navigation) has an important influence on this metapopulation.

A metapopulation model for the zebra mussel was based upon (Açkakaya and Baker 1998) an assessment of reported population data for zebra mussel dynamics and their abundances in the Mississippi River drainage. This effort was accomplished using the RAMAS(r) Metapop modeling software (Açkakaya 1998).

RESULTS OF METAPOPULATION MODELING: Parameter estimation for the metapopulation model indicated that survival rates have a very high temporal and spatial variation. For example, data from a large zebra mussel bed located on the Ohio River near Olmsted Lock and Dam exhibit extreme spatial variability due, in part, to substratum variability. Substrata here range from bedrock and gobble to gravel and shifting sand. Combined with sampling error (in estimating densities, or identifying sampling locations from previous years), the high variability of survival rates makes estimating a population mean very difficult. This suggested that a risk-based, medium-term approach was more appropriate than attempting to predict the exact density and distribution of zebra mussels from one year to the next.

The scale of spatial variability in rivers suggested the need for a regional metapopulation model. This model identified separate, yet connected, subpopulations for major reaches of the rivers, as well as the upstream or headwater lakes (Figure 1). Within each of these subpopulations, the dynamics were modeled with an age-structured model with three age classes: 0-1 year (0-16 mm), 1-2 years (17-27 mm), and 2-3 years (>27 mm). Survival rates (and their variation) for each age class were estimated from the available data (see Açkakaya and Baker (1998)).

Other important model parameters were recruitment and dispersal. All larval zebra mussels from a river population were assumed to drift to one or more downstream populations. In such a metapopulation model, the major recruitment source would be lakes with zebra mussel populations. The available data suggested that such recruitment may have high temporal (year-to-year) variation. Recruitment may even be zero in certain years. Dispersal rate estimates were closely linked with those of recruitment from upstream sources. Studies designed to estimate recruitment should give additional clues about dispersal.

USING THE ZEBRA MUSSEL METAPOPULATION MODEL: This metapopulation model can be used to address questions about the effect of various factors on the risk of a zebra mussel population explosion. The factors may include the frequency and amount of recruitment from lakes, downstream dispersal in rivers, instream reproduction, and mortality rates. The results of such a model are expressed as the probability (risk) that the abundance will exceed a certain threshold level within a given time period. This risk is calculated for a range of threshold levels, and plotted as a function of the threshold level (see Figure 2 for an example). Each point on the “risk curve” in Figure 2 gives the probability that a zebra mussel metapopulation (or part of it) will exceed a given threshold abundance within the next 20 years. Thus, there is about a 50-percent chance that the

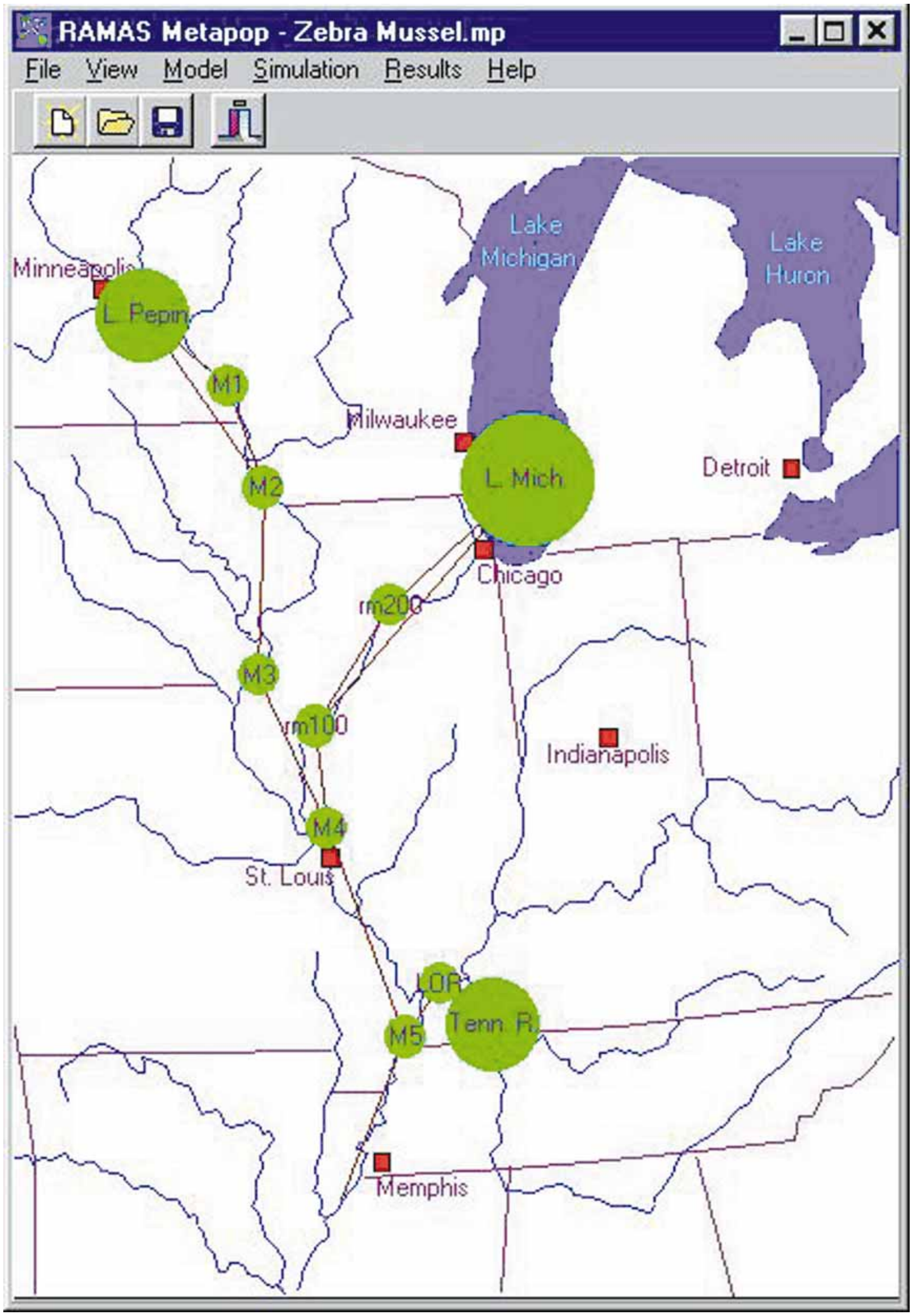

Figure 1. Spatial structure of a zebra mussel metapopulation in the upper Mississippi and lower Ohio Rivers. Circles represent subpopulations inhabiting lakes or sections of rivers. The sizes of the circles are proportional to the initial abundance or carrying capacity of the subpopulation. Lines represent potential dispersal among subpopulations. Each subpopulation may have a different age structure (distribution of the initial total abundance to age classes), or a different set of vital rates (survival and fecundity). Such differences are entered in the model as parameters.

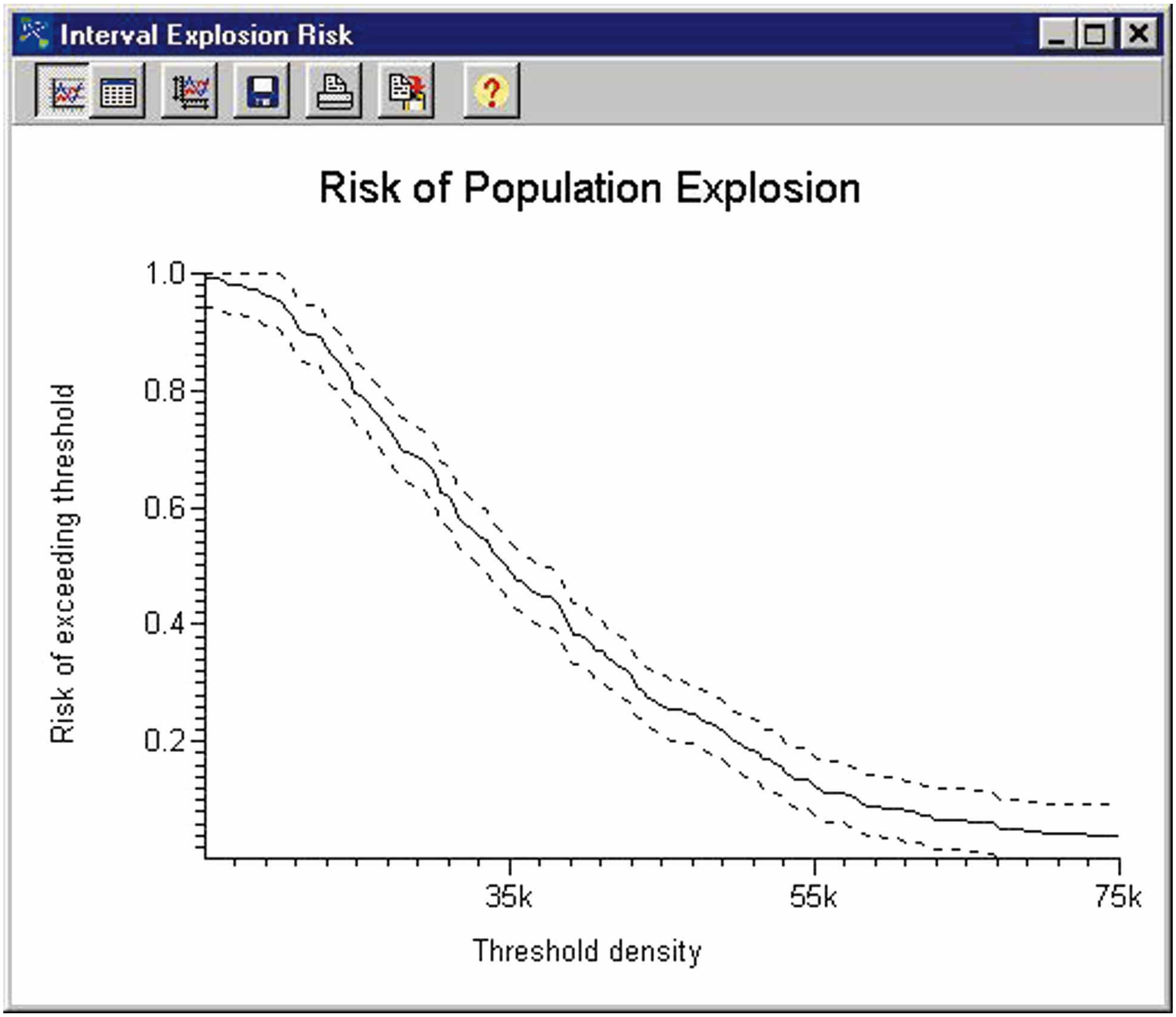

Figure 2. Risk curve showing the probability of a population explosion as a function of the threshold density

total abundance will exceed 35,000 individuals, and about a 20-percent chance that it will exceed 55,000. The dotted lines show the 95-percent confidence interval.

Each time the model is run, it produces a risk curve similar to that in Figure 2. The model can be run several times, each run with different assumptions about population dynamics or about management options. For example, the model can be run with the baseline parameters, and then rerun with parameters modified according to a “What if...” scenario. These scenarios can be evaluated by comparing their risk curves. Such comparisons are facilitated by the program, which allows superimposing risk curves from different model runs and reports the difference between them (and its statistical significance).

CONCLUSIONS AND RECOMMENDATIONS: The parameters of the metapopulation model (including survival, recruitment, dispersal rates and their variation) have been estimated from the available data. Because of the high temporal and spatial variability of zebra mussel population dynamics, and the short duration of the available data sets, these are not very precise estimates, and many model parameters are poorly known. The first step for improving the model should involve quantifying the uncertainties in model parameters. This can be done by assigning a range (instead of a single number) for each parameter. These ranges can then be used in a comprehensive sensitivity analysis. Sensitivity analysis allows the identification of the most important parameters (i.e., parameters to which the results are most sensitive.) The results of such an analysis indicate the most efficient way of reducing the uncertainty in the model. Carefully designed field studies would decrease this kind of uncertainty, originating from lack of information. For example, to estimate fertility more accurately would require further fieldwork on settlement rates, veliger density, and factors that affect reproduction (for details, see the "Recommendations" section in Açkakaya and Baker (1998)).

However, there is another source of uncertainty, which originates from natural variability in physical and biological factors affecting the zebra mussel populations, that cannot be reduced (but can be better understood) with additional fieldwork. This natural variability has both spatial and temporal components, and necessitates a risk-based, medium-term (5-10 years), large-scale (at the level of rivers, or river sections) model.

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> Kennedy, R. H., and Açkakaya, H. R. (1999). "Development of an age-structured metapopulation model of zebra mussels," *Zebra Mussel Technical Notes Collection* (ZMR-3-21), U.S. Army Engineer Research and Development Center, Vicksburg, MS. *www.wes.army.mil/el/elpubs/zebtnote.html*

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