

# A Multivariate Model for Predicting Population Fluctuations of *Dreissena polymorpha* in North American Lakes

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The European zebra mussel, *Dreissena polymorpha* (Pallas), has recently been introduced to North American freshwaters. *Dreissena* exhibits a wide range of population dynamics among different European lakes. In some lakes, long-term population size is fairly constant, while populations in other lakes can fluctuate greatly from year to year. Assessments of the potential ecological and economic effects of *Dreissena* in North America will be affected if populations show large interannual fluctuations in abundance. We develop a multivariate model for predicting population dynamics of *Dreissena* in novel lake systems. Our model uses the limnological differences between lakes with constant populations of *Dreissena* and those with variable populations to identify variables that may determine population dynamics. We find that lakes with more constant populations tend to have larger surface areas, lower levels of calcium, and higher levels of phosphate (PO<sub>4</sub>) compared with lakes with more variable populations.

La dreissénie européenne, *Dreissena polymorpha* (Pallas), a récemment été introduite dans les eaux douces de l'Amérique du Nord. Les *Dreissena* des lacs européens présentent une large gamme de dynamiques de population. Dans certains lacs, la taille de la population est passablement constante à long terme tandis que les populations d'autres lacs fluctuent grandement d'une année à l'autre. Les évaluations des effets écologiques et économiques éventuels des *Dreissena* en Amérique du Nord donneront des résultats variables si les populations présentent d'importantes fluctuations annuelles d'abondance. Nous avons élaboré un modèle à variables multiples pour la prévision de la dynamique des populations des *Dreissena* dans de nouveaux lacs. Le modèle fait appel aux différences limnologiques entre les lacs à populations constantes de *Dreissena* et ceux où les populations fluctuent pour la détermination des variables pouvant influencer sur la dynamique des populations. Nous avons trouvé que les lacs à populations plus constantes avaient tendance à présenter une plus grande surface, des teneurs en calcium moins importantes et des teneurs en phosphate (PO<sub>4</sub>) plus élevées que les lacs à populations plus variables.

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Since the turn of the century exotic invaders have greatly influenced the ecological history of many North American lakes, especially the Great Lakes (Christie et al. 1972; Smith and Tibbles 1980). For example, the abundance, growth habit, and population dynamics of lamprey (*Petromyzon marinus*), smelt (*Osmerus mordax*), and alewife (*Alosa pseudoharengus*) have had wide-ranging ecological effects. The most recent major invader, the European zebra mussel, *Dreissena polymorpha* (Pallas), has characteristics of other successful invaders (Hengeveld 1989). It has a high reproductive rate and a growth habit and feeding type that were not previously represented in these newly colonized lakes. In the past we have had to learn about the ecological effects of aquatic invaders over many years as communities responded to invasion and to the subsequent population dynamics of the new species. However, enough is known about *Dreissena's* physiology, life history, and ecology to develop predictive models of its ecological effects based on analyses of published data. We are using this approach in this paper to predict how environmental factors may affect the population dynamics of *Dreissena* in North American lakes.

Populations of *Dreissena* are now found in all Great Lakes basins (New York Zebra Mussel Information Clearinghouse 1990; Griffiths et al. 1991). They were introduced in the mid-1980's, probably through ballast water transport from ships (Hebert et al. 1989). The zebra mussel has also extended its range through most of Europe over the last two centuries (Wes-enbrug-Lund 1939; Stanczykowska 1977). The European experience forewarns of ecological and economic effects on North American freshwater ecosystems caused by *Dreissena* bio-fouling and feeding (Mackie et al. 1989).

Fluctuations in the size of zebra mussel populations can cause ecological consequences throughout a community (Carpenter 1988; Mills and Forney 1988). The life history of top predators can impose a periodicity which affects other system components (Carpenter and Leavitt 1991). Invasion of *Dreissena* may produce similar effects. With their high feeding rates, shoals of these benthic filter feeders can remove large percentages of primary productivity, which may reduce the energy available to pelagic food webs (Stanczykowska 1977; Mackie et al. 1989; Schneider 1991). Fluctuations in populations of *Dreissena*, whether caused by extrinsic factors or density dependence, may affect dynamics of phytoplankton, and thereby indirectly affect herbivorous zooplankton competitors. Fish recruitment and growth may also be affected by *Dreissena* population fluctua-

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tions. Although the effects of *Dreissena* on fish populations have not been thoroughly studied, dense overgrowths of zebra mussels on rocky fish spawning beds may deplete oxygen, causing egg mortality (O'Neill and MacNeill 1989). Small zebra mussels are consumed by many species of fish (Stanczykowska 1977). Interannual fluctuations in *Dreissena* abundance may affect the zooplankton and mussel forage base available to fish, and perhaps fish recruitment. *Dreissena* population dynamics may also be economically important. Biofouling of intake pipes, spawning beds, ships' hulls, and other waterworks may be severe enough to require management responses only during years of high abundance.

Reports of *Dreissena* population fluctuations seem to fall into two categories: (1) invasion dynamics and (2) irregular population increases and decreases (Stanczykowska 1977). A third pattern may be a regular cycle of population abundance, although only one study has demonstrated a weak periodicity (Lewandowski 1982). In Lake Mikołajskie, Poland, two population peaks appear 16 yr apart during a 20-yr period (Lewandowski 1982). A common invasion dynamic is an initial high abundance followed by a crash to low levels (Schlesch 1930; Sebestyén 1938). The boom-and-bust invasion of Lake Constance, Germany, is a well known example of this pattern (Walz 1974). The type of dynamic most often observed is an irregular pattern of population increases and decreases (Stanczykowska et al. 1975b) (Fig. 1).

The degree to which populations irregularly fluctuate varies widely among European lakes (Kajak and Dusoge 1975; Stanczykowska et al. 1975b). In some lakes, *Dreissena* abundance varies by no more than 15% among years over periods of 5-10 yr. In other lakes, populations can decline by two orders of magnitude within a few months and recover to their original level in several years (Stanczykowska et al. 1975b).

Several different mechanisms may underlie these population fluctuations, including resource depletion (e.g. food, oxygen, or attachment surfaces; Stanczykowska 1977) occasional high abundance of predators and parasites, fluctuations in larval recruitment (Lewandowski 1982; MacIsaac et al. 1991), and environmental changes. Dense populations of *Dreissena* show signs of physiological stress (reduced body mass; Stanczykowska 1964). A combination of overcrowding and low mid-winter oxygen levels have caused large die-offs of *Dreissena* (along with fish kills) in Lake Mikołajskie (Stanczykowska 1961; Stanczykowska et al. 1975b).

To allow better forecasts of the potential ecological and economic effects of *Dreissena* in North America, we develop a model for predicting *Dreissena* population fluctuations. We (1) quantify the potential range for interannual variance in population abundance, (2) identify limnological factors that may affect population variability, and (3) construct a model by using empirical, multivariate analysis of published data on the limnological environments of European lakes where different *Dreissena* populations have different dynamics. This is a powerful technique for predicting the behavior of a species during range expansion, based on its known population performance elsewhere (Pimm and Bartell 1980). This technique has already been successfully used to determine limnological factors that affect the distribution and abundance of native North American molluscs (Green 1971, 1972, 1974).

## Methods

Published data on both *Dreissena* abundance and on the biotic and abiotic environments of the European lakes they inhabit

were collected from a search of over 200 papers. These papers were found by searching through various American and European journals from 1900 to 1990, performing computerized library searches for key words (e.g. *Dreissena*) and authors (e.g. Stanczykowska, Lewandowski), and using the reference lists published in other papers on *Dreissena*. Of the more than 250 lakes for which data were collected, only 18 lakes had time-series data extending over a minimum of 10 yr and limnological data that were collected over a time period coincident to the *Dreissena* data for each lake (Appendix A).

Two of the lakes used in our analyses were in Germany (Lakes Stechlin and Nehmitz), one was in the USSR (Kuibyshev Reservoir), and the rest were in Poland's northern lake districts (Table 1). They were all studied between 1935 and 1975. *Dreissena* has occurred throughout these areas since the mid-1800's (Stanczykowska 1977). The lakes were in well-populated areas, and many received effluents from agriculture, industry, and municipal sewage (Kajak and Zdanowski 1983). Two lakes were oligotrophic, five were mesotrophic, and the rest were eutrophic. Water flow was controlled by dams in most of these lakes.

We made no a priori decisions about which lakes or variables should be retained in the dataset, but included data that would form as large a rectangular matrix as possible. The final dataset included 18 lakes and 17 limnological variables (Tables 1, 2). Several of the limnological variables that we used would have natural temporal variation on time scales of hours to years and spatial variation in both horizontal and vertical dimensions. For example, pH can show diurnal variations related to algal activity and can vary with water depth (Wetzel 1983). We dealt with this variation by averaging as many values as we could find for each parameter. Drainage basin area, lake surface area, and lake volume spanned four orders of magnitude within our dataset; therefore, values for these variables were log-transformed ( $\log_{10}$ ) to prevent undue influences of large lakes in our mathematical analyses. All variables were approximately normally distributed (Kolmogorov-Smirnov test of normality,  $p > 0.04$ , ( $\alpha = 0.003$  after adjustment by Bonferroni's inequalities for multiple comparisons; Snedecor and Cochran 1980).

The goal of our multivariate analyses was to distinguish lakes with variable populations of *Dreissena* from those with constant populations. We first categorized our lakes as having variable or constant populations based either on analysis of year-to-year fluctuations in *Dreissena* abundance or on studies of long-term population dynamics conducted by Stanczykowska et al. (1975b). We calculated coefficients of variation ( $V = (\text{standard deviation/mean}) \times 100$ , and is expressed as a percentage; Sokal and Rohlf 1981) of *Dreissena* abundance for each lake in our dataset for which we could find at least three estimates of *Dreissena* abundance (average number of mussels per square metre in the zone of occurrence) within a 15-yr period.  $V$  standardizes variance against the magnitude of the mean, so that lakes with low variance and large populations of *Dreissena* would not appear to be more variable than those with low variance and small populations. The number of observations of *Dreissena* abundance varied from two to seven for each lake. Lakes with values of  $V$  under 50% were considered to have constant populations (four lakes), while those with  $V > 50\%$  have variable populations (eight lakes). A threshold value of 50% divided the lakes into groups that agreed very well with reports of *Dreissena* population variability from authors who have long-term experience with these lake systems. Several lakes were classified as having either constant (three lakes) or

TABLE 1. Summary of *Dreissena* abundance data. "Density" is no. mussels • m<sup>2</sup> in the zone of occurrence averaged over several years (*n*). "Peak" is the peak density during that period, *V* is the coefficient of variation, and "criteria" is the method used to classify each lake as having either constant or variable populations (see text).

| Country                                | Lake       | Density | Peak    | <i>V</i> | <i>n</i> | Criteria                   |
|--|------------|---------|---------|----------|----------|----------------------------|
| <i>Lakes with constant populations</i> |            |         |         |          |          |                            |
| Poland                                 | Beldany    | 23.8    | 25.0    | -        | 2        | Stanczykowska et al. 1975b |
| Poland                                 | Boczne     | 960.0   | 1400.0  | 10.8     | 3        | V                          |
| Poland                                 | Dargin     | 566.7   | 600.0   |          | 2        | Stanczykowska et al. 1975b |
| Poland                                 | Dobskie    | 566.7   | 600.0   | -        | 2        | Stanczykowska et al. 1975b |
| Poland                                 | Niegocin   | 1060.0  | 1300.0  | 30.0     | 3        | V                          |
| Poland                                 | Sniardwy   | 510.0   | 600.0   | 17.8     | 3        | V                          |
| Poland                                 | Szymon     | 1500.0  | 1500.0  | 5.0      | 4        | V                          |
| <i>Lakes with variable populations</i> |            |         |         |          |          |                            |
| Poland                                 | Goldapiwo  | 531.3   | 542.5   |          | 2        | Stanczykowska et al. 1975b |
| Poland                                 | Jagonde    | 570.0   | 1125.0  | 93.8     | 4        | V                          |
| USSR                                   | Kuibyshev  | 1370.9  | 6698.0  | 174.52   | 3        | V                          |
| Poland                                 | Mikohjskie | 759.4   | 2200.0  | 116.6    | 7        | V                          |
| Germany                                | Nehmitz    | 2574.0  | 2574.0  |          | 3        | Other                      |
| Germany                                | Stechlin   | 7541.0  | 14435.0 | 81.7     | 3        | V                          |
| Poland                                 | Stregiel   | 1136.7  | 1700.0  | 71.4     | 3        | V                          |
| Poland                                 | Taltowisko | 1850.0  | 4500.0  | 99.5     | 5        | V                          |
| Poland                                 | Talty      | 1222.5  | 3600.0  | 170.4    | 3        | V                          |
| Poland                                 | Wojnowo    | 562.5   | 1100.0  | -        | 2        | Stanczykowska et al. 1975b |
| Poland                                 | Zabinki    | 1273.3  | 2000.0  | 70.5     | 3        | V                          |

variable (two lakes) populations based on the studies of Stanczykowska et al. (1975b). Estimates of *Dreissena* abundance in several lakes studied in 1962, and again in 1972, showed very large changes in population size in some lakes and nearly constant populations in others. Finally, one lake, Lake Nehmitz, was classified as having a variable population based on observations of *Dreissena* being abundant, rare, and then abundant again in successive years.

We used Discriminant Function Analysis (DFA) (SAS Institute Inc. 1990) on the limnological variables to find a mathematical function that best distinguishes lakes with constant from those with variable populations. We then used this model to predict *Dreissena* population dynamics in novel lake systems. For the DFA, each lake was assigned a prior probability of 1 for belonging to its own group (constant or variable) and 0 for belonging to the other group. A stepwise, parametric DFA identified which variables were most important in contrasting lakes with constant populations from those with fluctuating populations. Due to several missing values for variables, the stepwise DFA was conducted using all lakes except Beldany, Nehmitz, and Stechlin, and all variables except log(basin area), and chlorine. We ran a canonical DFA on the important variables identified by the stepwise DFA in order to create a predictive mathematical model. We tested the error rate of the model with a jackknife cross-validation technique.

## Results

*Dreissena* has a wide range of potential population variability (Table 1; Fig. 1). Populations vary by only 10-30% over time scales of 5-10 yr in about half of the lakes in our dataset, while in the other half, populations can crash by over two orders of magnitude in a few months. These populations can then recover within 4 yr (Stanczykowska et al. 1975b).

Long-term abundance of *Dreissena* did not differ significantly between lakes with constant and variable populations (t-test,  $p > 0.214$ ), despite the large differences in *V* between these two lake types (t-test,  $p < 0.002$ ) (Table 1). Lakes with constant populations did not occur in a different geographic area than those with variable populations. In fact, lakes with different population dynamics were sometimes connected by channels (Stanczykowska 1978).

Despite their proximity, lakes with constant and variable populations differed in their limnological characteristics (Tables 2, 3). DFA was very successful in distinguishing the two lake groupings (Table 4). The variables log(lake surface area), phosphate (PO<sub>4</sub>), and calcium provided the most contrast between the two lake types in the multivariate analyses. Lakes with constant populations had larger surface areas, lower levels of calcium, and higher levels of phosphate than lakes with variable populations. None of the other morphometric, physical, or chemical variables were important in distinguishing the lake types.

We tested the accuracy of the discriminant function at classifying populations as constant or variable by comparing our a priori classification of the lakes with the predictions from the model. The function correctly classified 13 of the 18 original lakes for a 72.2% success rate. Another, more conservative method for estimating success of a DFA model is a cross-validation procedure using a jackknife technique. In this method the discriminant function is recalculated as many times as there are lakes, each time deleting only one lake from the dataset. Each lake is predicted to have either constant or variable populations using the model that was derived without use of that lake. The success rate using cross-validation was also 72.2%. The values of the discriminant function at the centroids of each group were 0.928 and -0.591 for lakes with constant and variable populations, respectively. The discriminant scores of four of the five misclassified lakes ranged from -0.16 to 0.31 and indicated that these lakes did not associate strongly with either lake type.

TABLE 2. Morphometric and physical characteristics of lakes with the two population types. Log(BASIN) is log(drainage basin area (km<sup>2</sup>)), log(AREA) is log(surface area (km<sup>2</sup>)), log(VOL) is log(lake volume (10<sup>6</sup>m<sup>3</sup>)), Z<sub>m</sub> is maximum depth (m), Z is mean depth (m), EPI is depth of the epilimnion (m), TEMP is maximum summer bottom temperature (°C), O<sub>2</sub> is minimum summer bottom oxygen (mg • L<sup>-1</sup>), and SECCHI is depth of Secchi disk visibility (m). MEAN is the average value of each variable for lakes of one population type, so is standard deviation, MIN is the minimum value, and MAX is the maximum value.

| Lake                                   | log (BASIN) | log(AREA) | log(VOL) | Z <sub>m</sub> | Z     | EPI   | TEMP  | O <sub>2</sub> | SECCHI |
|--|-------------|-----------|----------|----------------|-------|-------|-------|----------------|--------|
| <i>Lakes with constant populations</i> |             |           |          |                |       |       |       |                |        |
| Beldany                                | 1.66        | 0.93      | 1.98     | 38.50          | 10.00 | 12.00 | 8.00  | -              | 1.89   |
| Boczne                                 | 1.71        | 0.28      | 1.20     | 15.00          | 8.60  | 10.00 | 16.00 | 0.00           | 3.00   |
| Dargin                                 | 1.50        | 1.40      | 0.83     | 37.30          | 10.60 | 15.00 | 10.00 | 0.00           | 5.00   |
| Dobskie                                | 1.94        | 1.25      | 2.15     | 21.00          | 7.90  | 15.00 | 16.00 | 0.00           | 4.18   |
| Niegocin                               | 1.42        | 1.40      | 2.41     | 40.00          | 9.90  | 12.50 | 11.00 | 0.00           | 2.96   |
| Sniardwy                               | 2.18        | 2.04      | 2.82     | 25.00          | 5.80  | 25.00 | 16.00 | 6.00           | 2.33   |
| Szymon                                 | 1.95        | 0.19      | 0.23     | 2.90           | 1.10  | 2.90  | 18.00 | 7.00           | 1.90   |
| Mean                                   | 1.77        | 1.07      | 1.66     | 25.67          | 7.70  | 13.20 | 13.57 | 2.17           | 3.04   |
|  | 0.271       | 0.660     | 0.930    | 13.903         | 3.331 | 6.633 | 3.823 | 3.371          | 1.173  |
| E N                                    | 1.42        | 0.19      | 0.23     | 2.90           | 1.10  | 2.90  | 8.00  | 0.00           | 1.89   |
| MAX                                    | 2.18        | 2.04      | 2.82     | 40.00          | 10.60 | 25.00 | 18.00 | 7.00           | 5.00   |
| <i>Lakes with variable populations</i> |             |           |          |                |       |       |       |                |        |
| Goldapiwo                              |             | 0.99      | 2.03     | 25.70          | 10.88 | 9.50  | 12.87 | 1.50           | 3.00   |
| Jagonde                                | 1.95        | 0.97      | 1.92     | 34.00          | 8.70  | 6.00  | 8.00  | 0.00           | 1.70   |
| Kuibyshev                              | 6.12        | 3.81      | 4.76     | 40.00          | 8.90  | 11.00 | 7.80  | 8.32           | 3.75   |
| Mokoeajskie                            | 1.05        | 0.66      | 1.75     | 27.80          | 11.00 | 9.00  | 6.40  | 2.20           | 1.72   |
| Nehmitz                                | 0.79        | 0.23      | 1.04     | 18.60          | 6.40  | 5.00  | 5.50  | 0.00           | 6.90   |
| Stechlin                               | 1.09        | 0.63      | 1.99     | 68.00          | 22.80 | 7.00  | 7.00  | 9.50           | 5.99   |
| Stregiel                               |             | 0.61      | 1.18     | 10.00          | 3.70  | 6.50  | 14.50 | 0.00           | 1.53   |
| Taltowisko                             | 1.86        | 0.51      | 1.66     | 36.50          | 14.00 | 12.00 | 6.40  | 3.00           | 4.50   |
| Tańty                                  | 1.73        | 1.07      | 2.20     | 37.50          | 13.60 | 9.00  | 11.00 | 0.50           | 1.62   |
| Wojnowo                                | 1.71        | 0.28      | 1.07     | 16.50          | 6.30  | 16.50 | 16.00 | 0.25           | 1.10   |
| Zabinki                                | -           | -0.39     | 0.60     | 42.50          | 9.86  | 9.00  | 5.87  | 1.65           | 2.40   |
| Mean                                   | 2.04        | 0.85      | 1.84     | 32.46          | 10.56 | 9.14  | 9.21  | 2.45           | 3.11   |
| SD                                     | 1.704       | 1.065     | 1.094    | 15.759         | 5.103 | 3.233 | 3.738 | 3.357          | 1.954  |
| MIN                                    | 0.79        | -0.39     | 0.60     | 10.00          | 3.70  | 5.00  | 5.50  | 0.00           | 1.10   |
| MAX                                    | 6.12        | 3.81      | 4.76     | 68.00          | 22.80 | 16.50 | 16.00 | 9.50           | 6.90   |

## Discussion

Fluctuations in each component of a community potentially affect the dynamics of all other components, but these effects are manifest over a wide range of time scales. The life span of individuals of a species can affect the degree to which the consequences of population fluctuations are either propagated or attenuated through the system. For example, in limnetic systems the dynamics of the dominant herbivore, *Daphnia*, can follow a predator-prey cycle with its phytoplankton food base (McCauley and Murdoch 1987). This pattern is possible because the life cycle of both components is on the order of days to weeks. The pattern is attenuated at higher trophic levels because planktivorous and piscivorous fishes cannot respond numerically on similar time scales (McQueen et al. 1986). On the other hand, in systems where fish predators exert controlling influences on their prey the effects of their population fluctuations may be propagated through the system by cascading interactions (Hurlburt et al. 1971; Carpenter et al. 1985).

Like fish, *Dreissena* is a relatively long-lived consumer that can remove large percentages of the production of its food base. Life span of *Dreissena* (estimated from shell annuli) varies among lakes from 3 to 11 yr, with an average of 3-5 yr (Stanczykowska 1963). In lakes where *Dreissena* is abundant it can remove up to 62% of littoral primary production (Hamburger

et al. 1990), up to 5-1 8% of total lake production (Stanczykowska 1975; Stanczykowska et al. 1975a), and can filter the entire volume of some lakes in a few days (Stanczykowska 1968). If *Dreissena* becomes abundant enough to have similar effects in North American lakes, the consequences of its population dynamics may affect many components of the limnetic community.

In habitats where *Dreissena* populations fluctuate, they may induce variability in several community components. *Dreissena* variability may affect phytoplankton dynamics which may, in turn, result in interannual fluctuations in zooplankton populations. Consumption of phytoplankton by *Dreissena* affects water clarity (Reeders et al. 1989), which indirectly affects the depth and density of macrophyte growth (e.g. Chambers and Kalff 1985; Dale 1986). If *Dreissena* becomes an important food source for fish and waterfowl, populations of these predators may also be affected by *Dreissena* fluctuations. The extent of economic damage caused by *Dreissena* would also vary with population size. Problems with biofouling, clogging of intake pipes, and encrusting of ships' hulls may be most severe during years of population peaks.

Understanding the causal mechanisms of *Dreissena* population dynamics is necessary for proper interpretation of our mathematical models. Spurious correlations and biases are most likely in small datasets. These must be identified before pre-

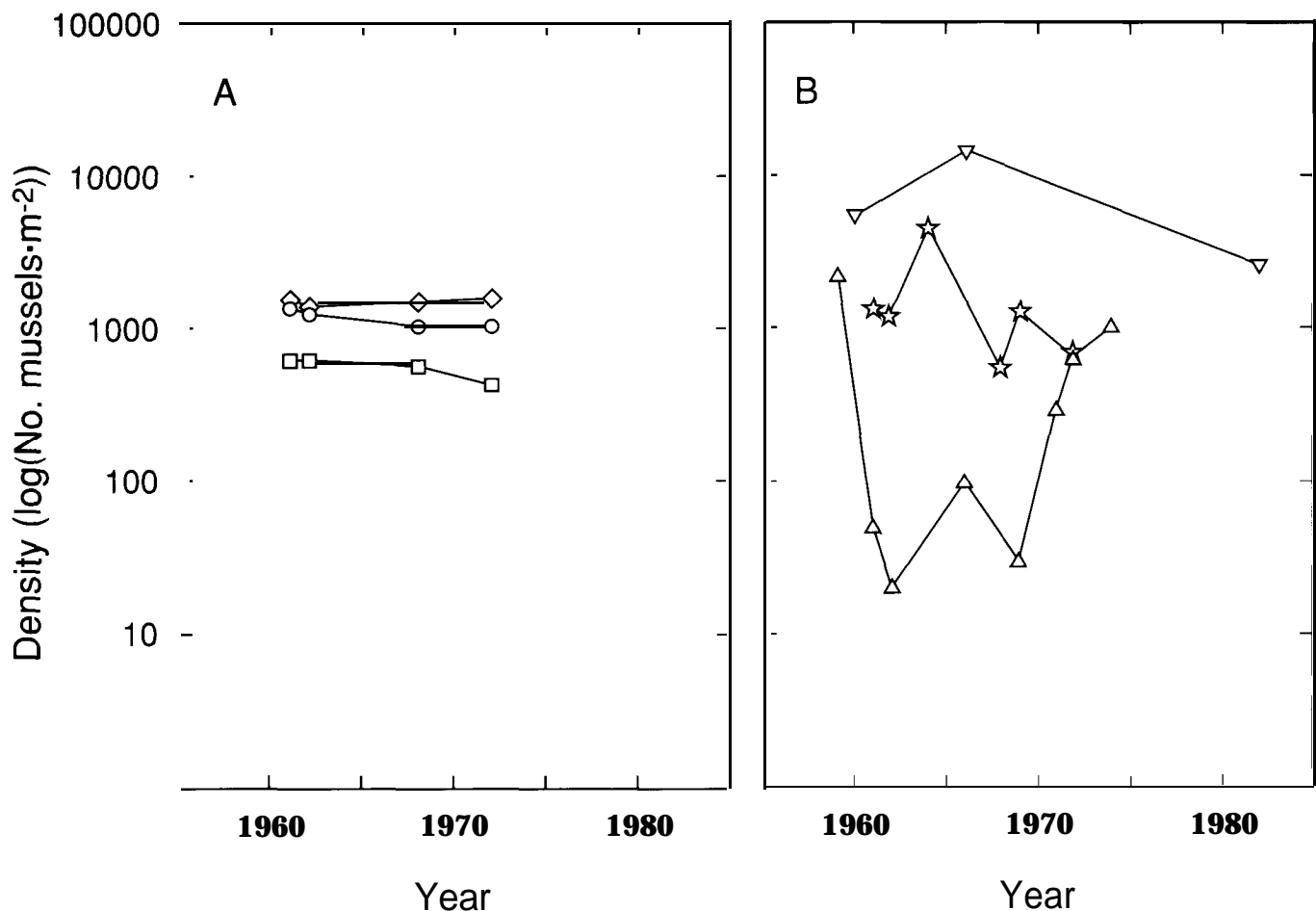


FIG. 1. *Dreissena* population dynamics in different European lakes from 1959 to 1985. Density is expressed as log., (no. mussels  $\cdot$  m<sup>-2</sup>) in the zone of occurrence. (A) Lakes with constant populations of *Dreissena*, (B) lakes with variable populations. Circles are Lake Boczne, squares are Lake Sniardwy, diamonds are Lake Szymon, downwards triangles are Lake Stechlin, upwards triangles are Lake Mikołajskie, and stars are Lake Tańtowisko.

dictions can be confidently made for novel lakes. Our mathematical model should reflect the biological mechanisms that underlie population dynamics.

Population fluctuations may be caused by several different mechanisms. Predators such as fish (e.g. Plizska 1956; Biró 1974) and waterfowl (e.g. Borowiec 1983) can consume substantial proportions of *Dreissena* production. *Dreissena* also has several parasites including *Sphenophyra dreissenae* (Ciliata, Holotricha, Thigmotrichida) (Dobranska 1958). However, at the population level, predators do not appear to be able to exert control over *Dreissena* (Stanczykowska 1990), and the effects of parasites are unknown (Stanczykowska 1977). A large population bottleneck for *Dreissena* appears to be high mortality in veliger and juvenile life stages (Walz 1978; Lewandowski 1982). Therefore, population fluctuations might be caused by interannual variation in factors such as wind mixing and temperature regime that may affect settling mortality and other aspects of larval recruitment variability.

In lakes with many diverse habitats, areas with reductions or extinctions of zebra mussels may be repopulated from elsewhere around the lake (habitat diversity hypothesis). Habitat diversity may be higher in larger lakes, just as it is in larger land masses (MacArthur and Wilson 1967). Therefore, lakes with larger surface areas should have more constant popula-

tions. This expectation is consistent with our model (Tables 2, 4).

Population fluctuations may also be a result of physiological stress caused by overcrowding, together with environmental variability (overcrowding hypothesis). Both the pattern of population fluctuations and physiological studies of mussel populations suggest that overcrowding is a factor in population crashes. *Dreissena* often reaches high abundance in the year prior to a precipitous population crash (Stanczykowska et al. 1975b; Lewandowski 1982). These crowded animals sometimes show signs of physiological stress (Stanczykowska 1977), perhaps as a result of resource limitation caused by their high abundance. They may weigh less for their body length in all size classes than animals grown under uncrowded conditions (Stanczykowska 1964). Environmental stresses such as a summer with reduced food supply or a winter with low oxygen may exacerbate physiological stress inducing population crashes. High abundance of *Dreissena* may have contributed to large winterkills in Lake Mikołajskie in 1959-60 and again in 1976-77.

Lakes that can support dense growths of *Dreissena* are more likely to have fluctuating populations (Stanczykowska et al. 1975b). We find that peak density of *Dreissena* is higher in lakes with fluctuating populations compared with lakes with constant populations (Table 1, t-test,  $p < 0.044$ ). In another

**TABLE 3.** Chemical characteristics of lakes with the two population types. pH is average pH value, and the other variables are concentrations of nutrients and ions expressed as mg • L<sup>-1</sup>. PO<sub>4</sub> is phosphate, NO<sub>3</sub> is nitrate, Ca is calcium ion, Na is sodium, Cl is chlorine, K is potassium, and Fe is total iron. MEAN is the average value of each variable for lakes of one population type, **SD** is standard deviation, MIN is the minimum value, and MAX is the maximum value.

| Lake                                   | pH    | PO <sub>4</sub> N | O <sub>3</sub> | Ca    | Na    | Cl    | K     | Fe    |
|--|-------|-------------------|----------------|-------|-------|-------|-------|-------|
| <b>Lakes with constant populations</b> |       |                   |                |       |       |       |       |       |
| Beldany                                | 7.80  | 0.14              | 0.10           | 41.00 | 4.75  | 9.23  | 2.14  | 0.08  |
| Boczne                                 | 8.15  | 0.16              | 0.05           | 53.50 | 9.40  | 16.68 | 4.35  | 0.13  |
| Dargin                                 | 8.15  | 0.10              | 0.07           | 41.50 | 6.50  | 12.58 | 3.33  | 0.00  |
| Dobskie                                | 8.15  | 0.07              | 0.08           | 40.67 | 6.60  | 12.66 | 3.31  | 0.00  |
| Niegocin                               | 8.15  | 0.18              | 0.14           | 49.40 | 8.94  | 17.09 | 4.32  | 0.13  |
| Sniardwy                               | 8.15  | 0.04              | 0.02           | 34.50 | 6.05  | 10.84 | 2.08  | 0.00  |
| Szymon                                 | 8.15  | 0.16              | 0.05           | 53.50 | 9.40  | 16.68 | 4.35  | 0.13  |
| Mean                                   | 8.10  | 0.12              | 0.07           | 44.87 | 7.38  | 13.68 | 3.41  | 0.07  |
| SD                                     | 0.132 | 0.051             | 0.039          | 7.315 | 1.855 | 3.156 | 0.999 | 0.065 |
| MIN                                    | 7.80  | 0.04              | 0.02           | 34.50 | 4.75  | 9.23  | 2.08  | 0.00  |
| MAX                                    | 8.15  | 0.18              | 0.14           | 53.50 | 9.40  | 17.09 | 4.35  | 0.13  |
| <b>Lakes with variable populations</b> |       |                   |                |       |       |       |       |       |
| Goldapiwo                              | 8.15  | 0.05              | 0.11           | 46.50 | 8.50  | -     | 3.97  | 0.00  |
| Jagonde                                | 8.15  | 0.16              | 0.08           | 50.50 | 9.66  | 14.20 | 4.50  | 0.13  |
| Kuibyshev                              | 7.50  | 0.05              | 1.66           | 76.07 | 16.72 | 34.82 | 16.72 | 0.10  |
| Mikołajskie                            | 8.00  | 0.14              | 0.04           | 43.67 | 6.72  | 11.72 | 3.20  | 0.10  |
| Nehmitz                                | 7.80  | 0.00              | 0.04           | 47.92 | -     | -     | -     | -     |
| Stechlin                               | 7.80  | 0.01              | 0.01           | 50.00 | -     | -     | -     | -     |
| Stregiel                               | 8.00  | 0.05              | 0.11           | 50.17 | 7.55  | 11.00 | 3.90  | 0.01  |
| Taltowisko                             | 8.00  | 0.11              | 0.10           | 49.00 | 6.15  | 15.45 | 4.10  | 0.10  |
| Tańty                                  | 8.00  | 0.11              | 0.11           | 49.00 | 6.15  | 15.45 | 4.10a | 0.10  |
| Wojnowo                                | 8.15  | 0.16              | 0.05           | 53.50 | 9.40  | 16.68 | 4.50  | 0.13  |
| Zabinki                                | 8.38  | 0.01              | 0.43           | 54.00 | 7.05  | -     | 3.13  | 0.00  |
| MEAN                                   | 7.99  | 0.08              | 0.25           | 51.85 | 8.66  | 17.04 | 5.35  | 0.07  |
| SD                                     | 0.233 | 0.061             | 0.483          | 8.539 | 3.292 | 8.105 | 4.292 | 0.054 |
| E N                                    | 7.50  | 0.00              | 0.01           | 43.67 | 6.15  | 11.00 | 3.13  | 0.00  |
| MAX                                    | 8.38  | 0.16              | 1.67           | 76.07 | 16.72 | 34.82 | 16.72 | 0.13  |

**TABLE 4.** Coefficients of limnological variables used by the canonical discriminant function.

| Variable          | Coefficient |
|-------------------|-------------|
| Ca                | -0.115      |
| PO <sub>4</sub>   | 12.783      |
| log(surface area) | 0.666       |
| Constant          | 3.788       |

study, we have found that *Dreissena* density tends to be higher in lakes with high calcium and low phosphate (C. W. Ramcharan, D. K. Padilla, and S. I. Dodson, unpubl. data). In this study, lakes with high calcium and low phosphate are more likely to have fluctuating populations. Together, these models suggest that populations may fluctuate more in lakes that can support high densities of *Dreissena* due, perhaps, to stresses caused by overcrowding.

*Dreissena* populations quickly recover from crashes. Within 1 yr, juveniles can settle in very high abundance on the empty shells left by the crash, and populations can grow by more than three orders of magnitude in 4 yr (compare Stanczykowska 1968 with Stanczykowska et al. 1975b for Lake Tańty). These rapid increases and declines are the characteristic pattern of

lakes with the most variable populations. *Dreissena* populations that are more constant may be unable to overexploit the resources of their lakes, and may live in more constant limnological environments.

Our model is based solely on empirical correlations. It does provide some support for both the habitat diversity and the overcrowding hypotheses. Nevertheless, no explanation of population variability can be eliminated by this analysis. We suggest that experimental work should be used to test among these hypotheses to determine the mechanisms responsible for *Dreissena* population fluctuations.

We expect that *Dreissena* population dynamics will be affected by similar ecological processes in Europe as in North America. The lakes used in model development are fairly typical of temperate zone lakes in terms of morphometry, and physicochemical environments, although degree of cultural eutrophication may be higher in Europe than in North America. Physiological biases in North American *Dreissena* populations caused by evolutionary founder effects are also unlikely. North American populations show a wide genetic diversity and may be the result of either several separate introductions or one very large introduction (Hebert et al. 1989). Our model should, therefore, be directly applicable to most North American lakes.

Predictions for lakes such as the Laurentian Great Lakes may be more problematical because of their size and physical com-

plexity. Morphometric variables for the Great Lakes cover a much wider range of values, and in some cases are orders of magnitude greater than the data that we used for model development. The Great Lakes also have more complex patterns of water mixing and thermal stratification than the smaller lakes that we studied. Predictions from our model should be interpreted in light of the morphological and physical differences between the Polish lake set used for model development and the Great Lakes.

Our model predicts that *Dreissena* populations should be constant in all Great Lakes basins, including Green Bay, Saginaw Bay, Lake St. Clair, and western Lake Erie. The model's prediction is primarily influenced by the very large size of these water bodies. Local populations of *Dreissena* may fluctuate in abundance; however, it is unlikely that all or most colonies will simultaneously decline in the many varied habitats found within each Great Lake.

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## Appendix A

TABLE A. 1. Sources of published data on lake morphometry (M), physical characteristics (P), chemical characteristics (C), and *Dreissena* abundance CD1 that were used in this study. References are grouped into sources of European and North American data.

*Data sources for European lakes*

MP BAJKIEWICZ-GRABOWSKA, E. 1983. Ecological characteristics of lakes in north-eastern Poland versus their trophic gradient. II. Lake catchment areas - physico-geophysical environment. Description of the region and 43 lakes. Ekol. Pol. 31: 257-286.

MPC BERNATOWICZ, S., AND J. ZACHWIEJA. 1966. Types of littoral found in the lakes of the Masurian and Suwalki lake-lands. Ekol. Pol. Ser. A. 28: 519-545.

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D DUSOGE, K. 1966. Composition and interrelations between macrofauna living on stones in the littoral of Mikojhskie Lake. Ekol. Pol. Ser. A 14: 755-762.

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MP GIEYSZTOR, M. 1959. On the thermal conditions of the littoral zone of lakes. Pol. Arch. Hydrobiol. 7: 171-193.

MPC GIEYSZTOR, M., AND Z. ODECHOWSKA. 1985. Observations on the thermal and chemical properties of Mazurian Lakes in the Gizičko region. Pol. Arch. Hydrobiol. 4: 123-152.

PC HEITMANN, M.-L. 1967. Die Physikalisch-chemischen Verhältnisse im Stechlin und Nehmitz-See. Limnologica 5: 307-329.

MPC JASINSKI, A. W. 1989. Anthropogenic impacts on Sniardwy Lake (Poland). J. Great Lakes Res. 15: 510-518.

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MPD MOTHEs, G. 1964. Die Mollusken des Stechlinsees. Limnologica 2: 41-421.

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MPC PATALAS, K. 1960. Stosunki termiczne i tlenowe oraz przyczynowość wody w 44 jeziorach okolic Węgorzewa (Thermal and oxygen conditions and transparency of water in 44 lakes of Węgorzewo District). Roczn. Nauk Roln. Ser. B Zootech. 77: 105-222.

MP PATALAS, K. 1960. Charakterystyka składu chemicznego wody 48 jezior okolic Węgorzewa (Characteristics of chemical composition of water in 48 lakes of Węgorzewo District). Roczn. Nauk Roln. Ser. B Zootech. 77: 243-297.

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