

Models to Predict Potential Occurrence and Density of the Zebra Mussel, *Dreissena polymorpha*

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Ramcharan, C. W., D. K. Padilla, and S. I. Dodson. 1992. Models to predict potential occurrence and density of the zebra mussel, *Dreissena polymorpha*. Can. J. Fish. Aquat. Sci. 49: 2611-2620.

Limnological features of different lakes may limit the density of, or even completely restrict, populations of the European zebra mussel, *Dreissena polymorpha*. We developed statistical models to predict the occurrence (presence or absence) and density (number per square metre) of *Dreissena* in lakes, based on multivariate correlations between the density of *Dreissena* populations and the limnological characteristics of the lakes they inhabit. We found that both occurrence and average density of *Dreissena* populations were highly correlated with water chemistry. *Dreissena* was not found in lakes with average pH values below 7.3 and concentrations of calcium ion below 28.3 mg·L⁻¹. Above these thresholds, *Dreissena* density was negatively related to concentration of the algal nutrients PO₄ and NO₃.

Certaines caractéristiques limnologiques de différents lacs peuvent limiter la densité, ou même anéantir, des populations de dreissena polymorphe (ou moule zébrée), *Dreissena polymorpha*. En vue de prédire l'occurrence (présence ou absence) et la densité (nombre par mètre carré) de *Dreissena* dans les lacs, nous avons élaboré des modèles statistiques à partir de corrélations à plusieurs variables entre la densité des populations de *Dreissena* et les caractéristiques limnologiques des lacs qu'elles fréquentent. Nous avons observé un degré de corrélation élevé entre les deux facteurs occurrence et densité moyenne et l'hydrochimie. *Dreissena* était absente des lacs dont le pH moyen est inférieur à 7,3 et la concentration en ions calcium inférieure à 28,3 mg·L⁻¹. Au-dessus de ces valeurs seuils, la densité de *Dreissena* était inversement proportionnelle à la concentration des PO₄ et NO₃ contenus dans les éléments nutritifs d'origine algale.

Received November 29, 1991

Accepted June 16, 1992

(JB310)

Reçu le 29 novembre 1991

Accepté le 16 juin 1992

The European zebra mussel, *Dreissena polymorpha* (Palas), has recently appeared in North America in the Laurentian Great Lakes (Hebert et al. 1989). This mussel can cause changes in freshwater communities and economic damage to man-made structures because of its feeding characteristics, sessile growth habit, and high fecundity (Stanczykowska 1977; Mackie et al. 1989; Griffiths et al. 1991). (Because an as yet unnamed, invasive, sibling dreissenid species has been identified (May and Marsden 1992), we will use *Dreissena* in the following study in the broad sense to represent both *D. polymorpha* and the sibling species.)

Useful forecasts of the potential ecological and economic impacts of invading *Dreissena* depend on estimates of both its occurrence (presence or absence) and density (mussels per square metre). Unfortunately, no method currently exists to predict occurrence and density of *Dreissena* in local habitats (Stanczykowska 1977). For example, extrapolation of the success of *Dreissena* in western Lake Erie (our primary North American experience with zebra mussels) to other water bodies can provide only a worst-case scenario. The colonization of western Lake Erie has been unusually successful compared with most European populations. We present statistical models to predict occurrence and density of *Dreissena* in lake habitats. Our models are developed from statistical correlations between *Dreissena* density in European lakes and limnological features of those lakes.

The success of *Dreissena* at colonizing several Great Lakes habitats and the rapidity with which it has spread across Europe do not necessarily indicate that this mussel will invade all North American freshwaters. The European experience shows that *Dreissena* is not found in all water bodies and that among those lakes in which *Dreissena* does occur, population densities can vary by several orders of magnitude. Since *Dreissena* is currently dispersed primarily by humans, some of its zoogeography can be explained by human activity patterns. For example, lakes along shipping channels were the first to be colonized, while *Dreissena* has only recently appeared in headwater lakes in the Alps (Siessegger 1969; Löffler 1979). Dispersal patterns alone, however, cannot fully explain patterns of occurrence. *Dreissena* is sometimes absent from lakes within a district that comprises many connected lakes (e.g. Lundbeck 1926). Population density can vary greatly among those lakes in a district that are colonized.

Low concentrations of dissolved calcium ion are known to affect zoogeographic distributions of several species of freshwater molluscs (e.g. Boycott 1936; Ökland 1983), since calcium is necessary for shell growth and other physiological processes. Stanczykowska (1964) found a weak relationship between calcium concentration and *Dreissena* density in 36 lakes. Sprung (1987) found in laboratory experiments that both fertilization success in eggs and survivorship of *Dreissena* embryos were enhanced by calcium concentrations above 47 mg · L⁻¹ and pH values of about 8.5.

Stanczykowska et al. (1983) and Stanczykowska (1984) found a tendency for *Dreissena* to be absent from highly

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eutrophic lakes that have high levels of phosphorus. Recently, Strayer (1991) found that the zebra mussel in Europe can tolerate such a wide range of climatic temperatures that its predicted zoogeographic distribution in North America may range from northern Canada to near the USA-Mexico border. Strayer (1991) also reported a tendency for European lakes in which *Dreissena* occurs to have higher concentrations of total ions (i.e. harder water).

Dreissena population density may also be affected by a variety of ecological factors. In some studies, fish (Plizska 1956; Biró 1974) and waterfowl (e.g. Borowiec 1983) consumed large amounts of zebra mussels, while in other studies, predation was negligible (Stanczykowska 1990). Negative effects of predation on *Dreissena* populations have yet to be demonstrated. Low food levels would rarely limit *Dreissena* populations in most freshwater environments (Walz 1978a, 1978b; Sprung and Rose 1988).

We searched for statistical relationships between density of *Dreissena* in different lakes and various environmental characteristics of those lakes. We built on previous studies (e.g. Stanczykowska 1964; Strayer 1991) by compiling data for a wide range of lake types and a broad spectrum of environmental variables. In addition, we provide statistical analyses that incorporate quantitative, predictive models.

Methods

Data on European *Dreissena* density and biotic and abiotic environments were collected from a search through over 350 papers published from 1900 to 1990. The literature search produced data for 278 lakes. We plan to make a complete set of our tabular data available in conjunction with a later paper through the Canada Institute for Scientific and Technical Information (Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Ont. KIA 0S2, Canada).

Our data set is restricted to European lakes inhabited by zebra mussels (*Dreissena* lakes) or lakes that in our judgement have received potential colonists but lack the mussel. We excluded from the data set any lakes to which *Dreissena* had probably not been introduced (e.g. high Alpine lakes and northern Scandinavian lakes). By excluding lakes that have probably not been colonized, we focused on factors that may determine the survival and growth of *Dreissena* populations in different lakes, exclusive of dispersal patterns that are already known to be strongly influenced by human activity (Stanczykowska 1977). Many lakes without *Dreissena* occurred in lake districts where they were in close proximity to other lakes that did support *Dreissena* (e.g. Lundbeck 1926; Schermer 1931, 1932; Dunn 1954). *Dreissena* also had a high probability of being introduced to lakes of the English Lake District and Scottish Highlands (which all lack *Dreissena*), as these lakes have been heavily used for recreational and commercial purposes; many are connected by locks and shipping canals to waterways inhabited by *Dreissena* (Kerney and Morton 1970; Macan 1970, 1984; Kemey 1974). Heavy boat traffic was the probable cause of the successful invasion of several species of molluscs and aquatic macrophytes into these highland lakes within this century (Macan 1970). Finally, a few lakes without *Dreissena* were located on river systems containing *Dreissena*. For example, although the Goczalkowice Dam Reservoir in Poland lacked *Dreissena*, it received veligers and adults from the Volga River (Krzyzanek et al. 1986).

We also excluded from the data set any lakes to which *Dreissena* had been introduced within the last 50 yr. *Dreissena* den-

sity may fluctuate early in an invasion, and population levels may differ from long-term, equilibrium density (Schlesch 1930; Ponyi et al. 1974; Walz 1974). All of the lakes in our data set occur in areas that had either been colonized by *Dreissena* or exposed to *Dreissena* introductions for at least 50 yr (Stanczykowska 1977).

Dreissena population dynamics show two interesting patterns (Stanczykowska et al. 1975; Lewandowski 1982; Ramcharan et al. 1992). First, *Dreissena* densities vary considerably among different lakes. Second, in more than half the lakes with *Dreissena*, mussel density is surprisingly constant from year to year (Stanczykowska et al. 1975; Ramcharan et al. 1992).

We made an effort to collect all published *Dreissena* data for each lake to determine the average density of *Dreissena* in the zone of occurrence. *Dreissena* density often varied among different habitats within a lake and from year to year. We dealt with variability among habitats by averaging as many density estimates as we could find. In some cases, we found only one density estimate for a lake, but these estimates were averaged values of samples that were taken from a range of depths and habitats within each lake. Where sites in a lake were sampled at a range of depths, we defined the zone of occurrence as extending from the shallowest to the deepest depths at which *Dreissena* was found and averaged these values to provide a density estimate. Estimates of density never included mussels smaller than 5 mm. Year-to-year fluctuations in density were also dealt with by averaging all the among-year density estimates that we could find for each lake.

For each lake, we searched the limnological literature for data on morphometry, physical and chemical characteristics, and algal productivity that were collected over the same period as the *Dreissena* data. Morphological variables included lake area, volume, depth, length, width, flushing rate, littoral zone area, and drainage basin area. Physical characteristics included maximum and minimum temperature and oxygen measured at the surface and near bottom, in summer and winter, epilimnion depths, and Secchi transparency. Chemical variables constituted most of the data set and comprised several different measures of phosphorus (total [P], total epilimnetic [P], spring turnover [P], [PO₄], nitrogen (total [N], [NO₂], [NO₃], [NH₃], [NH₄], and water hardness (pH, alkalinity, [HCO₃], [CaCO₃], as well as concentrations of Cl⁻, Mg²⁺, Ca²⁺, K⁺, and Na⁺ (all ion concentrations in milligrams per litre). Measures of phytoplankton were average summer total biomass and algal productivity.

Several limnological variables had natural temporal variation on time scales of hours to years and spatial variation in horizontal and vertical dimensions. We dealt with this variation by averaging all values for each variable. Drainage basin area, lake surface area, and lake volume spanned five orders of magnitude; log₁₀-transformed values for these variables reduced undue influences of large lakes in our statistical analyses.

Values for many of the above limnological variables were lacking for some of the 278 lakes of our original data set. To prepare the final data sets, lakes were eliminated if we could obtain values for less than 50% of the variables. We then prepared two different final data sets by eliminating variables that had missing values and lacked any correlations with either occurrence of *Dreissena* (for the presence-absence data) or density (for the density data). The final data (Tables 1-3) included lakes located in England, Scotland, France, The Netherlands, Denmark, Germany, Switzerland, Austria, Poland,

Hungary, Yugoslavia, Italy, the Commonwealth of Independent States (CIS, formerly the USSR), and Sweden.

Data on water chemistry for different basins of the Laurentian Great Lakes were collected from the literature and averaged using the same techniques as for the European data. In all Great Lakes cases, several values for each variable were averaged to provide a representative estimate for each basin.

We developed three different statistical models: one to predict *Dreissena* occurrence and two others to predict density in the zone of occurrence. All statistical analyses were performed with either SAS (version 6.06.01, SAS Institute), Systat (version 5.0, Systat Inc.), or SPSS-PC + (version 2.0, SPSS Inc.).

For the occurrence model, we used discriminant function analysis (DFA) on limnological variables to find a statistical function that best distinguished lakes with and without *Dreissena*. We first used a stepwise, parametric DFA to identify variables that were most important in distinguishing the two lake types. This DFA was run on eight lakes lacking *Dreissena* and 16 lakes with *Dreissena* for which we had values for surface area, volume, maximum depth, mean depth, maximum summer surface temperature, minimum summer bottom oxygen, Secchi depth, pH, [Ca], [PO₄], and [NO₃]. The variables pH and [Ca] were identified as most important in separating lakes with and without *Dreissena*. The final DFA model was run on 18 lakes without *Dreissena* and 58 lakes with *Dreissena*. These 76 lakes had records of pH and [Ca]. Error rate of the occurrence model was evaluated by jackknife cross-validation. With this technique the discriminant function is recalculated for each lake, each time deleting only that lake from the data set. The deleted lake is predicted to either have *Dreissena* or not using the model that was developed without use of that lake.

We developed two different models to predict *Dreissena* density. The first was a DFA model, similar to the occurrence model, except that we divided *Dreissena* abundance into three categories: absent, low density, and high density. Lakes with less than 3000 mussels • m⁻² were classified as low density, while those with greater density were classified as high density. The threshold between these two categories (3000 mussels • m⁻²) appeared to represent a natural break in the density frequency distribution (Fig. 1A). This DFA model was also evaluated by jackknife cross-validation.

The second model to predict density was developed by multiple regression using only data for lakes that had *Dreissena*. We first studied the relationships between *Dreissena* density and various water chemistry variables using several different univariate models. We developed the final density model with the variables pH, [PO₄], and [NO₃].

Predictions for the Great Lakes were prepared by using values of pH, [Ca], [PO₄], and [NO₃] for the open waters of different Great Lakes basins in our three final models. We limited our predictions to the Great Lakes for two reasons: (1) these lakes are the areas of immediate concern in terms of the invasion and (2) since *Dreissena* has already had the opportunity to colonize all Great Lakes basins, its patterns of occurrence are a test of our occurrence model.

Results

Latitudinal range was similar for lakes with and without *Dreissena*: lakes with *Dreissena* extended from Sweden to the southern CIS, and lakes potentially colonized by *Dreissena* (because of proximity or watershed) that lacked the mussel extended from Scotland to Yugoslavia.

Dreissena density varied considerably among lakes (Fig. 1A). Most of the limnological variables (Tables 1-3)

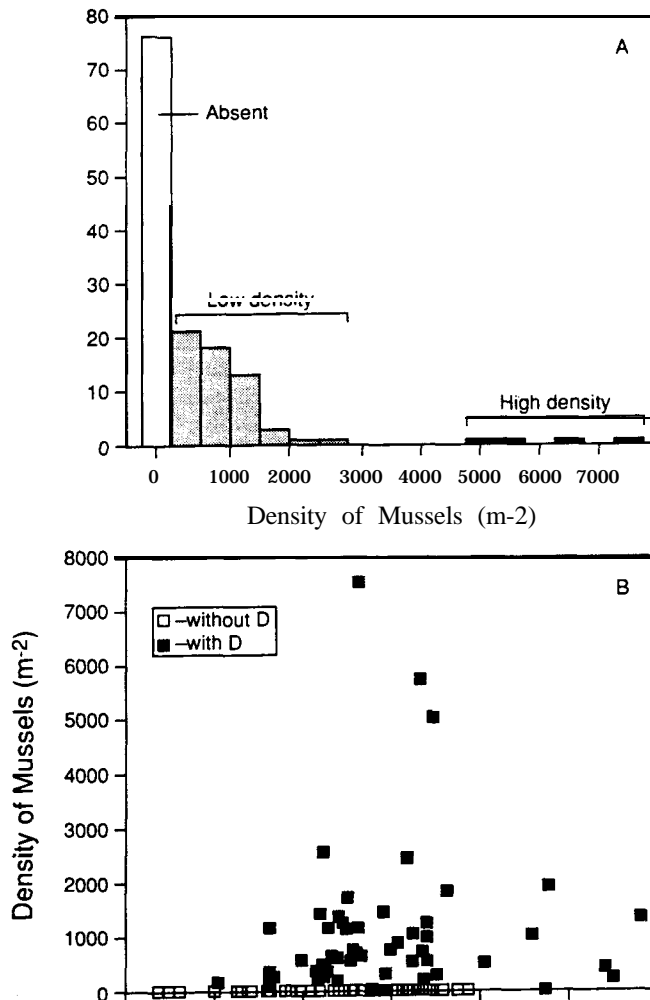


FIG.1.(A) Density-frequency distribution of *Dreissena* from European lakes used in our data set. The open bar indicates lakes from which *Dreissena* were absent. (B) Relationship between lake surface area (log₁₀ scale) and *Dreissena* density.

were unrelated to density of *Dreissena* and were unimportant in our predictive models. Lakes without *Dreissena* had a tendency towards smaller surface area than lakes with *Dreissena* (Fig. 1B; Table 1). Other morphological and physical variables, such as lake volume, maximum depth, mean depth, temperature, Secchi transparency, and oxygen, appear unrelated to *Dreissena* density; the stepwise DFA found that lakes with *Dreissena* did not differ morphometrically from those without.

The three final models are summarized in Table 4. The only variables necessary for predicting *Dreissena* occurrence and density in the DFA models were [Ca], pH, [PO₄], and [NO₃] (Tables 2,3; Fig. 2). Frequency distributions of these four variables did not differ significantly from normal (Kolmogorov-Smirnov test of normality, $p > 0.004$, $\alpha = 0.03$ after adjustment by Bonferroni's inequalities for multiple comparisons; Snedecor and Cochran 1980). The occurrence model (No. 1 in Table 4) used pH and [Ca] to distinguish lakes with *Dreissena* from those without, with 92.7% accuracy (cross-validation error rate). In our data set, no lakes with *Dreissena* had pH values below 7.3 or [Ca] below 28.3 mg • L⁻² (Fig. 2A, 2B).

In the DFA model that predicts density (model 2 in Table 4; Fig. 3), the variables pH and [Ca] were important for distin-

TABLE I. Morphometric characteristics and *Dreissena* abundance of lake groups used in the DFA. Density is *Dreissena* abundance, length is longest dimension. SE is standard error, and *n* is sample size.

	Density (no.m-2)	(Drainage) basin area (log(km2))	Lake surface area (log(km2))	Lake volume (log(106 m2))	Maximum depth (m)	Mean depth (m)	Epilimnion depth (m)	Length (km)	Max. width (km)
Presence-absence model									
<i>Dreissena</i> absent									
Mean	0.00	2.74	0.384	2.223	43.018	15.243	4.896	23.490	1.023
SE	0.000	0.187	0.341	0.726	14.703	5.288	0.610	6.552	0.234
Min.	0.00	2.23	-1.620	-0.854	2.900	1.500	2.900	0.230	0.150
Max.	0.00	3.25	1.852	3.872	189.90	37.000	7.000	41.000	1.950
<i>n</i>	18	5	14	7	15	7	8	7	7
<i>Dreissena</i> present									
Mean	813.53	2.583	1.21	2.26	43.40	15.79	10.687	92.48	8.772
	185.363	0.240	0.150	0.161	7.262	3.746	1.170	30.405	2.022
Min	22.00	0.79	-1.10	0.23	2.00	1.00	2.00	1.50	0.75
Max.	7541.01	6.12	3.81	4.76	286.00	145.20	25.00	546.00	56.00
<i>n</i>	58	35	55	50	56	50	28	30	30
Abundance model									
<i>Dreissena</i> absent									
Mean	0.00	2.70	1.13	2.60	74.19	12.78	3.27	25.56	1.012
	-	0.236	0.391	0.725	22.353	5.392	-	7.328	0.184
Min	0.00	2.23	-0.40	-0.23	3.27	1.50	3.27	1.00	0.55
Max.	0.00	3.25	1.75	3.87	132.00	32.00	3.27	41.00	1.45
<i>n</i>	5	4	5	5	5	5	1	5	5
Low abundance									
Mean	878.36	2.35	1.31	2.32	47.90	18.53	12.49	101.06	9.26
	103.601	0.265	0.210	0.243	12.916	6.291	1.483	47.816	1.940
Min.	2.00	1.05	-0.39	0.23	2.00	1.10	2.00	4.53	1.18
Max.	1979.29	6.12	3.81	4.76	286.00	145.20	25.00	546.00	27.000
<i>n</i>	27	24	27	26	27	26	19	14	14
High abundance									
Mean	3492.56	2.701	1.76	2.80	45.25	11.03	5.67	139.10	16.48
	1281.214	1.027	0.565	0.620	10.065	3.425	0.667	86.819	10.190
Min	3.00	0.79	0.23	1.04	18.60	5.50	5.00	3.50	0.80
Max.	7541.01	4.75	3.66	4.41	73.00	22.80	7.00	430.00	56.00
<i>n</i>	6	4	6	5	6	5	3	5	5

guishing lakes without *Dreissena* from those with low density, while $\ln([\text{PO}_4])$ and $\ln([\text{NO}_3])$ were used to discriminate between lakes with low density and those with high density (Table 5). The overall success rate of this model was 76.3% (Table 6). The model correctly classified 80.0% of the lakes without *Dreissena*, 74.1% of the low-density lakes, and 83.3% of the high-density lakes.

The regression-based density models used the variables pH, $[\text{PO}_4]$, and $[\text{NO}_3]$ to predict *Dreissena* density (Table 7). pH values above the threshold of about 7.3 were positively related to *Dreissena* density (Fig. 2B). $\ln([\text{PO}_4])$ and $\ln([\text{NO}_3])$ were negatively related to *Dreissena* density (Fig. 2C, 2D) and were also strongly correlated with each other. Therefore, only $\ln([\text{PO}_4])$ (the stronger predictor) and pH were used in the final regression model (Table 7, equation D; model 3 in Table 4).

Both the occurrence and density DFA models predicted that *Dreissena* will be present in all Great Lakes basins including Green Bay, except for Lake Superior. Except for Lake Huron, all of the Great Lakes had values of the discriminant function that strongly categorized them as lakes with or without *Dreissena*. The intermediate value for Lake Huron suggested that this lake cannot be confidently classified. The density DFA model predicts that *Dreissena* will form dense populations in western Lake Erie and Lake Ontario, while all other basins (except Superior) will have low-density populations. The regression-based density model predicted densities of 1200 and

3200 mussels $\cdot \text{m}^{-2}$ for Lake St. Clair and western Lake Erie, respectively.

Discussion

Human activity has strongly influenced zebra mussel distribution. Pleistocene deposits show that *Dreissena* was once widely distributed throughout Europe (Stanczykowska 1977) and Britain (Tate 1866). During the last glaciation, this mussel was restricted to areas around the Caspian and Aral seas, and the lower Volga river, where it was first discovered and described by Pallas (1771) (*Mytilus polymorphus*, Tate 1866). It is possible that *Dreissena* would have again extended its European range through natural colonization. However, this range expansion occurred within only 200 yr due to extensive ship traffic and connection of drainage basins by construction of shipping canals (Schlesch 1930). Most recently, the accidental introduction of *Dreissena* into the Laurentian Great Lakes (Hebert et al. 1989) will now allow this bivalve to colonize the freshwaters of North, Central, and South America.

Thus far, *Dreissena* has been very successful at colonizing North American lakes. Within 4 yr of the initial discovery in Lake St. Clair, colonies have appeared in all the Great Lakes, adjacent smaller lakes, and the Mississippi and Hudson rivers (Sea Grant 1992). Recent population densities in western Lake Erie are among the highest ever reported (3.0×10^4 mus-

TABLE 2. Physical characteristics of lake groups used in the DFA. Temperatures and oxygen were measured at maximum depth. SE is standard error and *n* is sample size.

	Max. summer bottom temp. (°C)	Max. summer surface temp. (°C)	Min. summer bottom oxygen (mg • L ⁻¹)	Secchi disc transparency (m)	Average pH
Presence-absence model					
<i>Dreissena</i> absent					
Mean	9.38	20.33	6.25	5.38	7.16
	2.988	0.882	2.400	1.079	0.184
Min.	4.00	19.00	2.12	1.72	5.25
Max.	17.93	22.00	10.43	11.00	8.25
<i>n</i>	4	3	3	8	18
<i>Dreissena</i> present					
Mean	10.56	20.31	5.12	3.64	8.08
	0.961	0.319	0.664	0.457	0.051
Min.	4.00	16.00	0.00	0.40	7.28
Max.	21.00	23.00	11.27	16.20	9.00
<i>n</i>	23	26	35	41	58
Abundance model					
<i>Dreissena</i> absent					
Mean	17.93	19.00	10.43	4.71	6.81
	-	-	-	1.132	0.250
Min.	17.93	19.00	10.43	1.72	6.14
Max.	17.93	19.00	10.43	7.98	7.68
<i>n</i>	1	1	1	5	5
Low abundance					
Mean	10.49	20.87	3.98	3.48	8.037
SE	1.058	0.216	0.802	0.618	0.052
Min.	4.50	19.00	0.00	0.73	7.34
Max.	16.00	22.50	11.27	16.20	8.54
<i>n</i>	15	18	23	25	27
High abundance					
Mean	7.86	20.09	6.26	4.14	8.04
SE	1.663	1.464	2.130	1.043	0.194
Min.	5.50	18.37	0.00	1.21	7.53
Max.	11.07	23.00	9.50	6.90	8.65
<i>n</i>	3	3	4	5	6

sels • m⁻², Griffiths et al. 1991); density in Lake St. Clair is up to 4.5 x 10² mussels • m⁻² (Hebert et al. 1989), while populations recently established in the other Great Lakes are at lower densities. Around Lake Erie, communities are already experiencing expensive blockages of water intakes, fouling of turbines, accumulations of shells of dead *Dreissena* on beaches, and overgrowth of fish spawning beds (Griffiths et al. 1989, 1991).

The European experience shows that *Dreissena* density can vary by several orders of magnitude among different lakes and that *Dreissena* is entirely absent from many lakes to which it has very likely been introduced. For example, several of Germany's Holstein lakes did not have *Dreissena*, while the Grosser Plöner See, in the same district, had peak densities of 1.34 x 10⁴ mussels • m⁻² (Lundbeck 1926). Among Polish lakes that had *Dreissena*, densities varied from 23 mussels • m⁻² in Lake Beldany to 7000 mussels • m⁻² in Lake Beloslawskie.

The economic and ecological impacts of *Dreissena* would only be evident in lakes that can support this mussel and would be worse in lakes with higher population densities. Therefore, useful predictions of the potential impact of *Dreissena* rely on accurate estimates of its potential density in different water bodies.

Occurrence Model

Most attempts to develop predictive models of either *Dreissena* occurrence or density have focused on limnological variables relating to water hardness. Both high calcium levels and high pH are necessary for shell production in many species of shell-bearing molluscs. For example, the zoogeographic distribution of snails in Norwegian lakes is strongly affected by water hardness (Okland 1983). Zoogeography of unionid clams in North American lakes is also affected by calcium levels (Green 1971, 1972). Stanczykowska (1964) found no relationship between calcium level and *Dreissena* density among the lakes she studied. Our study indicated that calcium acts as a threshold variable that affects *Dreissena* density only when it is in limiting supply. *Dreissena* density varied greatly among lakes, with levels of calcium above the threshold value of 28.3 mg • L⁻¹ (Fig. 2A). All of the lakes studied by Stanczykowska (1964) had levels of calcium well above this threshold. Stanczykowska (1965) also found that density was unrelated to Secchi disk transparency and that *Dreissena* tended to be absent from small ponds. Strayer (1991) has recently found that *Dreissena* can tolerate a very wide range of temperatures.

In laboratory experiments, Sprung (1987) found that the timing and success of fertilization, as well as development of

TABLE 3. Chemical characteristics of lake groups used in the DFA. All values are reported in mg·L⁻¹; SE is standard error and *n* is sample size.

	Ca ²⁺	Mg ²⁺	Cl	PO ₄ ³⁻	Total P	HCO ₃	NO ₃
Presence-absence model							
<i>Dreissena</i> absent							
Mean	20.31	2.82	11.25	0.01	—	—	0.02
SE	4.299	0.950	1.053	0.002	—	—	0.003
Min.	0.98	0.75	6.52	0.00	—	—	0.01
Max.	60.00	12.50	16.00	0.01	—	—	0.03
<i>n</i>	18	12	12	6	0	0	6
<i>Dreissena</i> present							
Mean	48.51	13.49	21.70	0.17	0.37	139.20	0.54
SE	1.801	2.644	3.360	0.061	0.245	10.103	0.202
Min.	28.33	0.70	0.13	0.00	0.01	27.33	0.01
Max.	85.84	59.22	170.00	2.15	6.23	284.00	7.80
<i>n</i>	58	30	51	43	25	31	41
Abundance model							
<i>Dreissena</i> absent							
Mean	7.65	3.19	8.54	0.01	—	—	0.02
SE	5.628	2.329	0.577	0.002	—	—	0.004
Min.	0.98	0.75	7.36	0.00	-	-	0.01
Max.	30.07	12.50	10.60	0.01	-	-	0.03
<i>n</i>	5	5	5	5	0	0	5
Low abundance							
Mean	49.09	19.69	14.14	0.09	0.14	158.97	0.29
SE	2.533	6.125	1.231	0.013	0.016	10.944	0.102
Min.	29.27	0.70	0.13	0.00	0.04	56.08	0.01
Max.	85.83	41.14	34.82	0.22	0.22	284.00	2.14
<i>n</i>	27	6	25	27	19	21	27
High abundance							
Mean	43.25	10.83	13.42	0.03	0.12	87.68	0.31
SE	4.343	4.446	9.647	0.019	0.102	24.330	0.171
Min.	28.33	2.50	1.40	0.00	0.01	58.56	0.01
Max.	52.73	22.68	32.50	0.12	0.22	136.00	0.92
<i>n</i>	6	4	3	6	2	3	6

TABLE 4. Three final models developed to predict zebra mussel occurrence or density. Ion concentrations are in mg • L⁻¹.

Final model	Prediction	Equation
1	Occurrence	A = 1.246pH + 0.045[Ca] - 11.696 Mussels present if A > -0.638
2	Density	DI = 2.773pH + 0.040[Ca] - 0.016(ln[PO ₄]) + 0.383(ln[NO ₃]) - 22.658 D2 = -0.342pH + 0.007[Ca] + 0.789(ln[PO ₄]) + 0.490(ln[NO ₃]) + 5.145 Use the scores of DI (which is the value of discriminant function 1) and D2 (value of discriminant Function 2) with Fig. 3 to make density category predictions
3	Density	Number·m⁻² = 2469pH - 88959e^{- PO₄ } - 8773}

embryos and young larvae. were strongly affected by levels of calcium and pH. Survivorship of *Dreissena* embryos was positively related to calcium concentration and also reached a peak at pH values around 8.4. Larval mortality was almost 100% at pH values below 7.3. We found that pH 7.3 is the lower limit for occurrence of *Dreissena*. Zebra mussels may be restricted from softwater lakes because of high larval mortality. Recently, Strayer (1991) also suggested that lakes with *Dreissena* tend to have higher levels of total ions.

Our study shows clearly that *Dreissena* is restricted from

lakes that have low levels of pH and calcium (Fig. 2A, 2B). The DFA uses only these two variables to correctly predict presence or absence of *Dreissena* with 92.7% accuracy. Other factors such as lack of suitable substrate may prevent *Dreissena* from colonizing those lakes that have pH values above 7.3 and calcium levels above 28.3 mg • L⁻¹. For example, several lakes without *Dreissena* and with high pH and calcium are Polish and Soviet reservoirs that were formed from flooded farmland. When flooded, the soil became a flocculent ooze (Pieczynska 1976; Mordukhai-Boltovskoi 1979) that cannot provide firm

TABLE 5. Coefficients and group centroids of the models that were developed by DFA. For the abundance model, function 1 primarily contrasts lakes with *Dreissena* from those with low density, while function 2 contrasts lakes with low density from those with high density.

Variable		Coefficient function 1	Coefficient function 2
Presence-absence model	pH	1.246	
	Ca	0.045	
	Constant	-11.695	
	Centroid of "absent"	-1.849	
	Centroid of "present"	0.574	
Abundance model	pH	2.773	-0.342
	Ca	0.040	7.752×10^{-3}
	$\ln(\text{PO}_4)$	-0.016	0.789
	MNO3	0.383	0.495
	Constant	-22.658	5.145
	Centroid of "absent"	-4.987	-1.331
	Centroid of "low"	0.811	0.418
	Centroid of "high"	0.505	-0.773

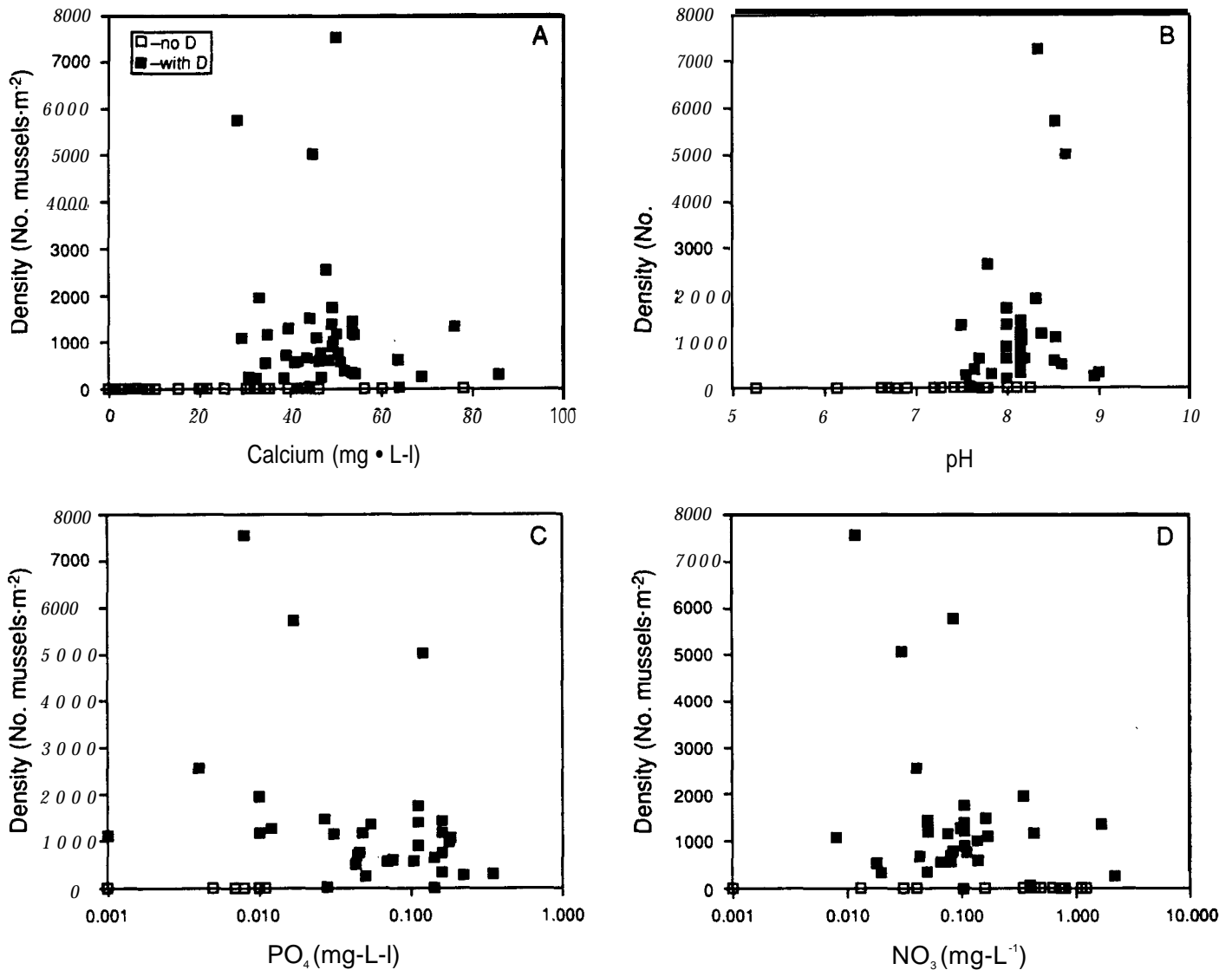


FIG. 2. Relationship between *Dreissena* density and (A) calcium concentration, (B) pH, (C) PO₄ concentration (log₁₀ scale), and (D) NO₃ concentration (log₁₀ scale).

TABLE 6. Cross-validation success rates (%) for the DFA model that predicts abundance. "Variables" indicates which limnological variable were important in distinguishing between two lake types. Values in parentheses are number of lakes. The overall success rate for correct classifications was 76.3%.

Observed	Predicted			Variables
	Absent	Low	High	
Absent	80.0 (4)	0.0 (0)	20.0 (1)	Ca, pH
Low	0.0 (0)	74.1 (20)	25.9 (7)	
High	0.0 (0)	16.7 (1)	83.3 (5)	ln(PO ₄), ln(NO ₃)

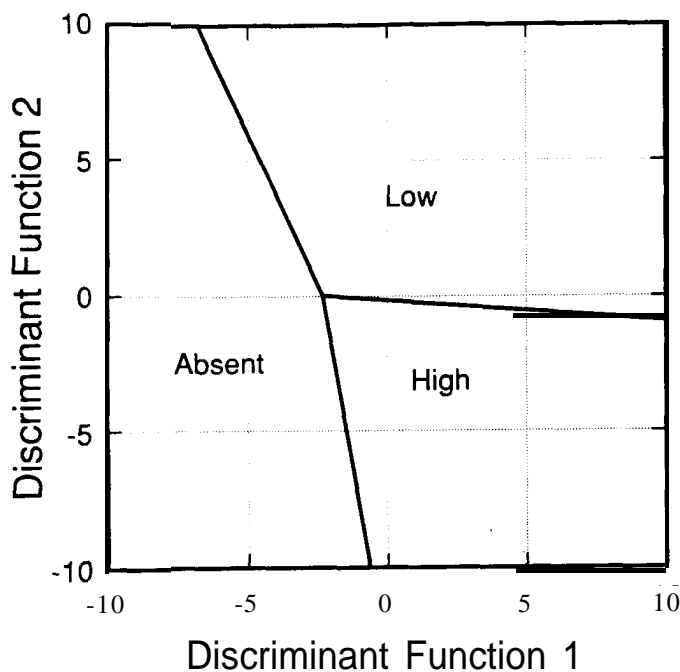


FIG. 3. Map (phase diagram) of the values of discriminant functions 1 and 2 for the model predicting density of *Dreissena* using the second model in Table 4. "High" density is over 3000 zebra mussels • m².

attachment sites for *Dreissena*. In other reservoirs, *Dreissena* commonly occurs on submerged rocks and trees (Mordukhai-Boltovskoi 1979).

Density Models

Although Stanczykowska (1964) found no strong relationships between *Dreissena* density and variables such as calcium and Secchi depth, she later found some evidence that *Dreissena* tended to be rare or absent in lakes with high levels of phosphorus (Stanczykowska et al. 1983; Stanczykowska 1984). In our study, *Dreissena* density was negatively related to both ln(PO₄) and ln(NO₃), suggesting that more eutrophic lakes are less suitable environments. Eutrophic lakes may be detrimental to *Dreissena* because high densities of algae, particularly blue-green algae, may clog their ctenidia (gills for filter-feeding, Stanczykowska 1984). Lakes with high primary productivity may also have lower levels of oxygen, due to high rates of bacterial decomposition of plant material.

TABLE 7. Nonlinear multiple regression models to predict *Dreissena* density. Predictions of model D are presented in Fig. 4.

Model	r ²	P
(A) 810.619pH - 5328.334	0.534	<0.0005
(B) -5578.540e ^{l[PO₄]} + 7540.236	0.489	<0.0005
(C) -144.134e ^{l[NO₃]} + 1643.642	0.451	<0.0005
(D) 2469.003pH - 8894.510e ^{l[PO₄]} - 8772.579	0.594	<0.0005
(E) 2834.425pH - 7762.502e ^{l[PO₄]} + 48.849e ^{l[NO₃]} - 13025.199	0.598	<0.0005

The lack of strong correlations between *Dreissena* density and limnological variables may indicate that density is more strongly determined by ecological factors than by physiological tolerances. While presence or absence of *Dreissena* may depend on the limitations of larval development and shell growth, density may more strongly depend on factors such as predation, food limitation, substrate availability, and recruitment. Several species of fish (e.g. Plizska 1956; Biro 1974) and waterfowl (e.g. Borowiec 1983) can consume substantial proportions of *Dreissena* production, although the ability of predators to control *Dreissena* populations has not been thoroughly studied (Stanczykowska 1990). The effects of parasites (Dobrzanska 1958) are also unknown (Stanczykowska 1977). Larval recruitment may be an important population bottleneck for *Dreissena* (Walz 1978b; Lewandowski 1982) as it is for many marine invertebrates (Underwood and Denley 1984). Variability in *Dreissena* density among different lakes may be caused by differences in factors that affect larval mortality such as lake morphology, temperature regimes, wind mixing (Lewandowski 1982), adult population density (MacIsaac et al. 1991), and substrate availability.

Interlake differences in abundance of algal food may or may not affect *Dreissena* density. This mussel can survive and grow at low food levels (Walz 1978a, 1978b; Sprung and Rose 1988). In laboratory experiments, both filtration and consumption rates follow a Type 2 functional response curve (Walz 1978a; Sprung and Rose 1988). However, consumption rate reaches a maximum at low food levels (1.6 x 10⁷ cells • mL⁻¹, Sprung and Rose 1988; 2.0 mg carbon • L⁻¹, Walz 1978a), while filtration rate continues to increase; excess filtered algae and rejected, inedible particles are expelled in pseudofeces. Even fairly oligotrophic lakes typically have phytoplankton concentrations of 1-5 mg carbon • L⁻¹ (Wetzel 1983), well within the range to support *Dreissena*.

The uncertainty in estimation of zebra mussel density in different lakes may affect the accuracy of our models. We had only a single estimate of *Dreissena* density for approximately half of the lakes in the data set that had zebra mussels. Because *Dreissena* densities fluctuate from year to year, single estimates may not accurately represent average, long-term density. Using single density estimates for lakes with fluctuating populations would probably have affected the regression models more than the DFA models, since the latter models assign lakes to broad density categories. Dense populations tend to fluctuate the most (Stanczykowska et al. 1975; Ramcharan et al. 1992); therefore, uncertainty in density estimates was greatest in lakes that should have had the strongest statistical influence on regression analyses. Moreover, we could find data for only a few lakes with high *Dreissena* densities, which probably caused the regression model to underestimate high densities (Fig. 4).

The difference in accuracy between our DFA and regression-based models may indicate the degree to which other factors, such as pollutants, predation by ducks and fish, and availability

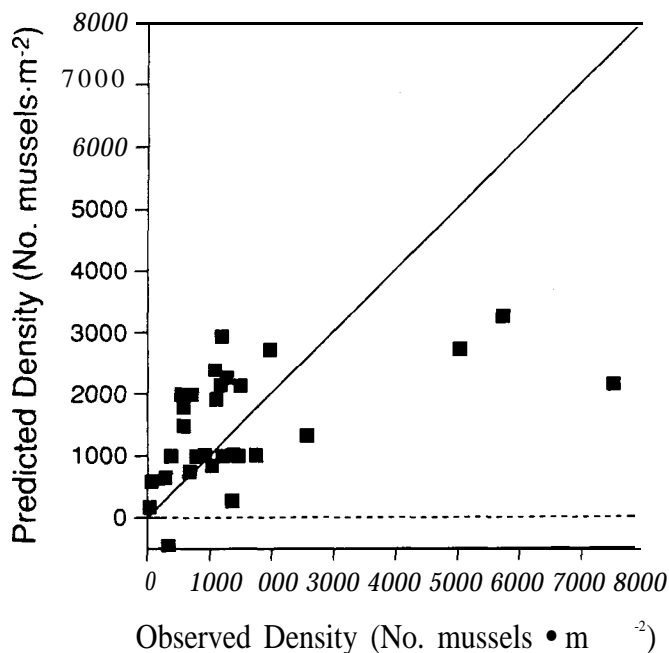


FIG. 4. Comparison of observed density of *Dreissena* and predictions of the regression-based abundance model (Table 7, equation D). The diagonal line ($y = X$) represents 100% accuracy of the model.

of firm substrate, affect the *Dreissena* density. Our occurrence and density models that were based on DFA used the variables pH, calcium, nitrate, and phosphate to obtain highly accurate predictions of *Dreissena* density levels with a low unexplained variance. The effects of factors other than the four chemical variables were apparently too weak to affect the categorization of lakes used in the DFA. For example, pollutants, shortage of firm substrate, and predation are unlikely to completely eliminate *Dreissena* from a lake. The density model that was based on multiple regression was less accurate than the DFA models and had a larger unexplained variance. Therefore, the effects of factors other than pH, calcium, nitrate, and phosphate are more evident at this finer scale.

We had also expected that substrate surface area would limit *Dreissena*, so we had searched for data on littoral zone area. Unfortunately, these data were scarce, and preliminary regression-based models that we had attempted showed no relationship between *Dreissena* density and littoral zone area. We did find many values for mean depth of our lakes and this variable should be statistically related to littoral zone area (deep lakes have small littoral zones and vice versa). We found that mean depth was not an important variable in any of our models.

Substrate quality as well as quantity may be important to *Dreissena*. Because they can only attach to firm materials, littoral zones made of sand and mud may restrict or reduce *Dreissena* populations. The growth habit of *Dreissena* in Europe indicates that availability of hard substrate is probably more important early in an invasion than later. In lakes with little hard substrate, *Dreissena* initially colonizes unionid clams, sticks and logs, and aquatic macrophytes. Veligers settle and grow on these early colonizers forming aggregations or druzes. Eventually, a *Dreissena* "mat" may form over the original soft substrates. These mats have been reported in Polish and Dutch lakes. The lakes in our data set have been colonized for so long that *Dreissena* would have had ample opportunity to form mats of hard substrate.

Our models to predict *Dreissena* occurrence and density should be directly applicable to North American lakes. The models were developed using typical temperate-zone lakes in terms of morphometry and physicochemical environments. It is unlikely that evolutionary founder effects have yet resulted in physiological differences between European and North American populations of *Dreissena* (Hebert et al. 1989). North American populations show a wide genetic diversity: they may have originated from either several separate introductions or one very large introduction (Hebert et al. 1989; May and Marsden 1992). However, it is possible that zebra mussel populations will eventually evolve genetic adaptations to local ecological conditions, as are found in the marine blue mussel, *Mytilus edulis* (Gartner-Kepkay et al. 1980; Dickie et al. 1984). Predicting the performance of *Dreissena* populations in very large lakes such as the Great Lakes is problematical because of heterogeneity in the chemical and physical environments of these basins. Chemical heterogeneity results from both natural and man-made influences. Each Great Lake spans a range of basin geology that has important effects on water chemistry (e.g. Adams 1972; Bahnick et al. 1972). Water mixing patterns are complex. Large inputs of several different nutrients and ions often occur at river mouths, near large urban centers, and all along the shoreline through surface runoff (Neil and Jackson 1982). Therefore, within each lake, water chemistry may vary greatly among different nearshore areas that *Dreissena* typically inhabits (Kinkead and Chatterjee 1974). Predictions can be improved using data from smaller subunits of each Great Lake, rather than average values for the entire lake as we have done for the present analysis. A good example is our prediction that *Dreissena* would be absent from Lake Superior, yet populations of zebra mussels are already found in Superior Harbour. Our prediction was based on chemical data for offshore stations in Lake Superior (Adams 1972). The water in Superior Harbour, influenced by outflow of the St. Louis River, has higher levels of calcium than the open lake and therefore would be predicted as zebra mussel habitat by our models.

Acknowledgements

We thank Anna Stanczykowska and Jim Kitchell for consultation during this study. We also thank Anna Stanczykowska, Petur Biró, H. Reeders, Ricardo DeBernardi, and Anna Maria Nocentini for providing published information on populations of *Dreissena* and characteristics of European lakes. We are grateful to Yvonne Allen for translations, Yalin Hu for statistical advice, Holly Cleator for providing several important papers, and Bill Feeny for preparation of figures. The comments of Steve Adolph and three anonymous reviewers are also appreciated. This project was funded by the University of Wisconsin Sea Grant Institute under grants from the National Sea Grant College Program, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, and the State of Wisconsin. Federal grant NA90AA-D-SG469, project AS48-9700-4, awarded to Allen H. Miller, D.K.P., and S.I.D. and grant NA16RG0531-01 awarded to D.K.P. and S.I.D.

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