

## Relationship between zebra mussel biomass and total phosphorus in European and North American lakes

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With 1 figure and 3 tables

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**Abstract:** We developed a regression model for predicting zebra mussel (*Dreissena polymorpha*) biomass from summer epilimnetic total phosphorus (TP) using published data from Polish lakes: dry tissue biomass =  $-10.8 + 11.0 \log_{10} \text{TP}$ ,  $R^2 = 0.19$ ,  $P < 0.04$ ,  $N = 24$ . This model was used to predict *Dreissena* biomass in six recently-invaded North American lakes. All of the North American observations fit within the 95% confidence limits of the Polish lake relationship. The predictive relationship for the combined Polish and North American data, dry tissue biomass =  $-7.1 + 9.0 \log_{10} \text{TP}$ ,  $R^2 = 0.24$ ,  $P = 0.007$ ,  $N = 30$ , should be useful as a necessary first step for predicting zebra mussel impacts, as well as for estimating reasonable stocking densities of zebra mussels for in situ experiments.

**Key words:** Predictive model, regression, *Dreissena*.

### Introduction

Since its invasion from Europe in the mid-1980s, the zebra mussel (*Dreissena polymorpha*) has spread rapidly into freshwater systems throughout eastern North America (HEBERT et al. 1991, LUDYANSKIY et al. 1993), with often dramatic effects on community structure and ecosystem processes (GILLIS & MACKIE 1994, JOHNGEN et al. 1995, LAVRENTYEV et al. 1995, MACISAAC et al. 1995, NALEPA et al. 1996, BASTVIKEN et al. 1998, PACE et al. 1998). Forecasting the effects of zebra mussels on ecosystems yet to be invaded is currently limited by, among other things, the ability to predict the eventual abun-

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dance of *Dreissena*. RAMCHARAN et al. (1992 a, b) were successful in building empirical models of steady-state (i.e., long-term average) abundance and population fluctuations based on lake characteristics, but these models only predict the density of mussels (number/m<sup>2</sup>). Many ecosystem impacts of invading species should be more closely linked to population biomass (g/m<sup>2</sup>) than to density (MELLINA et al. 1995, ARNOTT & VANNI 1996, YOUNG et al. 1996), so it would also be useful to develop empirical models that can predict zebra mussel biomass from easily-measured lake characteristics. For example, the relationship between zebra mussel body mass and the rate at which particles are filtered is only weakly nonlinear (log : log slope ~-0.9, KRYGER & RIISGÅRD 1988), so biomass predictions can be used to roughly predict potential filtration rates by future mussel populations. A predictive model for zebra mussel biomass would also be helpful in the selection of mussel stocking levels for manipulative experiments, especially in habitats where no estimates of natural abundance are available.

A number of lake characteristics may potentially influence the biomass of zebra mussels in freshwater lakes, including: lake depth, bottom slope, substrate type, degree of mixing, turbidity, nutrient concentrations, and phytoplankton biomass (HANSON & PETERS 1984, RASMUSSEN & KALFF 1987, RAMCHARAN et al. 1992 b, MELLINA & RASMUSSEN 1994). We expected mussel biomass to be positively related to TP, as seen for zoobenthic biomass in general (HANSON & PETERS 1984, RASMUSSEN & KALFF 1987), because of the strong influence of phosphorus in limiting lake, and in particular, phytoplankton productivity (SCHINDLER 1977, 1978). However, STANCZYKOWSKA (1984) reported a tendency for mussel density to be reduced in lakes with very high TP (>300 mg/m<sup>3</sup>) and RAMCHARAN et al. (1992 b) found a negative relationship between mussel density and orthophosphate concentration.

## Materials and methods

### Literature data

We found published data on zebra mussel biomass (reported here as dry tissue biomass) and one or more predictor variables, including: total phosphorus concentration (TP; summer and spring), calcium concentration (Ca<sup>+2</sup>), lake area and depth (mean and maximum), Secchi depth, and chlorophyll concentration (summer and spring). We were only able to find sufficient literature data for three of these potential predictors: depth, Ca<sup>+2</sup>, and summer TP. Of these three predictors, we did not expect there to be a strong influence of depth or calcium in the data set. Shallow lakes might be expected to have higher areal biomass than deep lakes, since a greater fraction of phytoplankton production should be available to benthic filter-feeders, and there should be less oxygen depletion near the bottom in shallow well-mixed systems. However, most literature data on zebra mussel abundance refer to biomass in the depth zone of mussel oc-

currence, so deep areas with no mussels would presumably not affect the average biomass reported for deeper lakes. This makes it less likely that lake depth, independent of lake productivity, will influence zebra mussel biomass as typically reported in the literature. In addition, we limited our analyses to lakes that contain zebra mussels, so presumably all lakes in the data set should have sufficient calcium for mussel growth. Consequently, we did not expect  $\text{Ca}^{+2}$  to be an important factor influencing zebra mussel biomass (SPRUNG 1987, RAMCHARAN et al. 1992 b). Finally, TP was expected to be influential in determining zebra mussel biomass because of its importance in limiting phytoplankton productivity in lakes (SCHINDLER 1977, 1978). The data set comprised 32 lakes in Poland and six lakes in North America (Tables 1, 2). Note that the set of studies that report mussel biomass is only a small fraction of all studies that have estimated zebra mussel density.

Several of the Polish lakes were part of three lake systems: Beldany-Mikolajskie-Sniardwy; Bozncne-Niegocin; and Dargin-Dobskie-Kisajno-Mamry. We followed RAMCHARAN et al. (1992 a) and considered each of these lakes as an independent observation, since there was considerable variation in mussel biomass, and both stable and unstable mussel populations (RAMCHARAN et al. 1992 a), among lakes within the same system. Treating these lakes as independent observations did not influence our conclusions with respect to the statistical significance (at  $P < 0.05$ ) of the two relationships between mussel biomass and predictor variables that we report.

We excluded data from studies in which we judged that the lake bottom was sampled in a biased manner; as in studies that collected samples only from hard substrates or reefs (e.g., HAMILTON et al. 1994, KORNOBIS 1977). We limited our data set to include only those studies that presented zebra mussel biomass as dry tissue mass except for Oneida lake where we calculated dry tissue mass from total dry mass (including shell) by using our own conversion factor (dry tissue mass = total dry mass  $\cdot$  0.0658; WILSON & SARNELLE, unpublished data). We relied on mean biomass values reported by the authors except for Lake Ontario and Gull Lake where we made our own determinations of lake-wide mean biomass. For Lake Ontario, we relied on depth-specific biomass estimates (reported as kg/10 min trawl) from Fig. 2 of MILLS et al. (1999) and their estimate of 0.73 ha swept per 10 min trawl. MILLS et al. (1999) reported dreissenid biomass for 8 depth strata ranging from 15 m to 85 m. We converted their depth-specific biomass estimates to an area-weighted lake average by determining the proportion of lake bottom within each of the sampled depth strata from a digitized bathymetric map (NOAA, National Geophysical Data Center).

### Gull Lake sampling

We estimated zebra mussel biomass in Gull Lake ( $42^{\circ} 24' \text{N}$ ,  $85^{\circ} 24' \text{W}$ ) on 8–9 July, 1999, 5 years after *Dreissena* was first sighted in this lake (see MOSS 1972 for a description of the lake). Four sampling sites were selected randomly from each of four depths: 2.5, 5, 7.5, and 10 m. SCUBA divers collected all mussels and macrophytes by hand within a  $1 \text{ m}^2$  quadrat from each site. Samples were frozen for a few days before sorting. We counted and measured all mussels larger than 15 mm, and subsampled smaller mussels. Some sites had large numbers of very small mussels attached to

**Table 1.** Lake characteristics and dreissenid abundance for Polish lakes. Mussel biomass expressed as dry tissue mass. Year of sampling (when known) in parentheses.

Lake	Mean depth (m)	Maximum depth (m)	TP (mg/m <sup>3</sup> )	Calcium (mg/L)	Mussel biomass (g/m <sup>2</sup> )
Beldany	10.0	31.0	55.0 <sup>k</sup> ('76)	33.0 <sup>l</sup>	0.2 <sup>i</sup> ('62)
Boczne	8.7	15.0	157.0 <sup>k</sup> ('76)	54.0 <sup>a</sup>	19.6 <sup>i</sup> ('62)
Dargin	10.6	37.0	63.0 <sup>k</sup> ('76)	63.1 <sup>a,i</sup>	7.7 <sup>i</sup> ('62)
Dobskie	7.8	21.0	60.0 <sup>k</sup> ('76)	53.2 <sup>a,i</sup>	5.4 <sup>i</sup> ('62)
Glebokie	11.8	34.3	62.5 <sup>b,f</sup>	—	5.0 <sup>j</sup> ('76)
Goldopiwo	—	24.5	—	46.5 <sup>e</sup>	9.7 <sup>i</sup> ('62)
Inulec	4.6	10.1	147.0 <sup>b,f</sup>	—	6.7 <sup>j</sup> ('76)
Jagodno	8.7	34.0	92.0 <sup>k</sup> ('76)	64.0 <sup>a</sup>	18.4 <sup>i</sup> ('62)
Jorzek	5.5	11.6	111.0 <sup>b,f</sup>	—	7.0 <sup>j</sup> ('76)
Kierzlinski	11.7	44.0	38.0 <sup>k</sup> ('77)	45.0 <sup>g</sup>	2.5 <sup>d</sup> ('77)
Kisajno	8.4	24.0	54.4 <sup>h,k</sup> ('76)	54.0 <sup>a</sup>	7.4 <sup>i</sup> ('62)
Kolowin	4.0	7.2	53.0 <sup>c,k</sup> ('78)	—	15.1 <sup>d</sup> ('78)
Kotek	1.0	2.5	103.0 <sup>k</sup> ('76)	50.0 <sup>a</sup>	4.7 <sup>i</sup> ('62)
Kuc	8.0	28.0	40.0 <sup>k</sup> ('77)	—	1.1 <sup>d</sup> ('78)
Majcz Wielki	6.0	16.4	18.5 <sup>f</sup>	—	12.0 <sup>d,j</sup> ('76)
Mamry	11.7	40.0	43.4 <sup>h,k</sup> ('76)	34.5 <sup>e,l</sup>	13.4 <sup>i</sup> ('62)
Mikolajskie	11.1	27.8	60.0 <sup>k</sup> ('76)	36.0 <sup>l</sup>	0.6 <sup>i</sup> ('62)
Niegocin	10.0	40.0	233.0 <sup>k</sup> ('76)	66.1 <sup>a,i</sup>	17.7 <sup>i</sup> ('62)
Olow	12.9	40.1	29.5 <sup>c,k</sup> ('77)	46.0 <sup>g</sup>	43.2 <sup>d</sup> ('78)
Pilakno	13.0	56.6	20.0 <sup>c,k</sup> ('77)	38.0 <sup>g</sup>	0.8 <sup>d</sup> ('77)
Probarskie	9.2	31.0	38.0 <sup>c,k</sup> ('77)	—	8.8 <sup>d</sup> ('77)
Ros	—	29.0	—	—	13.9 <sup>j</sup> ('62)
Sniardwy	5.9	25.0	38.0 <sup>k</sup> ('76)	32.0 <sup>l</sup>	5.2 <sup>i</sup> ('62)
Stregiel	—	12.5	—	49.0 <sup>c</sup>	51.3 <sup>i</sup> ('62)
Szymon	1.1	2.9	87.0 <sup>k</sup> ('76)	—	21.0 <sup>l</sup> ('62)
Tajty	7.6	34.0	55.0 <sup>k</sup> ('76)	54.0 <sup>a</sup>	17.1 <sup>i</sup> ('62)
Taltowisko	14.0	38.4	54.0 <sup>k</sup> ('76)	75.0 <sup>a</sup>	12.6 <sup>i</sup> ('62)
Talty	13.6	37.5	36.0 <sup>k</sup> ('76)	64.0 <sup>a</sup>	0.6 <sup>i</sup> ('62)
Wilkus	—	5.5	—	44.0 <sup>e</sup>	25.8 <sup>i</sup> ('62)
Zabinska	—	42.5	—	—	32.2 <sup>i</sup> ('62)
Zelwazek	3.7	7.4	—	—	5.5 <sup>j</sup> ('76)
Mean	8.5	26.2	69.9	50.1	12.7

Data sources: <sup>a</sup> = GIEYSZTOR & ODECHOWSKA 1958; <sup>b</sup> = HILLBRICHT-ILKOWSKA et al. 1984; <sup>c</sup> = KAJAK & ZDANOWSKI 1983; <sup>d</sup> = LEWANDOWSKI 1991; <sup>e</sup> = PATALAS 1960; <sup>f</sup> = PLANTER & WISNIEWSKI 1985; <sup>g</sup> = PRUSIK et al. 1989; <sup>h</sup> = SPODNIEWSKA 1978; <sup>i</sup> = STANCZYKOWSKA 1977; <sup>j</sup> = STANCZYKOWSKA et al. 1983; <sup>k</sup> = ZDANOWSKI 1982.

macrophytes. In these cases, macrophytes were subsampled by measuring the total wet weight of the macrophytes, then weighing out subsamples from which mussels were counted and measured. We developed a dry tissue mass (g) versus shell length (mm) relationship for fresh Gull Lake mussels: (log dry tissue mass = 2.5429\*log length - 4.9396, R<sup>2</sup> = 0.93, N = 50) to convert size distributions to biomass.

**Table 2.** Total phosphorus, mean depth and dreissenid abundance for North American lakes. Mussel biomass expressed as dry tissue mass.

Lake	TP (mg/m <sup>3</sup> )	Year invaded	Year sampled	Mean Depth (m)	Mussel biomass (g/m <sup>2</sup> )
Erie (eastern basin)	11.7 <sup>a</sup>	1988	'92-'93	25.0	7.7 <sup>b</sup>
Gull	14.0 <sup>k</sup>	1994	'99	12.5	6.1 <sup>k</sup>
Oneida	19.9 <sup>d,j</sup>	1991	'92-'00	6.8	2.2 <sup>d,j</sup>
Ontario	9.3 <sup>e</sup>	1990	'95	86.0	0.9 <sup>g</sup>
Saginaw Bay, Lake Huron (inner bay)	19.0 <sup>c</sup>	1990	'93	7.2	4.5 <sup>h</sup>
St. Clair	22.5 <sup>f</sup>	1986	'90-'94	3.8	3.8 <sup>i</sup>

Data sources: <sup>a</sup> = BERTRAM 1993; <sup>b</sup> = DERMOTT & KEREC 1997; <sup>c</sup> = FAHNENSTIEL et al. 1995; <sup>d</sup> = IDRISI et al. 2000; <sup>e</sup> = JOHNGEN et al. 1994; <sup>f</sup> = MELLINA et al. 1995; <sup>g</sup> = MILLS et al. 1999; <sup>h</sup> = NALEPA et al. 1995; <sup>i</sup> = NALEPA et al. 1996; <sup>j</sup> = Cornell Biological Field Station, unpublished data; <sup>k</sup> = this study.

The epilimnion of Gull Lake was sampled four times from June to August, 1998, with a depth integrating tube sampler. Water samples were filtered through Whatman GF/F glass fiber filters on the day of collection. Total phosphorus (the sum of dissolved and particulate fractions) was measured via persulfate digestion (VALDERRAMA 1981) followed by molybdate blue colorimetry (MURPHY & RILEY 1962).

### Data analysis

Much of the mussel biomass data represented single-year estimates, and most of the measurements of Ca<sup>+2</sup> and TP (summer averages for the epilimnion) in the Polish data set were made many years after zebra mussel biomass was estimated (Table 1). Although Ca<sup>+2</sup> should not change drastically from year to year, large temporal changes in TP are possible particularly due to human influence. These factors should increase the unexplained error of a predictive relationship, especially given that zebra mussel abundance can vary greatly from year to year (RAMCHARAN et al. 1992 a, STANCZYKOWSKA 1984, STANCZYKOWSKA & LEWANDOWSKI 1993). Restricting the data set to lakes in which mussel biomass and TP were measured within three years of each other did not improve fit (N = 6). We log-transformed the TP data which greatly reduced skewness in this variable.

Initial statistical analyses indicated the presence of two very large outliers (Lake Olow and Lake Stregiel, Table 1) in the Polish data set. For example, when we regressed mussel biomass against TP, Ca<sup>+2</sup> and mean depth, the standardized residual for Lake Olow was 6.1, indicating an extreme outlier. There were no TP data for Lake Stregiel, so inclusion/exclusion of this lake was inconsequential to analyses involving TP. These two lakes had unusually high biomass (>40 g/m<sup>2</sup>) and were responsible for strong skewness in the mussel data that could not be alleviated via transformation. Consequently, we excluded these two lakes from all subsequent statistical analyses. We strongly suspect that values of mussel biomass greater than 40 g/m<sup>2</sup> represent transient, nonsustainable excursions from long-term average biomass (see Discussion). For

this reason, we also restricted the data from Saginaw Bay. Lake Huron to data collected in 1993. Mussel biomass in Saginaw Bay increased from 10 g/m<sup>2</sup> in 1991 (first year after invasion) to 62 g/m<sup>2</sup> in 1992, then declined to 4.5 g/m<sup>2</sup> in 1993 (NALEPA et al. 1995), suggesting that zebra mussel biomass was far above long-term sustainable levels in 1992.

## Results

The Polish data consisted of mesotrophic to hyper-eutrophic lakes (mean and range of TP: 70, 19–233 mg/m<sup>3</sup>) with mean depths from 1–14 m, and Ca<sup>+2</sup> concentrations from 32–75 mg/L (Table 1). Not surprisingly, mean depth and maximum depth were highly intercorrelated ( $r = 0.81$ ,  $P < 0.0001$ ,  $N = 25$ ), so we only used mean depth in regression analyses. There was only a marginally significant correlation between Ca<sup>+2</sup> and logTP ( $r = 0.43$ ,  $P = 0.09$ ,  $N = 16$ ) and no significant correlation between mean depth and logTP ( $r = -0.32$ ,  $P = 0.13$ ,  $N = 24$ ) in the Polish data. Stepwise multiple regression indicated that Ca<sup>+2</sup> and mean depth had no statistically significant influence on mussel biomass in these data ( $P > 0.3$ ). The latter result was robust to the order in which variables were entered and whether variables were forced into the model. Multiple regression indicated that logTP was the only potentially influential variable (Table 3). Based on these results, we calculated a predictive equation for the Polish data (Fig. 1): mussel biomass =  $-10.8 (\pm 8.8) + 11.0 (\pm 4.9) \log_{10} \text{TP}$ ,  $R^2 = 0.19$ ,  $P = 0.04$ ,  $N = 24$  (standard errors in parentheses).

The TP range of the six North American lakes (Table 2, mean and range of TP: 16.1, 9.3–22.5 mg/m<sup>3</sup>) was much smaller and extended lower than the range of TP in the Polish data, and all of the biomass estimates in these recently-invaded North American lakes fit within the 95% confidence limits of predictions from the equation above (Fig. 1). Combining the Polish and North American data and excluding Lake Olow, we calculated the following predictive equation: mussel biomass =  $-7.1 (\pm 5.2) + 9.0 (\pm 3.1) \log_{10} \text{TP}$ ,  $R^2 = 0.24$ ,  $P = 0.007$ ,  $N = 30$  (standard errors in parentheses).

**Table 3.** Multiple regression statistics for the influence of mean depth (m), calcium (mg/L) and log total phosphorus (mg/m<sup>3</sup>) on zebra mussel biomass in Polish lakes.  $N = 16$ .

Variable	Slope	Standard error	P
Log mean depth	5.5	5.8	0.36
Log calcium	11.7	13.9	0.42
Log total phosphorus	16.9	6.8	0.03
Full model			0.04

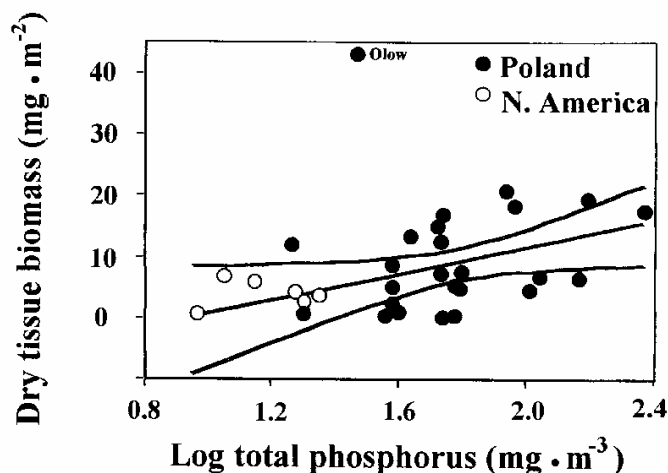


Fig. 1. Relationship between total phosphorus and dreissenid biomass for Polish and North American lakes. Data from Tables 1 and 2. Regression line and 95% confidence bands for equation estimates were calculated for Polish lakes after excluding the outlier (Lake Olow).

## Discussion

Total phosphorus was the only variable that significantly predicted zebra mussel biomass in the Polish data set. Lack of  $\text{Ca}^{+2}$  influence was expected, since  $\text{Ca}^{+2}$  concentrations were above 30 mg/L in every lake (Table 1), a level that is above minimum thresholds for successful *Dreissena* growth and reproduction (RAMCHARAN et al. 1992b). Likewise, mean and maximum depth should have little direct influence given that mussel biomass is generally reported from Polish lakes for the restricted depth zone of mussel occurrence.

The amount of variation in mussel biomass explained by TP ( $R^2 = 0.19, 0.24$ ) was low but comparable to that reported for total zoobenthic biomass by RASMUSSEN & KALFF (1987) ( $R^2 = 0.20, 0.26$ ). In contrast, HANSON & PETERS (1984) found a stronger relationship between zoobenthic biomass and TP (1984;  $R^2 = 0.48$ ), which may be related to the lower TP range in their study (3–117 mg/m<sup>3</sup>) relative to the range in RASMUSSEN & KALFF (4–390 mg/m<sup>3</sup>) and our study (9–233 mg/m<sup>3</sup>). The response of lake productivity (as indexed by phytoplankton biomass) to increases in TP tends to be weaker for lakes with TP greater than ~200 mg/m<sup>3</sup> (SARNELLE et al. 1998). At high levels of TP other factors begin to limit lake productivity (SMITH 1982, McCAULEY et al. 1989), so the influence of increased phosphorus on benthic biomass should weaken.

Given that the response of a single species to enrichment is likely to be much more variable than the response of total zoobenthic biomass, the statistical significance of the TP: zebra mussel relationship is encouraging. How-

ever, we were only able to establish a TP influence after excluding data from one lake (Lake Olow) with mussel biomass  $>40 \text{ g/m}^2$ . The status of this excluded lake is thus critical to our analysis.

Based on both Polish and North American data, we propose that a dreissenid biomass in excess of  $\sim 40 \text{ g/m}^2$  is not sustainable (i.e., much higher than steady-state biomass) in lakes. This hypothesis is supported by evidence suggesting that mussel populations in outlier lakes were unstable at the time that biomass was measured. One of the two high-biomass lakes (Lake Stregiel, Table 1) was classified as having an unstable mussel population by RAMCHARAN et al. (1992 a), based on the magnitude of interannual density fluctuations. Lake Olow, the other high-biomass lake, was not explicitly classified as unstable by RAMCHARAN et al. (1992 a), but we note that mussel density was reported as  $1830/\text{m}^2$  in 1978 (the year in which biomass was estimated, LEWANDOWSKI 1991) and as  $514/\text{m}^2$  (year unspecified) by STANCZYKOWSKA & LEWANDOWSKI (1993). Lake Olow undergoes transient periods of hypolimnetic anoxia during the summer (KAJAK & ZDANOWSKI 1983), which have been shown to be lethal for zebra mussels (KARATAYEV et al. 1998). Thus, the mussel population in Lake Olow may have been at a transient high biomass level in 1978. The propensity for zebra mussel populations to initially overshoot carrying capacity, as documented in Saginaw Bay (NALEPA et al. 1995), suggests that this type of boom and bust population cycle is common and should be considered when estimating natural densities for inland lakes.

To examine population instability as a factor producing residual variation in the TP:mussel biomass relationship, we restricted the Polish data to lakes classified as stable by RAMCHARAN et al. (1992 a), and recalculated the logTP:biomass regression. This restriction improved the fit: mussel biomass =  $-33.5 (\pm 16.3) + 23.2 (\pm 8.4) \log_{10}\text{TP}$ ,  $R^2 = 0.60$ ,  $P = 0.04$ ,  $N = 7$  (standard errors in parentheses). We caution against using this equation for prediction because it is based on very few lakes, but the improvement in fit suggests that population instability may be a major source of residual variation in the TP-mussel biomass relationship. Additional factors that may account for residual variation are: substrate quality (MELLINA & RASMUSSEN 1994), the temporal mismatch between measurements of TP and mussel biomass for most of the Polish lakes, and within-lake spatial variation in mussel biomass estimates. Standard deviations of single-year biomass estimates for North American lakes vary from 45% (Oneida Lake) to  $\geq 100\%$  (Lake Erie, Lake St. Clair, Saginaw Bay) of the mean (NALEPA et al. 1995, 1996, DERMOTT & KERIC 1997), so this source of residual variation may be important.

With the exception of the first two years after invasion, we found no evidence to suggest that time since colonization influences steady-state dreissenid biomass. North American lakes three years after invasion do not seem to support detectably higher biomass of zebra mussels than Polish lakes in which



mussels have existed for >50 years. The limited data available on population dynamics immediately after invasion (Saginaw Bay, NALEPA et al. 1995) support the suggestion that dreissenid populations in North America require only about three years to approach steady-state biomass. Ironically, mussel populations in some recently invaded North American lakes may be closer to steady-state biomass than populations in some European lakes. Long-term presence is no guarantee that a mussel population will be near steady-state biomass in any given year, especially when one considers the precipitous declines and rapid recoveries that characterize some long-established populations (STANCZYKOWSKA et al. 1975). More study of *Dreissena* population dynamics is needed.

To compare the response of dreissenid biomass to TP enrichment with the response of total zoobenthic biomass reported in previous studies requires conversion of the data to common scales. To this end, we calculated  $\log_{10}TP$  vs.  $\log_{10}$ biomass and  $\ln TP$  vs.  $(\text{biomass})^{0.1}$  regressions for the combined Polish and North American data to enable comparison with the relationships reported by HANSON & PETERS (1984) for profundal benthos, and RASMUSSEN & KALFF (1987) for profundal and sublittoral benthos, respectively. For both of these comparisons, the slope of the zebra mussel response to TP enrichment (log : log slope : 0.56, ln : tenth root slope: 0.07) was roughly similar to the slope for total zoobenthic biomass (log : log slope: 0.71, ln : tenth root slope: 0.08–0.09). These comparisons suggest that dreissenid biomass increases at a roughly similar rate with enrichment as total zoobenthic biomass. The elevation of the dreissenid regression was similar to those reported by RASMUSSEN & KALFF (1987), but somewhat lower than that reported by HANSON & PETERS (1984) (–0.25 versus –0.09). A lower elevation is expected for the response of a single taxon relative to total zoobenthic biomass.

The positive relationship that we found between dreissenid biomass and TP is not surprising given that zoobenthic biomass responds positively to nutrient enrichment, but contrasts with the negative correlation found between mussel density and orthophosphate concentration by RAMCHARAN et al. (1992 b). It is difficult to compare these contrasting results because of the difference in independent variables employed, but we can suggest that the data set analyzed by RAMCHARAN et al. (1992 b) included lakes with much higher levels of phosphorus loading than the lakes that we analyzed. Their data set included 15 lakes with orthophosphate concentrations in excess of  $100 \text{ mg/m}^3$ . Many of these lakes probably had TP in excess of  $233 \text{ mg/m}^3$ , the maximum in our data set. In extremely eutrophic waters, anoxia and toxic cyanobacteria may lead to reduced zebra mussel biomass, as suggested by STANCZYKOWSKA (1984). In any case, orthophosphate concentration is a poorer surrogate variable for lake productivity than TP, because the former is subject to much greater seasonal variation and is under much greater control by the biota (via uptake and excretion) and by sorption to non-living particles than is TP.

In conclusion, we found that dreissenid biomass can be predicted from TP for lakes with TP less than  $233 \text{ mg/m}^3$ , and that steady-state biomass in recently invaded North American lakes fits the positive TP:biomass relationship for Polish lakes. The latter fit, however, is at least in part a function of the low  $R^2$  of the Polish relationship. The TP:biomass relationship for Polish and North American lakes combined can be used to predict future zebra mussel biomass in uninfested lakes, and to suggest reasonable biomass stocking levels for experiments in habitats for which biomass estimates are lacking. These predictions, however, carry a large degree of uncertainty, much of which may stem from large interannual and spatial variation in mussel abundance for individual lakes. To refine these predictions, more unbiased estimates of dreissenid biomass over multiple years are needed. We recommend that dry tissue mass (rather than total or shell-free wet mass) be determined in future studies given that most existing studies report dry tissue mass and that dry mass estimates are more reliable and reproducible.

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