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Predicting the intensity and impact of *Dreissena* infestation on native unionid bivalves from *Dreissena* field density

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Abstract

Introduced dreissenid mussels (Dreissena polymorpha and D. bugensis) foul native unionid bivalves by attaching to their shells in large clusters and may critically impair many North American unionids that are already threatened by habitat degradation. Using literature and new field data, we examined patterns of Dreissena infestation on unionids, and the relationships between Dreissena field density, infestation intensity, and unionid mortality. Linear regression models showed that Dreissena field density strongly predicts (i) the proportion of unionids colonized by dreissenids ($r^2=0.90$, $p<0.0001$) and (ii) the mean number of dreissenids attached to unionids ($r^2=0.81$, $p<0.0001$). We fitted a compound Poisson model that accounts for dreissenid clustering and predicts both the proportion of colonized unionids and the mean infestation intensity as effectively as our empirically-derived models. The proportion of unionids colonized by Dreissena follows a saturation curve, increasing rapidly with Dreissena densities up to 200/m^2, and reaching a plateau at 70-80% colonization. Unionid mortality (reflected by the proportion of dead unionids) is strongly correlated with Dreissena field density ($r^2=0.82$, $p<0.002$) at densities above 1000/m^2. Our models predict that severe unionid mortality (>90%) occurs when Dreissena density and mean infestation intensity reach 6000/m^2 and 100 dreissenids/unionid.

Introduction

Freshwater bivalves of the family Unionidae play an important role in nutrient recycling in aquatic systems (Lewandowski and Stanczykowska 1975; Kasprzak 1986; Nalepa et al. 1991a), and are potentially valuable indicators of water quality (Imlay 1982; Green et al. 1989). North America has the richest freshwater mussel fauna in the world, with close to 300 described species and subspecies (Williams et al. 1993). However, over the past few decades, unionid abundance and species diversity have severely declined throughout North America, largely because of habitat degradation (Fuller 1974; Nalepa et al. 1991b; Williams et al. 1993); 70% of our native unionids are currently considered to be endangered, threatened, or of special concern (Williams et al. 1993).

A new, potentially fatal stress on North American unionid populations has been caused by the introduction of the European zebra mussel, Dreissena polymorpha (Hebert et al. 1989). Using their adhesive byssal threads, zebra mussels may attach to any solid substrate, including the shells of other molluscs (e.g., Lewandowski 1976; Mackie 1990). Evidence from field and laboratory studies suggests that zebra mussels preferentially colonize living unionids (Biryukov et al. 1964; Wolff 1969; Lewandowski 1976; Mackie 1990; Ricciardi 1994). Unionids are fouled by byssally-attached zebra mussels wherever they are sympatric in Europe (Wagner 1936; Sebestyen 1938; Zhadin and Gerd 1961; Wiktor 1963; Biryukov et al. 1964; Kuchina 1964; Wolff 1969; Lewandowski 1976; Arter 1989) and North America (Hebert et al. 1989, 1991; Mackie 1990; Schloesser and Kovalak 1991; Hunter and Bailey 1992; Tucker 1994; Ricciardi 1994; Gillis and Mackie 1994; and others). The infestation intensity varies by several orders of magnitude among these habitats; in extreme cases, zebra mussels settling on unionid shells may form encrusting colonies of more than 10,000 individuals, and weigh 3-4 times as much as the unionid (Hebert et al. 1991; Schloesser and Kovalak 1991). The more recently introduced quagga mussel (D. bugensis) may also contribute to unionid fouling, but probably to a much lesser extent than the zebra mussel because it does not show a preference for unionids as substrates (Conn and Conn 1993). Dreissenid infestations are believed to negatively affect unionids primarily by smothering siphons, preventing valve opening and closure, and interfering with normal feeding and burrowing activity (Mackie 1990; Schloesser and Kovalak 1991; Haag et al. 1993). Heavy infestations of Dreissena may cause reduced glycogen reserves (Haag et al. 1993), significant depletion of biomass and total energy stores (Ricciardi, in prep.), and shell deformation in unionids (Wolff 1969; Lewandowski 1976; Mackie 1990; Hunter and Bailey 1992). These impacts may have major consequences for unionid populations, as indicated by the significant mortality and loss of species richness that have often followed Dreissena invasions (Sebestyen 1938; Arter 1989; Hunter and Bailey 1992; Gillis and Mackie 1994; Haag et al. 1993; Ohnesorg et al. 1993; Maleski and Masteller 1994; Ricciardi, in prep.).

Relocation of unionid populations has been advocated as a conservation measure to protect them from Dreissena infestation (Waller et al. 1993; Havlik 1994). But since Dreissena is expected to successfully invade most North American water bodies (Strayer 1991; Ramcharan et al. 1992), massive relocation of unionids into refugia that are inaccessible to Dreissena may be both futile and impractical. Future conservation practices, whatever form they may take, will likely involve decisions regarding levels of Dreissena infestation that are tolerable to particular unionid populations. Such decisions will require a method of predicting the level of infestation on unionids prior to a Dreissena invasion.

Dreissena population densities are highly variable among different aquatic habitats (Stanczykowska 1977). There has been some recent success in developing predictive models of Dreissena abundance from environmental variables (Ramcharan et al. 1992; Mellina and Rasmussen 1994), and more refined models may be available in the future. Therefore, it may be possible to predict the infestation intensity (and correlated impacts) of Dreissena on unionids from environmental variables if infestation can be quantitatively related to local Dreissena abundance. This would permit us to identify habitats and unionid populations that are at great risk, in advance of a Dreissena invasion. The first step in developing these larger predictive models, and the main objective of our investigation, is to quantify relationships between the infestation intensity of Dreissena on unionids and Dreissena density. Secondly, we examine whether Dreissena density and infestation intensity can be used to predict unionid mortality.

Methods

We examined patterns of unionid infestation across a range of habitats and geographic regions, using data obtained from the literature combined with our own field data collected from the St. Lawrence River. The primary data set consisted of 36 records, including 13 from the Laurentian Great Lakes (Hebert et al. 1989; Hebert et al. 1991; Schloesser and Kovalak 1991; Gillis and Mackie 1994; Masteller and Schloesser 1992; Haag et al. 1993), 9 from the St. Lawrence River (this study), 8 from the upper Mississippi River Basin (Tucker et al. 1993; Tucker 1994), and 6 from the Mazurian lakes of northeastern Poland (Lewandowski 1976). Data on infestation intensity included (i) the percentage of unionids colonized by Dreissena, (ii) the mean number of dreissenids per unionid (=mean infestation intensity), and (iii) the maximum number of dreissenids found on a unionid (=maximum infestation intensity). These data were coupled with estimates of Dreissena field density for each site, wherever possible (Table 1); when more than one literature source was required to obtain these data, only data collected within the same year were used. The mean number of dreissenids per unionid includes all unionids (including those not colonized by Dreissena) in a given population. The Mississippi River studies (Tucker et al. 1993; Tucker 1994) gave mean infestation intensities for colonized unionids only, and therefore were multiplied by the proportion of colonized unionids to obtain the mean infestation for the entire population.

TABLE 1
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Data collected from St. Lawrence River sites

Unionids were collected from six sites on the upper St. Lawrence River in Québec: two sites on Lake St. Louis (near Lachine), one site on Lake St. François (near Les Cèdres), one site at the Port of Montréal, and two sections of the Soulanges Canal at Pointe-des-Cascades (approx. 45°20'N 73°58'W).

Collections at the Soulanges Canal sites were made monthly during the summers (June-August) of 1992-1994. Lake St. François was sampled once in July 1992. Two sites in Lake St. Louis were sampled in September 1992; one of these sites was revisited in June 1994. The Port of Montréal site was sampled once in July 1994. All unionids, including empty shells, were removed by hand from a 1-m^2 PVC quadrat randomly placed on the bottom substrate using SCUBA. The upper 10 cm of sediment within the quadrat was probed by hand to locate living and recently dead individuals buried immediately beneath the surface. An underwater light was used to aid collections in areas of low visibility. We decided _a priori_ to use five replicated quadrats at each site, since this was expected to yield a precision of approximately 20% when sampling unionid densities of 10-30 mussels/m^2 (Downing and Downing 1992). The sole exception to our sampling protocol was the Port of Montréal, where unionid and dreissenid densities were not sampled; living and recently dead unionids were randomly collected by SCUBA, and provided by a local environmental consulting firm (Subdev Canada Inc.).

Dreissena became established in the upper St. Lawrence River ca. 1990 (Griffiths et al. 1991); settled mussels, including adults, were present in L. St. Louis and L. St. François in the spring of 1991 (Ricciardi, pers. obs.). Dreissenid densities were estimated using SCUBA and randomly placed 1-m^2 quadrats (at least five replicates) at L. St. Louis and L. St. François sites, since preliminary surveys (in 1992) showed that these sites had relatively small _Dreissena_ populations ($10^2/m^2$). Smaller (25 cm x 25 cm, or 0.0625-m^2) quadrats were used at the Soulanges Canal sites, where dreissenid densities were on the order of $10^3/m^2$. Objects with attached mussels were removed from quadrats placed at sites in L. St. Louis, L. St. François, and the west section of the Soulanges Canal. In the east section of the Soulanges Canal, where the bottom substrate is predominantly mud, quadrats were placed on the concrete canal walls at 3-5 m depths and dreissenids were scraped into bags by a SCUBA diver using a knife. In the laboratory, dreissenids were removed from unionids and other substrates, using a knife and a bristle brush (for small specimens). All dreissenids were washed through a 1-mm mesh sieve, and counted under a dissecting microscope. Data from sites that were sampled more than once during a year were averaged for that year.

Development of predictive models

Our analysis consisted of modelling the relationships between Dreissena density and infestation variables by three approaches. We first analyzed these relationships empirically with simple linear regression models using SAS procedures (SAS Institute Inc. 1988). Proportion data (i.e., colonized unionids; unionid mortality) were transformed as $\sin^{-1}(\text{proportion}^{0.5})$ to achieve a better linear fit. The remaining variables spanned two to four orders of magnitude in range (Table 2), and thus were $\log_{10}$-transformed to stabilize their variances and reduce the influence of extreme values (Zar 1984). Our second approach investigated the possibility that the colonization of unionids by dreissenids is a simple space-occupancy problem controlled by stochastic processes. We thus derived a model to predict unionid colonization based on the Poisson distribution, and fitted it to the percentage colonization data using a non-linear iterative regression technique (Wilkinson 1989). We verified this model by testing (i) its ability to predict the proportion of unionids colonized by Dreissena, and the mean infestation intensity, and (ii) the expected 1:1 correspondence between mean infestation and variance required for a simple Poisson distribution (Zar 1984). Our analysis led us to consider a third approach in which we fitted a compound Poisson model (Thomas 1949) that accounted for the tendency of dreissenid mussels to aggregate and form clusters on unionid shells.

TABLE 2
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Estimating unionid surface area

In the process of developing our simple Poisson model, we needed to determine the allometric relationship between unionid shell length (cm) and surface area (cm^2). To do this, we randomly selected fifty unionids from L. St. Louis and Soulanges Canal collections. The surface area of each unionid was estimated by spreading a sheet of aluminum foil over the entire shell, subsequently weighing the foil, and multiplying this weight by an area-to-weight ratio determined from sample masses of foil. The maximum length of the shell was measured to the nearest millimeter, using dial callipers.

The $\log_{10}$-transformed shell length and surface area variables were related by linear regression (SAS Institute Inc. 1988). This equation permitted us to estimate the surface area available for colonization by Dreissena, using data from unionids in the Great Lakes--St. Lawrence River system.

An indicator of mortality: the proportion of dead unionids in a population

TABLE 3
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Data on the proportion of dead unionids in populations within the Great Lakes-St. Lawrence River system comprised a second data set (Table 3) that was used to determine if Dreissena density and infestation intensity are significant predictors of unionid mortality. We considered a high proportion of recently dead unionids in a population to indicate relatively high mortality, since we found few studies that provided a direct measure of mortality. A similar measure, the ratio of live to dead unionids, was used in other studies as an indicator of increased mortality due to Dreissena fouling in Lake St. Clair (Hunter and Bailey 1992), western Lake Erie (Haag et al. 1993), and the Detroit River (Ohnesorg et al. 1993). An increase in the proportion of dead unionids was correlated with both a decrease in living unionid density and an increase in Dreissena density across sites in Lake St. Clair (Hunter and Bailey 1992). Therefore, we chose to use this proportion as an indicator of unionid mortality in order to investigate its correlation with Dreissena abundance and infestation across a number of different habitats. Living and recently dead unionids (distinguished from older dead shells by the presence of mussel tissue or an intact ligament, and by the absence of severe shell erosion) were obtained from five sites on the St. Lawrence River (L. St. Louis, L. St. François, two sections of the Soulanges Canal, and the Port of Montréal), and these data were supplemented by similar data from the North American literature (Hebert et al. 1991; Hunter and Bailey 1992; Haag et al. 1993; Gillis and Mackie 1994) (Table 3).

We recognize that a simple measure of the proportion of recently dead unionids in a population is not as meaningful an indicator of mortality as the change in unionid density over time, but there is a paucity of data concerning these density changes in the literature. Our previous experiences in sampling unionid populations in rivers and inland lakes throughout southwestern Quebec suggested the proportion of dead unionids in populations occupying relatively pristine habitats (e.g., many southwestern Quebec lakes), or even habitats that are subject to some perturbation (e.g., the lower Ottawa River), is usually well below 10%. This is considerably lower than the proportions recorded in habitats invaded by *Dreissena* (Table 3). Therefore, we assumed that if *Dreissena* density and infestation were strong correlates of unionid mortality, then we would be able to detect these relationships using our surrogate variable.

Results and Discussion

Empirical relationships between infestation and Dreissena field density

The proportion of unionids colonized by *Dreissena* at a given site is strongly dependent on the density of the *Dreissena* population at that site ($r^2=0.90$, $p<0.0001$), and follows a saturation curve that increases rapidly with *Dreissena* density up to ca. $200/m^2$, where it plateaus at 70-80% colonization (Fig. 1). Typically, over 90% of unionids are colonized when *Dreissena* densities reach 10^3 mussels/m^2.

The mean number of dreissenids on each unionid (mean infestation intensity) is strongly correlated with *Dreissena* field density (Fig. 2; Table 4), which accounts for 81% of the variance. This relationship is equally applicable to lentic and lotic habitats (ANCOVA, F=1.85, $p>0.19$), although infestation intensities tended to be lower in lotic situations. The maximum number of *Dreissena* attached to a unionid (maximum infestation intensity) at a given site is also correlated with *Dreissena* field density ($r^2=0.58$, $p<0.0001$), but is significantly lower in lotic situations (ANCOVA, F=11.27, $p<0.005$; Fig 3), which may reflect the greater availability of alternative hard substrates in running waters.

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The mean infestation intensity remains low until the majority of unionids in a population is colonized (Fig. 4). Unionids are then subject to rapid increases in infestation (Table 5), possibly due to

(i) the attraction of larvae and young-of-the-year to established mussel clusters on unionids (gregarious settlement), or (ii) self-recruitment by unionid-bound dreissenid populations. In both cases, larval settlement is enhanced by the increased surface area provided by dreissenid shells themselves (Mackie 1990), thus the rate of infestation should increase over time. However, during initial colonization, the rate of infestation should be limited by the low abundance of larvae in the water column, i.e., infestation levels should be dependent on factors influencing larval settlement. The initial colonization of unionids by Dreissena in the Illinois and Mississippi Rivers consisted primarily of single attachments, and larger unionids were more likely than smaller specimens to bear attached Dreissena (Tucker et al. 1993); during subsequent colonization, infestation varied exponentially with unionid shell length (Tucker 1994). At low infestations, unionid shell length explained 19% of the variance in the number of Dreissena attached to unionids in the upper St. Lawrence River (Ricciardi, In prep.), between 23% (Mackie 1990) and 43% (Hebert et al. 1989) for unionids in the Great Lakes, and as much as 97% for unionids in the upper Mississippi River (Tucker 1994).

Predicting infestation from a Poisson model

We attempted to fit a stochastic model to the data based on the null hypothesis that the colonization of unionids by dreissenid mussels, both as settling larvae and as migrating young-of-the-year mussels, is a process characterized by a large element of chance or randomness. We assumed that the exposed surface area on a unionid shell contains a large number (n) of locations that can be occupied by a byssally-attached dreissenid, and that each of these locations has the same probability (p) of being occupied. The probability that exactly r of these locations will be occupied is described by the binomial distribution:

$$(1) \qquad P_{k=r} = (n!/[r!(n-r)!])\ p^{r}\ (1-p)^{n-r}$$

Let us assume that np (the mean of the binomial distribution) can be represented as a linear function of the overall dreissenid density, D (number of mussels per m^2), in the environment containing the unionids. We can express this function as

(2) $np=\mu sD$

where s is the mean colonizable space (in m^2) available on each unionid, and μ is a measure of the preference of Dreissena for this space, relative to other available substrate in the surrounding habitat. Assuming also that n is very large, p is small, np is of moderate magnitude, and r is negligible compared to n, then the probability of r locations being occupied (i.e., r dreissenids on a unionid) is given by

(3) $P_{k=r} = (1/r!)\ (\mu sD)^r\ (1-\mu sD/n)^n \approx (1/r!)\ (\mu sD)^r\ e^{-\mu sD}$

Equation 3 is the Poisson distribution (Zar 1984) with a mean and variance equal to μsD, which is the expected infestation per unionid. We estimated s using our allometric regression equation relating surface area to shell length for St. Lawrence River unionids:

(4) $\text{Log}_{10}(\text{surface area}) = 1.981\ \text{Log}_{10}(\text{shell length})$ $r^2=0.92$, SE=0.053

Assuming a mean unionid shell length of 9.5 cm (based on combined data from Mackie 1990, Schloesser and Kovalak 1991, and this study), and correcting for backtransformation bias, Eq. 4 gives us a mean surface area of 87.7 cm^2. In most cases, only the posterior region of a unionid (partially buried in sediment) is available for Dreissena colonization (Mackie 1990; Schloesser and Kovalak 1991; Hunter and Bailey 1992; Haag et al. 1993; Ricciardi, pers. obs.), hence we estimate an exposed surface area (s) of approximately 44 cm^2 (0.0044 m^2). Our Poisson null model then predicts the proportion of uncolonized unionids ($P_{k=0}$) to be

(5) $e^{-0.0044\mu D}$

and the proportion colonized to be

(6) $1-e^{-0.0044\mu D}$

We tested the fit of this model using non-linear regression (Wilkinson 1989), and found it to be nearly as effective (r^2=0.78) as our previously determined empirical model (Table 3) at predicting the proportion of colonized unionids from *Dreissena* field density. The estimated value for the preference parameter (μ) obtained from this non-linear fit was 2.2 (95% C.I. = 1.2-3.2), which suggests that *Dreissena* (primarily *D. polymorpha*) is about twice as likely to colonize unionids compared with other substrates in the surrounding habitat, and thus corroborates laboratory and field observations of the preferential colonization of unionids by *Dreissena* (Biryukov et al. 1964; Wolff 1969; Lewandowski 1976; Mackie 1990; Ricciardi 1994). The predicted mean infestation per unionid (μsD) becomes 0.0097D, and we obtain the following relationship:

(7) Predicted colonization = $1 - e^{-0.0097D}$ r^2=0.783, SE=0.032

A further test of this model was obtained by comparing predicted and observed mean infestations for given values of *Dreissena* field density, D. We found that the model provides useful rough estimates, but it generally underestimates mean infestation intensities, probably because it does not account for the effect of contagious infestation. The relationship between the mean infestation and variance suggests that dreissenids are contagiously distributed on unionids (Fig. 5) and that our simple Poisson model, although useful as a basis for further modelling, is inappropriate in its current form to

FIG 5 NEAR HERE

accurately describe infestation patterns.

Using a compound Poisson model to predict infestation

TABLE 6 NEAR HERE

Analysis of variance-to-mean ratios for unionid-bound dreissenids in the St. Lawrence River indicated that young-of-the-year dreissenids are more contagiously distributed than adult dreissenids (Table 6). Furthermore, young-of-the-year dreissenids tend to aggregate around adult (one- and two-year-old) dreissenids and thus form structured clusters on unionid shells (Ricciardi, pers. obs.). We therefore fitted a compound Poisson model (Thomas 1949) to account for this clustering tendency. The model is based on two parameters: λ, which describes the Poisson distribution of adult dreissenids on unionid shells, and β, which describes the distribution of young-of-the-year dreissenids around adults. The probability of k dreissenids on a unionid, P(k), is given by the following equation adapted from Thomas (1949):

$$(8) \qquad P(k) = \sum [\lambda^{r} e^{-\lambda}/r!][(r\beta)^{k-r} e^{-r\beta}/(k-r)!]$$

The mean infestation per unionid is given by

$$(9) \qquad \lambda(1+\beta)$$

and the variance is given by

$$(10) \qquad \lambda(1+3\beta+\beta^{2})$$

We calculated λ and β for each record in our data set that contained mean and variance estimates (n=17), $\log_{10}$-transformed both parameters, and then related them to Dreissena density (D) by linear regression. Backtransformation of the regression equations produced the following power functions:

(11) $\lambda = 0.119\ D^{0.453}$ $r^2=0.69$, $p<0.002$, SE=2.37

(12) $\beta = 0.103\ D^{0.5}$ $r^2=0.50$, $p<0.018$, SE=26.7

The predicted proportion of colonized unionids is thus given by

(13) $1-e^{-\lambda}$

where λ is derived from Eq. 11. After fitting both Eq. 11 and Eq. 12 into Eq. 9, we obtain the following:

(14) Predicted mean infestation = $0.119\ D^{0.453}(1+0.103D^{0.5})$

We tested Eq. 13 and Eq. 14 on our entire data set and found that they performed better than equations from the previous Poisson model, and explained similar proportions of variance in percent colonization ($r^2=0.89$, $p<0.0001$; Fig. 1) and infestation intensity ($r^2=0.82$, $p<0.0001$; Fig. 2), respectively, as our empirical models. The compound Poisson model may also be used to predict the number of unionids having a given level of infestation using Eq. 8; thus, the number of unionids with infestations exceeding a critical threshold, c, may be estimated by calculating $P(k \geq c)$.

Can dreissenid density and infestation be used to predict unionid mortality?

Some studies have linked an increase in the proportion of dead unionids and a decline in living unionid density with an increase in dreissenid density (Hunter and Bailey 1992; Haag et al. 1993; Ohnesorg et al. 1993). We have confirmed these relationships for the unionid population in the

FIGS 6-8 NEAR HERE

Soulanges Canal (Fig. 6). Furthermore, linear regression analysis shows that Dreissena density explains 64% (82% for densities > 10^3 mussels/m^2; Fig. 7), and mean infestation intensity explains 69% (Fig. 8), of the variability in the proportion of dead unionids in populations across the Great Lakes-St. Lawrence River system. These results corroborate previous studies that correlated significant increases in unionid mortality (declines in unionid density) with increases in local Dreissena abundance, both temporally (Arter 1989; Gillis and Mackie 1994) and spatially within a habitat (Hunter and Bailey 1992; Ohnesorg et al. 1993). Infestation intensity would probably explain an even greater amount of the variance in unionid mortality if the size-structure (biomass) of attached dreissenids is considered. Haag et al. (1993) hypothesized that a unionid suffers an energy loss in maintaining its proper orientation in the substrate under the destabilizing weight of dreissenids concentrated on its posterior shell; a cluster of large dreissenids may therefore cause a greater impact than the same number of smaller (e.g., young-of-the-year) mussels.

The variance in unionid mortality that is explained by Dreissena is remarkable, given that much of the decline of native freshwater mussels during the past century has been attributed to habitat destruction from impoundment, erosion, channelization, and contaminants (see Williams et al. 1993 for review). For example, a decline in water quality coupled with periodically low oxygen levels is the hypothesized cause of the long-term reduction of a rich unionid population in western Lake Erie (Nalepa et al. 1991b). However, although water quality in the Great Lakes has generally improved in recent years following phosphorus abatement (Great Lakes Water Quality Board 1987; Nicholls and Hopkins 1993), high mortality and local extinction of unionid communities have recently occurred in western Lake Erie (Haag et al. 1993), eastern Lake Erie (Maleski and Masteller 1994), Lake St. Clair (Hunter and Bailey 1992; Gillis and Mackie 1994), the Detroit River (Ohnesorg et al. 1993), and the upper St. Lawrence River (this study), wherever high densities of Dreissena have become established. Therefore, the introduction of Dreissena may be the critical stress that causes the extirpation of threatened unionid populations throughout most of North America.

Since habitat characteristics may be used to predict dreissenid densities (Ramcharan et al.

1992; Mellina and Rasmussen 1994), they may also indirectly predict unionid impacts. Impacts should therefore be maximal in lentic habitats with high pH, high calcium and low phosphate concentrations, i.e., habitats that typically support high densities of Dreissena (Ramcharan et al. 1992; Mellina and Rasmussen 1994). These limnological variables may also prove useful in predicting infestation intensities on unionids, including the critical thresholds that precede significant population declines. At present, there are few available data from which the density and infestation thresholds that cause mortality may be accurately determined. Although minor impacts such as shell deformities have been reported at mean infestations as low as 20 dreissenids/unionid (Lewandowski 1976), heavy mortality and extirpations in lakes are often associated with mean infestations on the order of 10^2/unionid. Significantly reduced survival was observed in Lake Erie populations having a mean infestation of 216/unionid (Haag et al. 1993), and a mean infestation of 642/unionid preceded the extirpation of unionids at a site in Lake St. Clair (Gillis and Mackie 1994). Hundreds of attached zebra mussels were found on unionids in Lake Balaton, Hungary (Sebestyen 1935, cited in Lewandowski 1976), less than two years before the unionid population suffered a major decline (Wagner 1936; Sebestyen 1938). However, some evidence suggests that, at least for some unionid populations, the mortality threshold is much lower than that which has been observed for these large lentic habitats. Very few unionids from our upper St. Lawrence River sites were found alive with infestations exceeding 100 dreissenids/unionid, even though a large number of dead unionids were found with these infestation levels (Ricciardi, pers. obs.); a sharp increase in mortality among unionids in Soulanges Canal occurred when the mean infestation reached 20/unionid (Fig. 6), at a zebra mussel field density near 4000/m^2. Unionid mortality increased noticeably in a small inland lake when the mean infestation exceeded 70/unionid at a Dreissena density near 1000/m^2 (Garton 1994; D.W. Garton, Indiana University, Kokomo, Indiana 46904-9003 U.S.A, pers. comm.). When we excluded sites with densities less than 1000/m^2, we obtained a much stronger correlation (r^2=0.815, p<0.0021) between mortality and Dreissena density (Fig. 7), suggesting that mortality sharply increases at Dreissena densities above 1000/m^2. According to this model, unionid mortality greater than 90% is associated with Dreissena densities exceeding 6000/m^2. The mean and maximum infestation intensities are near 100/unionid and 700/unionid, respectively, at these densities (Fig. 2). Therefore, a *Dreissena* density of 1000/m^2 appears to be a critical threshold above which unionid mortality increases significantly with *Dreissena* density until the population becomes virtually extirpated at a density and mean infestation intensity of approximately 6000/m^2 and 100/unionid, respectively. These critical values probably vary according to the size-structure of attached dreissenids and the species composition of the unionid population.

Unionid morphologies and behaviours (e.g., burrowing activity) that are intrinsic to gender or species may potentially enhance or reduce fouling, and thus cause differential impacts within a unionid population (Haag et al. 1993). In Europe, *Dreissena* occurs more frequently and in greater numbers on *Anodonta* shells than on *Unio* shells (Kuchina 1964; Lewandowski 1976; Arter 1989), probably because *Unio* is almost completely buried in its natural position in the substrate and thus provides little surface area for colonization, whereas *Anodonta* normally exposes a large portion of its shell (Arter 1989). In the Mississippi River, unionids are differentially colonized; thick-shelled, ornamented species are more heavily colonized than thin-shelled, unornamented species (Tucker 1994). Species-specific and sex-specific differences in impacts and survival are likely to become significant after infestation levels rise (Haag et al. 1993). Differences in mortality among infested species have already been observed in Lake St. Clair (Hunter and Bailey 1992; Gillis and Mackie 1994) and Lake Erie (Haag et al. 1993).

In habitats that support *Dreissena* densities of at least 1000/m^2, virtually all unionids become infested in 2-3 years, as found in Lake St. Clair (Gillis and Mackie 1994), the Detroit River (Ohnesorg et al. 1993), eastern Lake Erie (Masteller and Schloesser 1992), the upper Mississippi River (Tucker 1994), and the upper St. Lawrence River (Ricciardi 1994). High infestation and heavy mortality may occur shortly thereafter, if the local dreissenid density continues to rise. Large numbers of dead unionids were found washed up on shore, and unionid populations declined noticeably, less than five years after *Dreissena* invaded Lake Balaton (Wagner 1936; Sebestyen 1938). Severe (90-100%) reductions in unionid density were recorded in Lake St. Clair (Gillis and Mackie 1994) and the Detroit River (Ohnesorg et al. 1993) approximately four years after *Dreissena* invaded these habitats.

Similarly, an 83% decline in unionid density in Presque Isle Bay, Lake Erie, occurred three years after the establishment of a Dreissena population (Maleski and Masteller 1994). The unionid population around Kelley's Island in western Lake Erie was virtually eliminated five years after Dreissena invaded the region (J. R. Hageman, F.T. Stone Laboratory, Put-in-Bay, Ohio, 43456-0119 USA, personal communication). Unionid communities in the upper St. Lawrence River appear to be following the same pattern; in the Soulanges Canal, unionid density has varied inversely with Dreissena density over time and the population is on the verge of extirpation, four years after Dreissena became established in that section of the river (Ricciardi, In prep.). These data suggest that the extirpation of a unionid population will occur within 4-5 years of a Dreissena invasion, provided that the Dreissena population grows to sufficient levels (> 6000/m^2). Viable unionid populations in North America may ultimately be restricted to soft-water habitats or geographic regions that are either invulnerable to Dreissena invasion or support very low densities of dreissenids (Strayer 1991; Ramcharan et al. 1992; Mellina and Rasmussen 1994).

Conclusions

Our study demonstrates that the infestation of unionids by Dreissena follows a very predictable pattern with increasing dreissenid density. The proportion of unionids colonized by Dreissena follows a saturation curve with rapid colonization at Dreissena densities up to 200/m^2. Dreissenids aggregate preferentially on unionids, forming a cluster whose size is correlated with the total population density of Dreissena in the habitat. These infestations may be accurately described by a compound Poisson model that takes into account the clustering tendency of young-of-the-year dreissenids. Unionid mortality (reflected by the proportion of recently dead unionids in a population) associated with these infestations varies strongly with the local Dreissena density. We predict sharply accelerated mortality at Dreissena densities above 1000/m^2, and heavy (>90%) mortality of unionids when the Dreissena density and mean infestation intensity reach 6000/m^2 and 100 dreissenids/unionid, respectively.

Extirpation of unionid populations will occur within five years after the establishment of Dreissena in habitats that support dreissenid densities of at least 6000/m^2. The general significance of these thresholds can be further tested as the Dreissena invasion of North American drainages continues and densities increase.

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Table 1. Field data used in the analysis. Numbers in parentheses for St. Lawrence River sites are standard errors.

Site	Dreissena Density No./m^2	Unionid Density No./m^2	% of Unionids Colonized	Mean No. of Dreissena per Unionid	Max. No. of Dreissena per Unionid	Sources of data
St. Lawrence River						
Soulanges Canal						
East site 1992	1990 (384)	21.0 (3.4)	74	3.1 (0.6)	12	1, 2
East site 1993	1819 (283)	15.0 (4.7)	95	9.9 (0.9)	75	1, 2
East site 1994	3712 (247)	3.0 (1.7)	100	19.6 (6.0)	61	1
West site 1994	2944 (539)	5.3 (3.4)	100	43.8 (9.2)	134	1
L. St. Louis-1 1992	101 (21)	19.2 (4.0)	58	0.8 (0.2)	4	1
L. St. Louis-2 1992	123 (28)	48.0 (9.2)	59	1.3 (0.4)	6	1
L. St. Louis-2 1994	851 (307)	48.6 (16.0)	62	8.7 (3.8)	92	1
L. St. François 1992	165 (39)	120.5 (16.0)	55	1.2 (0.04)	9	1
Port of Montréal 1994			100	23.1 (2.8)	42	1
Laurentian Great Lakes						
L. St. Clair-2	48.0	5.7	70	2.3		3
L. St. Clair-3			87	4.3		3
L. St. Clair-4			47	1.4		3
L. St. Clair-5			60	1.9		3
L. St. Clair-7	195.0	11.3	90	8.2	38	3
L. St. Clair-8			92	17.1		3
L. St. Clair-9			73	1.7		3
L. St. Clair-10			93	3.9		3
L. St. Clair-13	6000.0			5496.0	10520	4, 5
L. St. Clair-Puce	5000.0	1.7	100	642.0	1991	4, 6
L. Erie-Presque Ile			100	234.0		7
Western L. Erie	15000.0		100	216.0		8, 9, 10
Monroe Canal	700000.0			6777.0	10732	11
Mississippi River Basin						
Peoria	1.2	12.0	10	0.1		12
LaGrange	1.2	6.4	6	0.1		12
Alton	7.3	8.2	27	0.6		12
L. Swan-outflow	0.3	12.9	2			12
L. Swan-interior	2.7	8.7	20			12

Table 1. (Continued).

Site	Dreissena Density No./m²	Unionid Density No./m²	% of Unionids Colonized	Mean No. of Dreissena per Unionid	Max. No. of Dreissena per Unionid	Sources of data[a]
Grafton	1.5	4.9	27	0.3		12
Piasa Creek	1.1	2.3	18	0.3		12
Mile 217			100	37.3	219	13
Mazurian Lakes, Poland						
L. Mikolajskie 1972	700.0	0.4	85	20.0	99	14, 15, 16
L. Mikolajskie 1974	1000.0		92	52.0	132	14
L. Beldany	25.0				40	14
L. Jagodne	125.0				80	14
L. Sniardwy	425.0				85	14
L. Niegocin	1300.0				186	14

[a] Sources of data: 1) This study; 2) Ricciardi 1994; 3) Hebert et al. 1989; 4) Griffiths 1993; 5) Hebert et al. 1991; 6) Gillis and Mackie 1994; 7) Masteller and Schloesser 1992; 8) Haag et al. 1993; 9) Garton and Haag 1993; 10) J.R. Hageman, F.T. Stone Laboratory, Put-in-Bay, Ohio, pers. comm.; 11) Schloesser and Kovalak 1991; 12) Tucker et al. 1993; 13) Tucker 1994; 14) Lewandowski 1976; 15) Stanczykowska 1975; 16) Stanczykowska et al. 1976.

Table 2. Ranges and mean values of field data in Table 1.

Variable	Range	Mean (S.E.)	Median	N
Dreissena field density	0.3 - 700000	27464 (25874)	195.0	27
Unionid density	0.4 - 120.5	18.9 (6.3)	8.7	19
% unionids colonized	2.0 - 100	66.7 (6.0)	73.5	30
Mean no. of Dreissena per unionid	0.1 - 6777	454.3 (285.6)	6.3	30
Max. no. of Dreissena per unionid	4.0 - 10732	1227.9 (725.2)	82.5	20

Table 3. Data on unionid mortality, with associated infestation intensity and zebra mussel density from sites in the Great Lakes-St. Lawrence River system.

Site	Dreissena Density No./m^2	No. of Dreissena per Unionid	Proportion of dead unionids	Reference
L. St. Clair-West	152		3.8	Hunter and Bailey 1992
L. St. Clair-Central	2847		52.6	Hunter and Bailey 1992
L. St. Clair-East	11655	c.5500	98.0	Hunter and Bailey 1992; Hebert et al. 1991
L. St. Clair-Puce	5000	642	98.4	Gillis and Mackie 1994
L. Erie, Put-in-Bay		216	32.4	Haag et al. 1993
L. Erie, Kelley's Island		216	43.2	Haag et al. 1993
Detroit River	c.5000		90.0	Ohnesorg et al. 1993
L. St. François 1992	165	1.2	14.7	This study
L. St. Louis 1992	123	1.3	27.3	This study
Port of Montréal 1994		23.1	39.0	This study
Soulanges Canal-East 1992	1990	3.1	16.6	This study
Soulanges Canal-East 1993	1819	9.9	25.0	This study
Soulanges Canal-East 1994	3712	19.6	57.0	This study
Soulanges Canal-West 1994	2944	43.8	60.0	This study

Table 4. Linear regression models used to predict infestation and impact on unionids[a].

Model	r^2	p	n	SE_{est}
$LOG_{10}(AVGINFEST) = 0.812\ LOG_{10}(DENSITY) - 1.073$	0.807	<0.0001	21	0.630
$SIN^{-1}(PCOL^{0.5}) = 0.302\ LOG_{10}(DENSITY) + 0.332$	0.902	<0.0001	21	0.150
$LOG_{10}(MAXINFEST) = 0.751\ LOG_{10}(DENSITY)$	0.584	<0.0001	18	0.641
$SIN^{-1}(PMORT^{0.5}) = 0.498\ LOG_{10}(DENSITY)$	0.644	<0.0029	11	0.269
[b]$SIN^{-1}(PMORT^{0.5}) = 1.350\ LOG_{10}(DENSITY) - 3.858$	0.815	<0.0021	8	0.181
$SIN^{-1}(PMORT^{0.5}) = 0.262\ LOG_{10}(AVGINFEST) + 0.363$	0.692	<0.0015	11	0.213

[a] Abbreviations used:
AVGINFEST= Mean no. of Dreissena per unionid;
MAXINFEST= Maximum no. of Dreissena per unionid.
DENSITY= Dreissena field density (No./m^2);
PCOL= Proportion of unionids colonized by Dreissena;
PMORT= Proportion of dead unionids in a population.

[b] Excluding Dreissena densities < 1000/m^2

Table 5. Percentage increases in *Dreissena* infestation of unionids.

Site	Year	Percentage of unionids colonized	Mean no. of *Dreissena* per unionid	% Increase in infestation
L. Erie (east)[1]	1990	100	121	
	1991	100	234	93%
L. Mikolajskie (Poland)[2]	1972	85	20	
	1974	92	52	160%
Soulanges Canal (east site)[3]	1992	74	3.1	
	1993	95	9.9	219%
L. St. Clair (Puce, Ont.)[4]	1989	c.100	143	
	1990	c.100	642	349%

[1] Masteller and Schloesser 1992.
[2] Lewandowski 1976.
[3] Ricciardi 1994.
[4] Gillis and Mackie 1994.

Table 6. Variance to mean ratios for young-of-the-year (YOY) and adult dreissenids attached to unionids (n=146) in the upper St. Lawrence River)[1].

	Mean number per unionid, m	Variance, s^2	s^2/m
YOY dreissenids	3.2	46.9	14.7
Adult dreissenids	4.9	18.3	3.7

[1] Note that a contagious distribution is indicated by values of $s^2/m > 1$ (Elliott 1977).

FIGURE LEGENDS

FIG. 1. Proportion of unionids colonized by Dreissena versus Dreissena field density over the range 0-1000/m^2; values greater than 1000/m^2 converge to 100% colonization (Table 1) and are omitted for clarity. Closed circles denote observed values; open circles denote values predicted by the compound Poisson model (Eq. 14).

FIG. 2. Mean infestation intensity versus Dreissena field density (both variables are $\log_{10}$-transformed). Curved line denotes infestation predicted by the compound Poisson model (Eq. 14). Straight line denotes infestation predicted by linear regression model (Table 4). Points represent observed values from Table 1.

FIG. 3. Maximum infestation intensity versus Dreissena field density (both variables are $\log_{10}$-transformed). Closed circles denote lentic habitats ($Y = 1.095\ X$, $r^2=0.69$, $p<0.001$); open circles denote lotic habitats ($Y = 0.880\ X - 1.202$, $r^2=0.91$, $p<0.005$). Regression lines are significantly different (ANCOVA, $p<0.005$).

FIG. 4. Mean infestation intensity plotted against the percentage of unionids colonized by Dreissena.

FIG. 5. Variance versus mean infestation intensity (both variables are $\log_{10}$-transformed). Solid line represents 100% correspondence between mean and

variance.

FIG. 6. Upper graph: Changes in the density of living unionids and the percentage of dead unionids in the population at the Soulanges Canal (east site), 1992-1994. Lower graph: Changes in Dreissena infestation intensity on unionids over this same time period.

FIG. 7. Proportion of dead unionids in a population ($\sin^{-1}x^{0.5}$ transformed) versus Dreissena field density ($\log_{10}$-transformed). Line denotes $Y = 1.350 X - 3.858$.

FIG. 8. Proportion of dead unionids in a population ($\sin^{-1}x^{0.5}$ transformed) versus infestation intensity ($\log_{10}$-transformed): $Y = 0.262 X + 0.363$.

Fig. 1

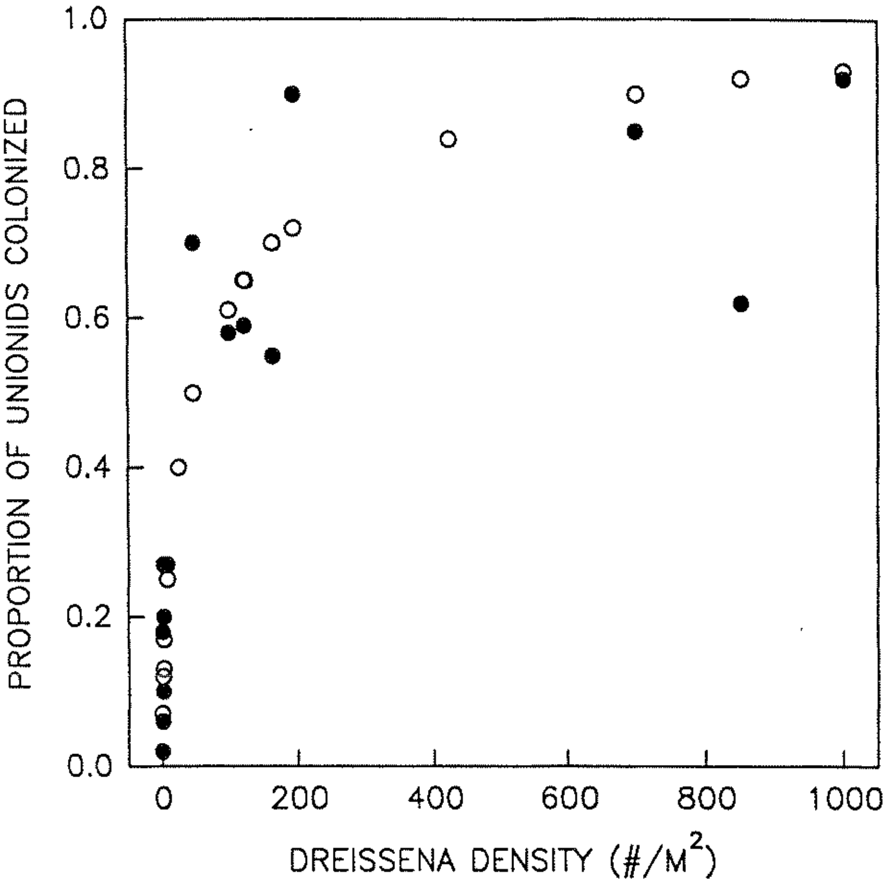
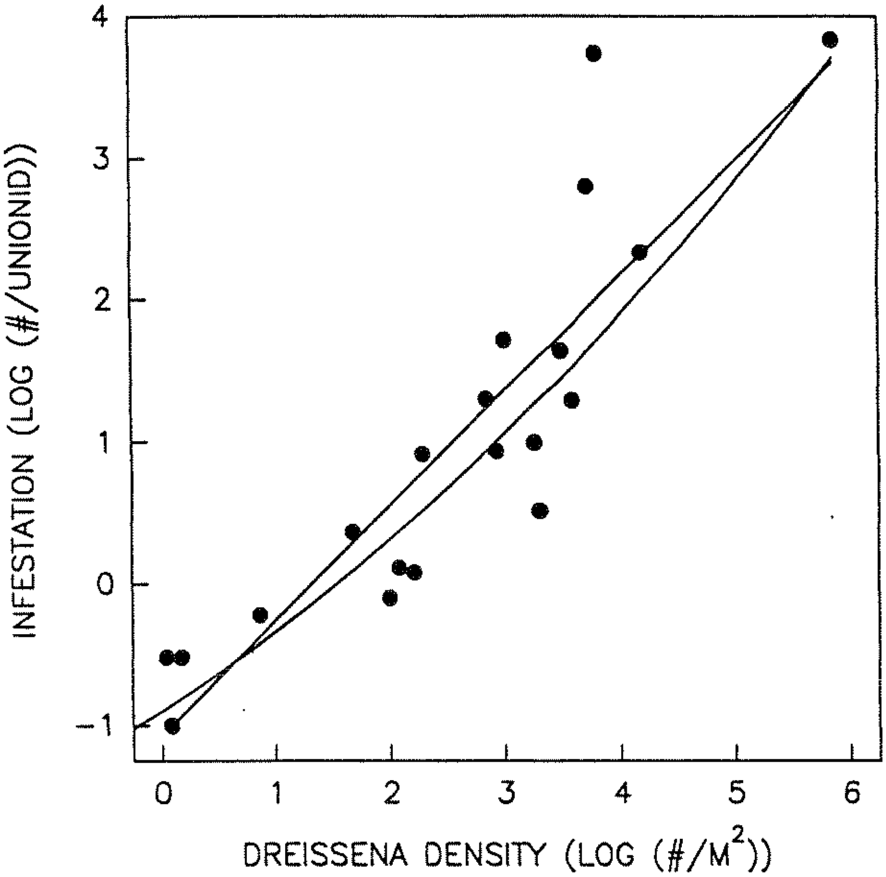
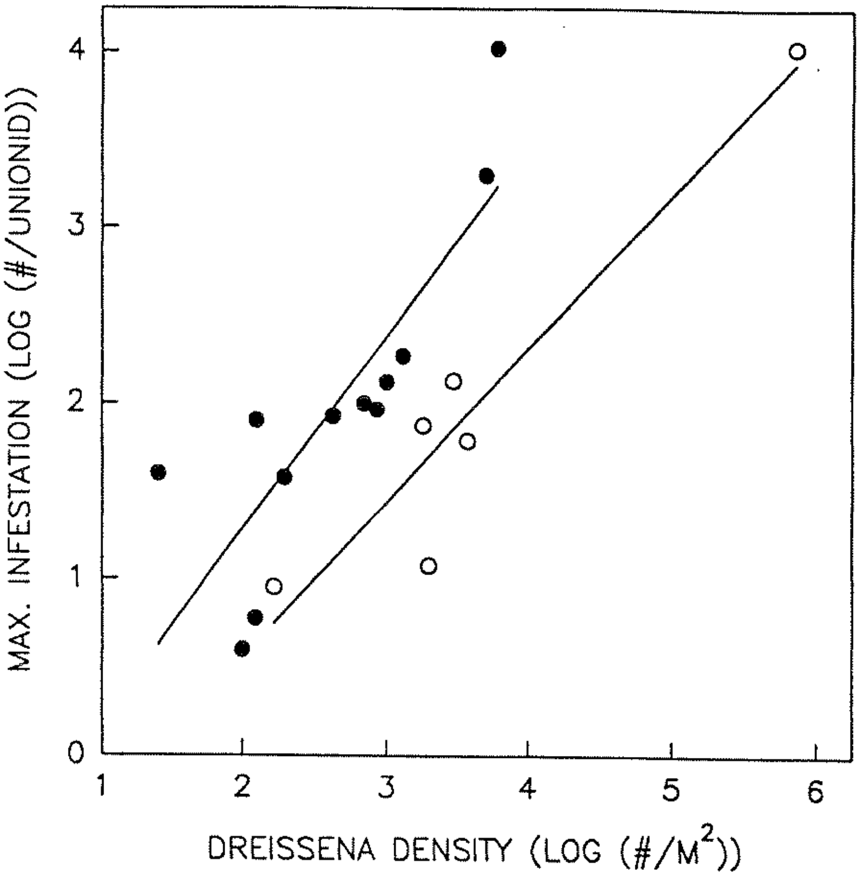

PROPORTION OF UNIONIDS COLONIZED
1.0
0.8
0.6
0.4
0.2
0.0
0
200
400
600
800
1000
DREISSENA DENSITY (#/M^2)

FIG. 2



4
3
2
1
0
−1
INFESTATION (LOG (#/UNIONID))
0
1
2
3
4
5
6
DREISSENA DENSITY (LOG (#/M^2))

Fig. 3



MAX. INFESTATION (LOG (#/UNIONID))
0
1
2
3
4
1
2
3
4
5
6
DREISSENA DENSITY (LOG (#/M²))

FIG. 4

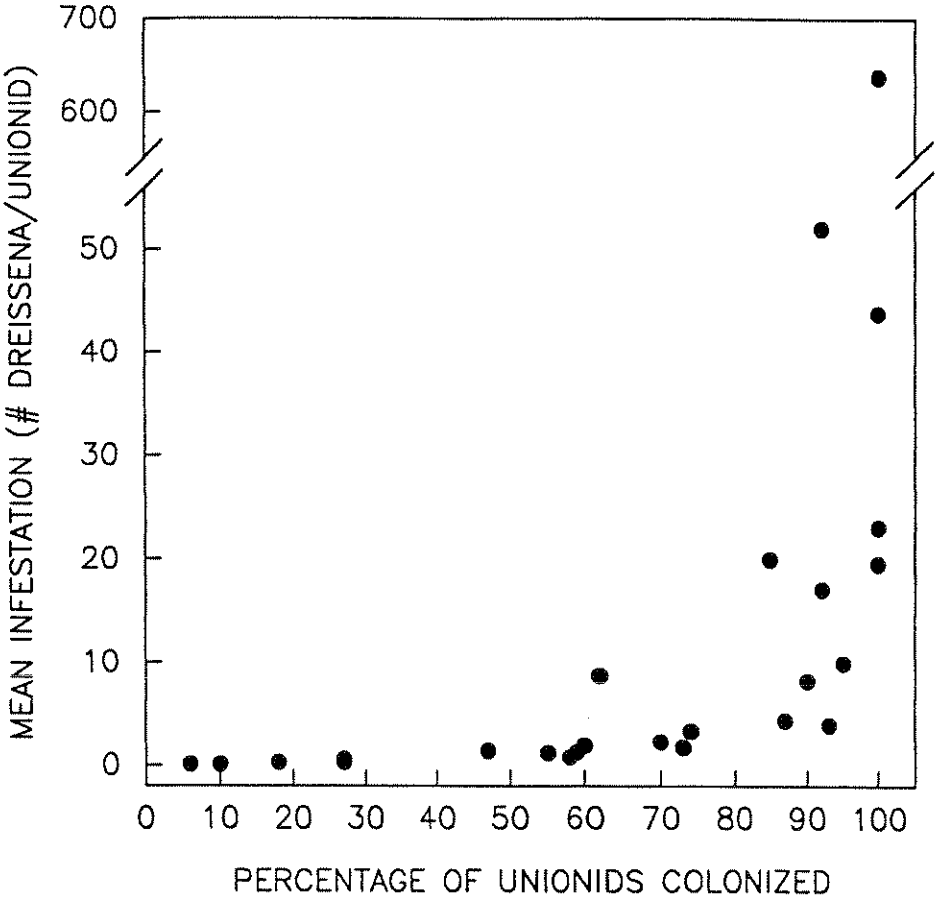

700
600
50
40
30
20
10
0
0
10
20
30
40
50
60
70
80
90
100
MEAN INFESTATION (# DREISSENA/UNIONID)
PERCENTAGE OF UNIONIDS COLONIZED

FIG. 5

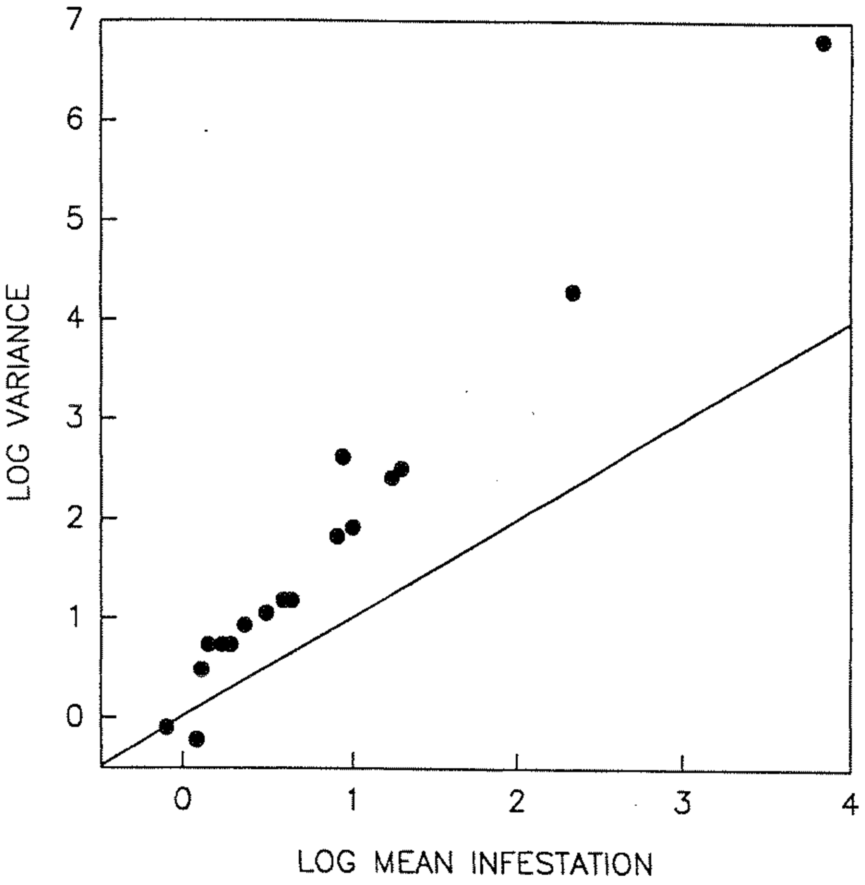
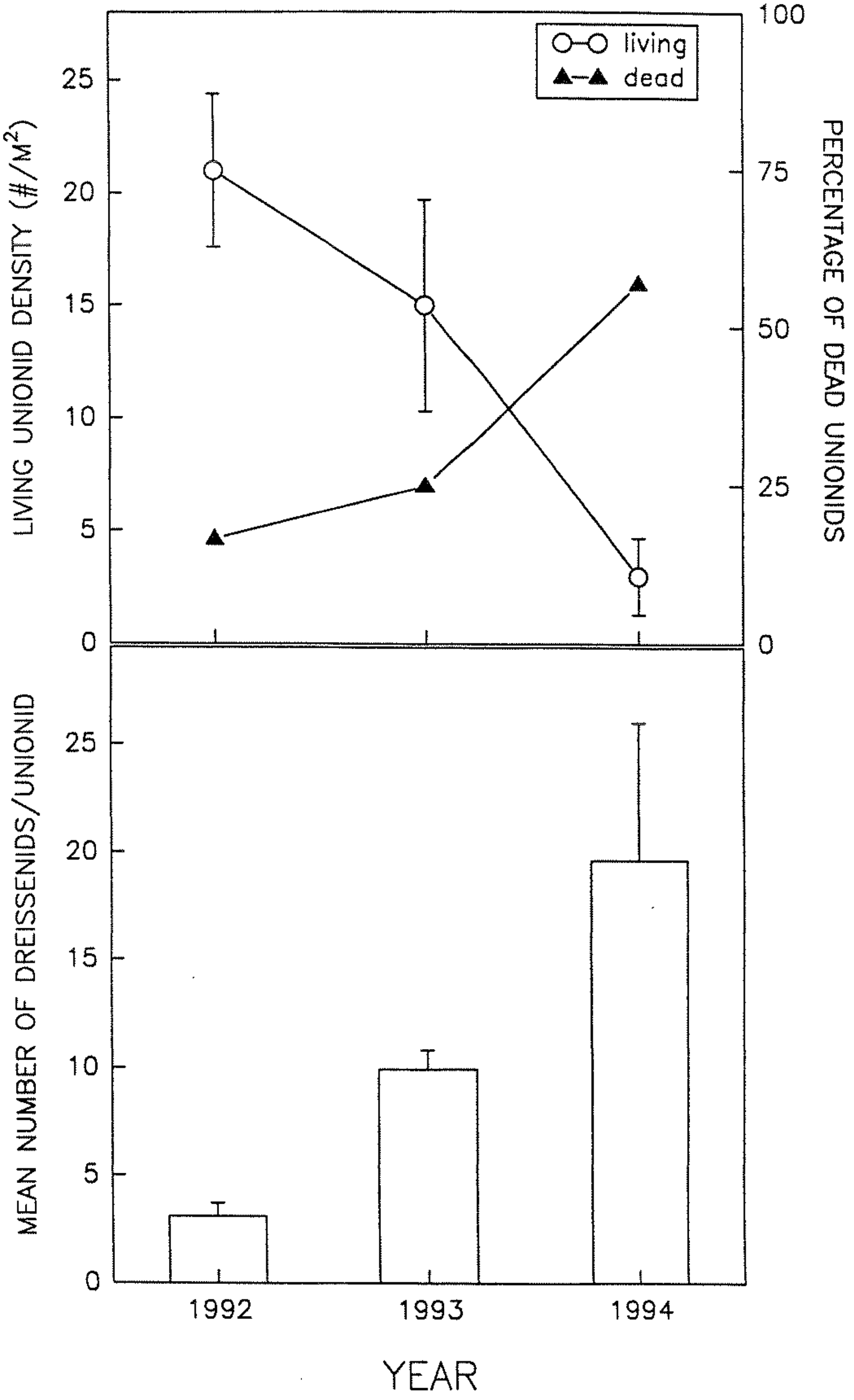
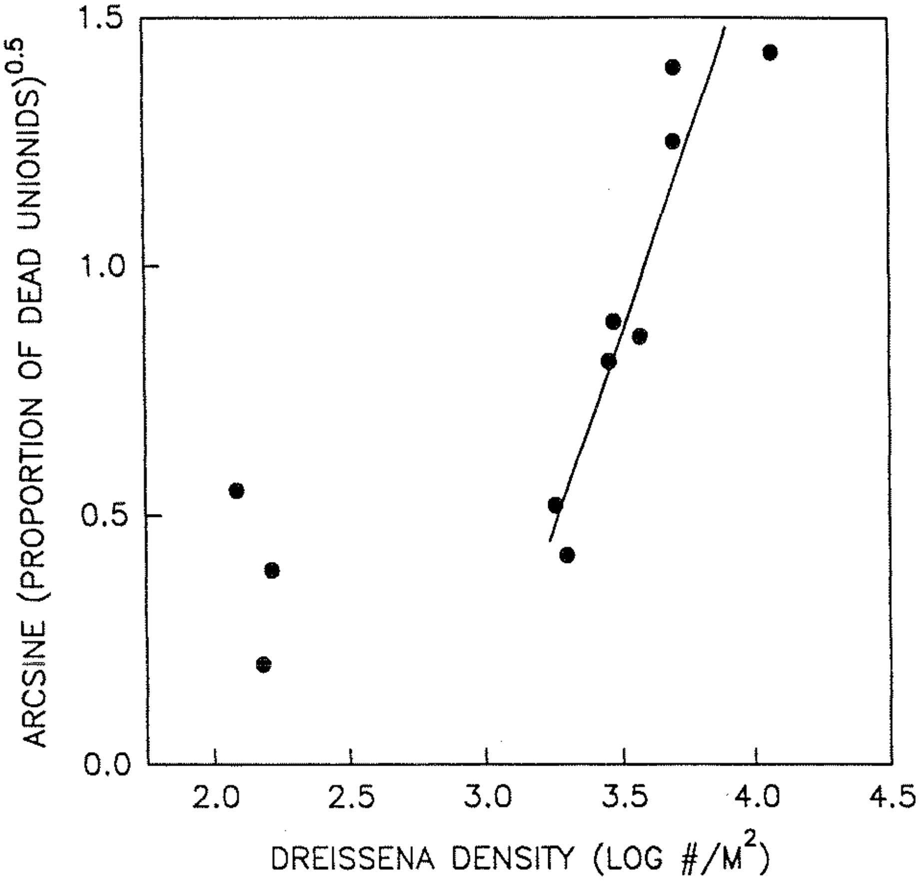


FIG. 6



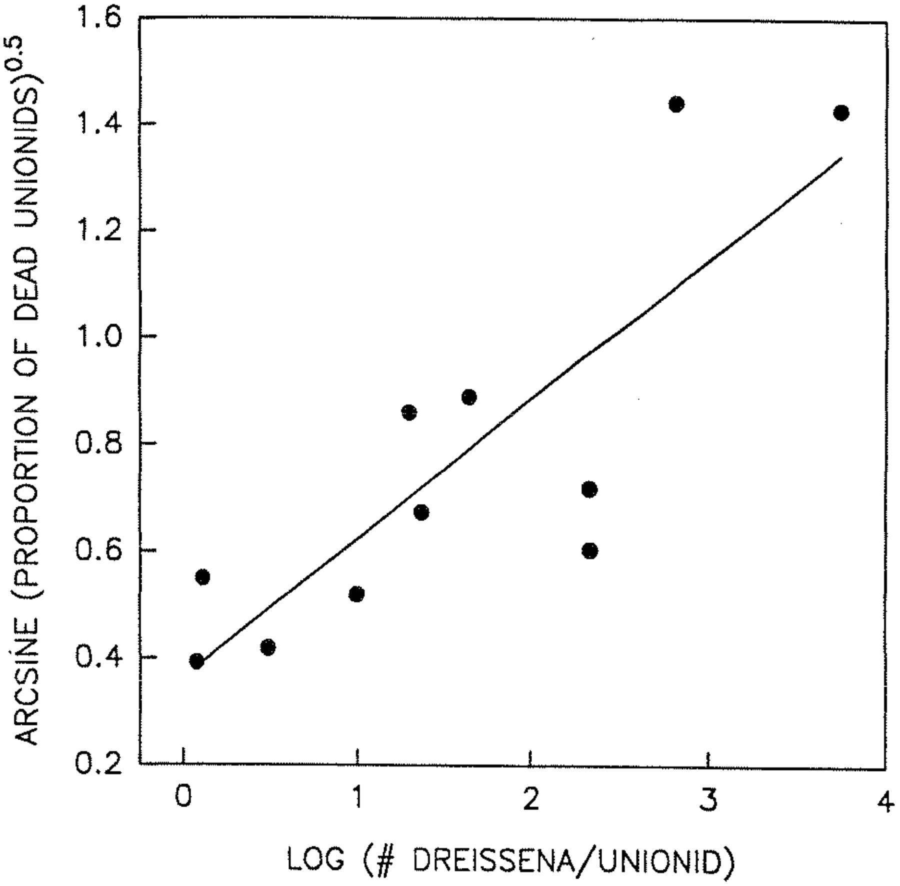
living
dead
LIVING UNIONID DENSITY (#/M²)
PERCENTAGE OF DEAD UNIONIDS
0
5
10
15
20
25
0
25
50
75
100
MEAN NUMBER OF DREISSENIDS/UNIONID
0
5
10
15
20
25
1992
1993
1994
YEAR

FIG. 7



ARCSINE (PROPORTION OF DEAD UNIONIDS)$^{0.5}$
1.5
1.0
0.5
0.0
2.0
2.5
3.0
3.5
4.0
4.5
DREISSENA DENSITY (LOG #/M^2)

FIG. 8



1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
1
2
3
4
ARCSINE (PROPORTION OF DEAD UNIONIDS)$^{0.5}$
LOG (# DREISSENA/UNIONID)