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J. R. Straka
Iowa State University

J. A. Downing
Iowa State University, downing@iastate.edu

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Distribution and Abundance of Three Freshwater Mussel Species (Bivalvia: Unionidae) Correlated with Physical Habitat Characteristics in an Iowa Reservoir

J. R. STRAKA¹ and J. A. DOWNING

Department of Animal Ecology, Iowa State University, Ames, Iowa 50011

A rapid drawdown (<4 weeks) of a reservoir allowed us to determine the combined influence of water depth, maximum effective fetch, bottom slope, and substrate characteristics on abundance of three species of freshwater mussels. The three principal mussel species were significantly ($P < 0.001$) correlated in different ways with characteristics of their physical habitat, implying separation of habitat requirements. *Pyganodon grandis* (Say) was most abundant on deeper shelves (ca. 3 m depth, slope <0.15 m/m, where fetch was great (>1 km), and sediment organic matter content was moderate (<3.5%). *Lampsilis siliquoidea* (Barnes), however, was most abundant in shallow water (<1.5 m), in flat, sheltered areas with low slope (<0.10 m/m) and fetch (<0.4 km), on substrates with 1-3% organic matter content. *Potamilus alatus* (Say) had a more cosmopolitan depth distribution, but was found only on bottoms with low slope (<0.01 m/m), where fetch was less than 0.8 km. The results of this study agree with previous studies with one important exception. Abundance of *Pyganodon grandis* was found to be negatively affected by increasing substrate organic matter content. This result stands in contrast to other studies that have suggested that abundance of *Pyganodon grandis* was positively correlated with substrate organic matter content.

INDEX DESCRIPTORS: Unionidae, *Pyganodon*, *Potamilus*, *Lampsilis*, habitat, reservoir, depth, fetch, bottom slope, substrate, spatial distribution, population density.

Freshwater mussels are an ecologically important group of organisms that are poorly understood and many are declining rapidly to extinction. Mussels may be the most endangered of all animal groups in North America with over 70 percent of mussel species threatened or endangered (Williams et al. 1993). More than seven percent of North American mussel species may have become extinct in the last century alone. Their loss will impact the ecology of fish populations, phytoplankton, benthic communities, and the water chemistry of those ecosystems (see review by Downing and Downing 1992).

Mussels are of economic and historic importance. Mussels are the source of freshwater pearls (Kunz 1893, Lopinot 1967, Thiel and Fritz 1993), and buttons (Coker 1919, O'Hara 1980). For example, from 1989 through 1990, over 6 million kilograms of mussels were harvested from the Mississippi and Illinois rivers, valued at greater than \$9 million (Thiel and Fritz 1993). Mussels were used by indigenous cultures as a food source (Parmalee and Klippel 1974, Stoltman 1983, Lightfoot et al. 1993), as temper in pottery (Stoltman 1983, Roosevelt et al. 1991), as tools (Gradwohl 1982, Stoltman 1983), and as beads and other jewelry (Stoltman 1983, Yerkes 1983, Seymour 1988).

Habitat degradation has been implicated in the decline of mussel populations (Bogan 1993). Erosion due to agricultural practices and logging can cause increased siltation, which can cover mussel beds (Coker et al. 1921, Hartfield 1993, Mehlhop and Vaughn 1994). Agricultural and industrial effluents introduce fertilizers, herbicides, insecticides, and toxic chemicals which may cause mussel die-offs and decreased viability (Cvancara 1970, Strayer 1980, Keller and

Zam 1991, Keller 1993, Fleming et al. 1995) and reproduction (Mehlhop and Vaughn 1994).

In spite of the ecological, economic, and historic importance of freshwater mussels, basic ecological questions about the suitability of aquatic habitats need to be resolved (Salmon and Green 1983, Strayer et al. 1994). Further, mussel habitats may diverge greatly among species (Parmalee 1967, Clarke 1981). In order to protect mussels, it is necessary to know the factors influencing their distribution and abundance in aquatic ecosystems.

Many factors are thought to influence mussel habitat suitability. Chemical and climatic factors such as pH, alkalinity, food, oxygen, nutrients, and temperature influence the large-scale distribution of freshwater mussels (e.g., Coker et al. 1921, Chamberlain 1930, Wilbur and Owen 1964, Cvancara 1970, Cvancara and Freeman 1978, Green 1980, Rooke and Mackie 1984, Hinch et al. 1986). Within a given ecosystem, however, mussel abundance and distribution is likely to be influenced by physical factors that impact their ability to collect food or stay firmly anchored in the substrate. Wave action and current can positively influence mussel distribution by increasing the amount of food available in the water column (Hinch et al. 1986). Wave action can also dislodge mussels, however, and water currents can cause substrate instability. Therefore, mussel distributions may be negatively affected by extreme wave exposure (Coker et al. 1921, Ghent et al. 1978). High turbidity associated with turbulence may also limit mussel distribution (Cvancara 1970). Because wave energy is greatest in shallow water and in areas of greatest fetch (Håkanson and Jansson 1983), mussels may be rare or absent in exposed, shallow areas of lakes.

The influence of depth on mussel abundance is controversial. Matteson (1948) reported that the abundance of *Elliptio complanata* (Lightfoot) was negatively correlated with depth but ultimately con-

¹ Current Address: Bear Creek Archaeology, Inc., P.O. Box 347, Cresco, IA 52136.

trolled by temperature. Negus (1966) suggested that an interaction between depth and temperature limited *Anodonta* and *Unio* abundance. Green (1980) and Strayer et al. (1981) found a parabolic relationship between the abundance of two species (*Pyganodon grandis* (Say) and *Elliptio complanata*) and depth, with maximum abundances occurring at 2–3 meters. Stern (1983) suggested that mussels are least abundant at great depth, but only because current velocity and substrate type vary along a depth gradient. The influence of depth on mussel distribution may therefore vary with other physical variables.

The effect of bottom slope on mussel abundance is less controversial. Steep slopes may make it impossible for mussels to affix themselves to the substrate. For example, Ghent et al. (1978) found that when slopes were severe, *Pyganodon grandis* was not able to anchor into the substrate and slid into unfavorable habitat. Green (1980) found a negative linear effect of slope on *Pyganodon grandis* abundance. Strayer et al. (1981) also suggested that slope had a negative effect on *Elliptio complanata* abundance. The literature, therefore, suggests that high slopes are detrimental to freshwater mussels, but none of these studies offered quantitative estimates of slopes optimal for mussels.

The influence of substrate composition on mussel distribution and abundance is less clear (Kat 1982). Mussels have been found in a wide variety of substrates, from mud to fine sand and coarse gravel (Parmalee 1967, Clarke 1981). Many mussel species appear to have divergent substrate optima because no systematic effect of substrate type on mussel distribution has been discerned (Parmalee 1967). Both positive and negative effects of mud on species' distributions have been observed (Coker et al. 1921, Cvancara and Freeman 1978, Strayer et al. 1981, Hinch et al. 1986). The literature also suggests varied effects of sand and gravel substrates on the distribution of mussels (Baker 1928, Cvancara 1970, Harman 1972, Stern 1983).

The interaction of substrate composition with other physical variables has resulted in some confusion in the literature. In shallow water lakes, for example, wave action can be extreme (Håkanson and Jansson 1983) leading to coarse and impenetrable substrata, enhancing the danger of being dislodged by turbulence. Coker et al. (1921) suggested that the substrate affinities of mussels may be difficult to interpret because of interactions between substrate type and current velocity and other physical variables. Cvancara (1970) and Stern (1983) both observed that mussels were absent from shifting substrates. Some mussel species can apparently exist in almost any type of substrate if other physical variables are favorable for survival (Cvancara 1970).

In spite of the importance to conservation efforts of determining the habitat characteristics influencing mussel abundance and distribution, analyses of mussel distributions in entire habitats have been rare. This is probably due to the immense sampling effort that would be required to extensively sample large ecosystems. The present study took advantage of a unique research opportunity to determine the factors influencing mussel distribution in an entire reservoir. The level of a 23 year old reservoir was lowered more than 6 m in the autumn of 1995 to allow shoreline armoring and construction of silt dikes and jetties. This allowed us to efficiently locate and sample mussel populations and determine their physical habitat. Thus, we were able to test the influence of water depth, maximum effective fetch, bottom slope, and substrate characteristics on mussel abundance across the entire reservoir.

METHODS

This study was carried out in Big Creek Lake (Fig. 1; 41° 47' 30" N; 93° 43' 45" W). This dimictic, eutrophic (Bachmann et al. 1992) reservoir has a surface area of 357 ha and an annual mean total

phosphorus concentration of 124 µg/L. In autumn of 1995, the water level of Big Creek Lake was drawn down by > 6 m. The draw-down occurred so rapidly (<4 weeks) that mussels were not able to burrow into the sediment or retreat into permanently wet sediments. This allowed the spatial distribution of stranded mussels to be determined at several sites.

Sampling of the lake was stratified from upstream to downstream into three arbitrary sections of equal length. Next, a preliminary survey was carried out by walking the shore of the lake estimating mussel densities by eye. Potential sample sites were placed into one of three arbitrary strata: areas of high, medium, or low mussel density. These strata were used to ensure that sampling sites spanned a wide range of mussel densities along the lake's axis. Sites were also chosen considering depth and slope in order to include a wide range of habitat conditions in the samples.

A total of 27 sites were selected: nine from each lake division (upper, middle, lower), three sites per density stratum per lake division. At each site, a 15 m by 15 m grid was placed on an arbitrary center over what was judged to be the center of the mussels distributed at each site. The grid was oriented with one edge parallel to the shoreline. A stake was placed at the normal zero depth water line on the shore nearest to each site. This stake marked the point on shore from which depths and slopes would be measured using an autolevel. A total of 243–25 m² quadrats were sampled exhaustively for mussels: nine quadrats at each site, nine sites from each lake division, three sites from each mussel density stratum. The loose surface layer of all quadrats was searched by hand for mussels. Our sampling scheme was therefore among the most exhaustive employed in freshwater lakes (Downing and Downing 1992).

All mussel shells visible in part or in whole were collected from each of the nine 5 m by 5 m quadrats at each of the twenty-seven sites. A substrate core sample (2.5 L) was collected from the center of each quadrat in order to determine substrate organic matter content in each sample unit. The sediment core sample was fifteen centimeters in diameter and 15 centimeters deep. Normal water depth estimates were obtained relative to the normal shoreline using an autolevel and stadia rod. The autolevel was positioned on the shoreline perpendicular to each site. Sixteen depth values were recorded at each of the sixteen quadrat corners within each grid. Bottom slope was calculated from the side of the site parallel and nearest the normal shoreline, to the side of the site parallel and farthest from the normal shoreline. Because fetch (a measure of the free water surface over which wind may generate wave action) should be a viable predictor of turbulence at each site, we estimated the maximum effective fetch according to Håkanson and Jansson (1983).

The number of mussels that had been living at each site prior to the draw-down was estimated from the number of whole shells found. We counted whole shells which still contained decaying soft tissue to avoid adding long-dead shells to the estimates of mussel abundance. Shells were identified to species and counted. Identifications were confirmed using several sources (Baker 1928, Burch 1973, Clarke 1981, Cummings and Mayer 1992). Shells were paired with their opposing valve to avoid double counting individuals.

Sediment organic matter in substrate samples taken from each of the 243 quadrats was determined by mass-loss on ignition (Downing and Rath 1988). Each substrate sample was homogenized with a spatula. Three subsamples were then taken from each sample, massed wet, then dried for 24 hours at 70° C to constant mass. The dry samples were then ignited in a muffle furnace for six hours at 500° C and allowed to cool to room temperature in a dessicator. The samples were then massed to determine organic matter loss. Percent loss was calculated as loss on ignition divided by the dry mass of each sample.

Before statistical analysis, the number of mussels found in each

Table 1. Density of freshly dead mussels of each species found at each site. Densities are averaged over all nine 25 m² quadrats at each site and are expressed as number of mussels per m². PG = *Pyganodon grandis*; PA = *Potamilus alatus*; LS = *Lampsilis siliquoidea*; UT = *Unio merus tetralasmus*; CF = *Corbicula fluminea*.

Site	PG	PA	LS	UT	CF
1	0.036	0.049	0	0	0
2	0.022	0.022	0.004	0	0
3	0.036	0.022	0.004	0	0
4	0.036	0.089	0	0	0
5	0.182	0.036	0.080	0.036	0
6	0.089	0.018	0.133	0	0
7	0.147	0.720	0.222	0	0
8	0.022	0.040	0.631	0.004	0
9	0.258	0.067	0	0.004	0
10	0.102	0.027	0	0	0
11	0.036	0.009	0	0	0
12	0.040	0.009	0	0.004	0
13	0.076	0.040	0.018	0	0.004
14	0.204	0.044	0.004	0.076	0.004
15	0.169	0.013	0	0	0.004
16	0.662	0.013	0	0.009	0
17	0.680	0.040	0	0.040	0.009
18	0.204	0.009	0	0	0.004
19	0.044	0.009	0	0	0
20	0.053	0	0.013	0	0
21	0.031	0.004	0	0	0
22	0.138	0	0	0	0
23	0.129	0.004	0	0.009	0
24	0.040	0.004	0	0	0
25	0.218	0	0.004	0	0
26	0.098	0.013	0	0	0
27	0.142	0	0	0	0

quadrat was transformed using a square root transformation to stabilize the variance (Downing and Downing 1992), making them amenable to parametric analysis (Scheffé 1959). This transformation normalized our data. Two shell collections were unrepresentative of natural or living mussel densities and were thus withdrawn from the analyses. One quadrat contained 233 *Pyganodon grandis* shells which were obviously deposited by wind and wave action, while another quadrat was removed from the analyses because the shells were found in an obvious small mammal midden.

Bivariate relationships between the abundance of mussel species and site characteristics were sought using correlation analysis (Green 1979). Multiple regression analysis using backwards elimination variable selection (Hocking 1985) was used to determine the multivariate influences of site characteristics on mussel abundance. The multivariate regression model contained thirteen candidate variables: slope, depth, sediment organic matter content, fetch, the squares of slope, depth, and sediment organic matter content, and the following interaction terms: slope by depth, slope by fetch, slope by sediment organic matter content, depth by fetch, depth by sediment organic matter content, and fetch by sediment organic matter content. Squared terms for slope, depth and sediment organic matter content were included in the regression to determine whether parabolic relationships suggested by previous authors were shown by mussels in this lake. The interaction terms in the analysis were included to test for relationships between mussel abundance and combinations of en-

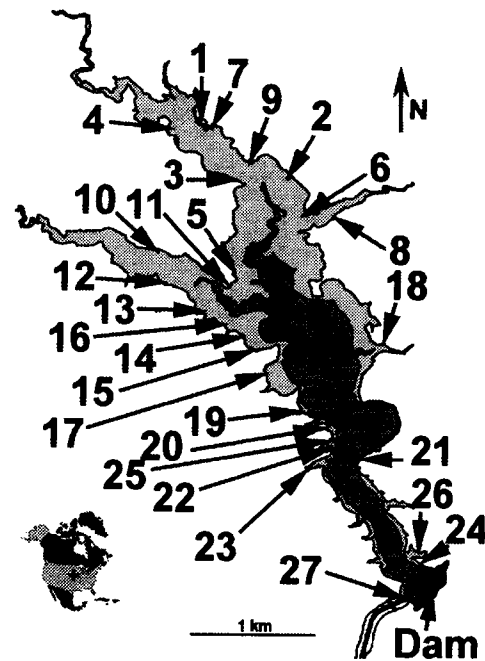


Fig. 1. Location of twenty-seven sampling sites in Big Creek Lake, Polk County, Iowa, USA. The dark gray shaded area indicates the part of the lake that was deeper than the draw-down depth (6 meters).

Table 2. Average values of physical variables for 27 sampling sites at Big Creek Lake, Iowa. Data were collected during November and December of 1995. Z = water depth; S = slope; F = maximum effective fetch; C = sediment organic matter content estimated as loss on ignition. "Quadrat" refers to a 5 m by 5 m sampling unit.

	Z (m)	S (m/m)	F (km)	C (%)
Median	2.16	0.06	0.94	2.09
Mean	2.32	0.11	0.96	2.34
Sample Variance	2.18	0.01	0.25	2.31
Quadrat maximum	5.76	0.48	—	6.7
Quadrat minimum	0.09	0.001	—	0.06
Site maximum	5.44	0.31	1.59	5.73
Site minimum	0.16	0.0062	0.08	0.61

vironmental characteristics. The initial regression model was therefore:

$$A = b_0 + b_1Z + b_2Z^2 + b_3S + b_4S^2 + b_5C + b_6C^2 + b_7F + b_8SZ + b_9SC + b_{10}SF + b_{11}ZC + b_{12}ZF + b_{13}CF \quad (1)$$

where A = square-root transformed abundance, Z = water depth, S = slope, C = sediment organic matter content, F = fetch, and b_0 - b_{13} are fitted regression coefficients. The initial regression was fitted for each species, eliminating insignificant ($P > 0.05$) variables stepwise, beginning with the variable explaining the least variance in mussel abundance (Hocking 1985).

Because multivariate relationships are often difficult to interpret intuitively, three-dimensional response surface plots were used to examine the form of the multidimensional equations. Abundance con-

tours were plotted based on regression predictions made from each final regression equation for each of the mussel species encountered (Straka 1997).

RESULTS

Five species of large bivalves were found in Big Creek Lake (Table 1). In decreasing abundance they were: *Pyganodon grandis* (Say), *Potamilus alatus* (Say), *Lampsilis siliquoidea* (Barnes), *Unio merus tetralasmus* (Say), and *Corbicula fluminea* (Müller). The first four species are native to Iowa's reservoirs, lakes and rivers (Frest 1987) but *Corbicula* is an introduced exotic (Counts 1986).

The spatial distributions of the three most abundant species; *Pyganodon*, *Potamilus*, and *Lampsilis* overlapped throughout the lake. *Pyganodon grandis* was the most prevalent species, made up almost 60 percent of the mussels found, and was the only species that was found at every site (Table 1). The majority of *Lampsilis* (>96%) were collected from the upstream section of the lake. Few *Unio merus* (41) and very few *Corbicula* (6) were found. *Corbicula* are relatively rare within the state of Iowa (Kelly Arbuckle, pers. comm., Counts 1986) while *Unio merus* is most often found in small streams and ponds and is thus probably a holdover from pre-impoundment (pers. comm., Kevin Cummings, Illinois Natural History Survey, Champaign, Illinois). Mussel densities ranged widely among and within sites at Big Creek Lake (Fig. 1, Table 1).

Habitat conditions also varied widely in this lake. Depth of the quadrats ranged from 0.09 m to 5.76 m (Table 2). The sampling sites with the maximum pre-draw-down water depths were recorded in the lower section of the lake, near the dam. The shallowest depth of a sampling site (0.16 m) was found in the upper section, at the northern tip of the lake, near the creek entrance. As is typical in reservoirs (Håkanson and Jansson 1983), there was a general increasing gradient in site depths from the upstream reaches of the lake to downstream sites.

Bottom slopes at various sites varied from 0.006 to 0.31 m/m (Table 2). There was a general increase in average slope from upper lake to lower lake, although the linear correlation is weak ($r^2 = 0.22$, $P < 0.0001$). This is expected since deeper sites, and thus steeper possible slopes, must occur near the dams in reservoirs.

Sites varied from sheltered to very exposed (Fig. 1). The maximum effective fetch varied from 0.08 km to 1.59 km (Table 2). Because the lake is widest in the middle, those sites generally had the greatest maximum effective fetches. The upper section of the lake was generally narrower and therefore lower in fetch. The lake also narrows near the dam, resulting in low maximum effective fetch (<0.56 km) for sites nearest the dam.

Because fetch, slope, and depth were highly variable, so too was estimated substrate organic matter content; however, correlations among environmental variables all had correlation coefficients (r) < 0.35 (Straka 1997). Organic sediments accumulate at unexposed sites of low slope, at greater depths (Håkanson and Jansson 1983). The maximum mean substrate organic content estimate (5.73%) was found at the sheltered site number one (Fig. 1). The minimum mean organic content (0.61%) was close to the organic content of pure silica sand (Håkanson and Jansson 1983). There was a slight tendency for sediment organic matter content to decrease with increasing slope ($r^2 = 0.21$, $P < 0.0001$) (Fig. 2A). This occurs because organic sediments have a specific gravity close to that of water and therefore are less likely to accumulate on steep slopes.

Site characteristics were generally consistent with what would be expected in a reservoir. Such characteristics included the increasing gradient in site depth from upstream to downstream, increasing slope from upstream to downstream, and decreasing substrate organic matter content from upstream to downstream. These observations

indicate that the draw-down did not greatly modify distributions of habitat characteristics like sediment organic matter content. Although there was a slight linear correlation between depth and slope ($r^2 = 0.12$, $t = 5.59$, $P < 0.0001$), the distribution appeared to be slightly parabolic (Fig. 2B). Slope was frequently low at great depth, indicating littoral shelves in the lake basin. Slope was greatest at intermediate depth (2–4 m) indicating the area of transition between the upper and lower shelf. Because correlations among environmental characteristics were weak (i.e., $r < 0.35$, Straka 1997), interpretation of correlations between environment and mussel abundance should be unconfounded by collinearities (Gujarati 1978).

Bivariate correlations between mussel abundance and individual environmental characteristics were generally weak and varied among species. *Pyganodon grandis* were slightly more abundant at sites with great fetch and were less dense with increasing substrate organic content (Table 3). Maximum *Pyganodon* densities appeared between depths of one and three meters. *Potamilus alatus* abundance decreased with increasing slope and depth (Fig. 2C). *Lampsilis siliquoidea* abundance decreased with increasing depth (Fig. 2D). All *Lampsilis* were collected at depths of less than four meters, with almost 92 percent (230) found between one and two meters depth. *Lampsilis* were found primarily (>96%, 242 individuals) in low slope areas (<0.21 m/m) in the upper portion of the lake. In contrast to *Pyganodon*, *Lampsilis* were less abundant at sites where fetch was great. The two least abundant species found at Big Creek Lake, *Unio merus tetralasmus* and *Corbicula fluminea*, showed almost no significant ($P < 0.05$) relationship with environmental characteristics studied here. Densities of *Unio merus tetralasmus* were greatest at depths between one and three meters, although *Unio merus* abundance and depth were not significantly correlated ($r = 0.03$, $P = 0.615$; Table 3). *Unio merus* was never found at depths greater than four meters, at sites where slope was greater than 0.2 m/m, or in substrates that contained >4% organic matter.

Table 4 and Figs. 3A–D show that mussel densities were correlated with several site characteristics in Big Creek Lake. Multiple regression showed that the density of *Pyganodon grandis* generally varied as:

$$A_{PG} = 0.211 + (0.613Z) - (0.110Z^2) + (3.41S) + (1.51F) - (6.95SF) - (0.208CF) \quad (2)$$

where A_{PG} is transformed *Pyganodon grandis* abundance, Z is depth in meters, S is bottom slope in m/m, F is maximum effective fetch in km and C is sediment organic matter content in percent. The interactions and polynomial terms in this equation show that *Pyganodon grandis* abundance was negatively related to bottom slope and sediment organic content, but positively related to fetch and most abundant at intermediate depth.

Lampsilis siliquoidea abundance was negatively correlated with slope, depth and fetch. *Lampsilis* abundance was greatest at intermediate levels of sediment organic matter content. Multiple regression showed that *Lampsilis* varied as:

$$A_{LS} = 2.96 - (0.567Z) - (6.03S) - (0.0681C^2) - (1.97F) + (5.18SF) + (0.0679ZC) + (0.245ZF) + (0.160CF) \quad (3)$$

Potamilus alatus abundance decreased with slope, depth, and fetch. Sediment organic matter content was uncorrelated with *Potamilus* abundance. Multiple regression showed that *Potamilus* abundance varied as:

$$A_{PA} = 1.62 - (0.115Z) - (5.21S) - (0.557F) + (2.96SF) \quad (4)$$

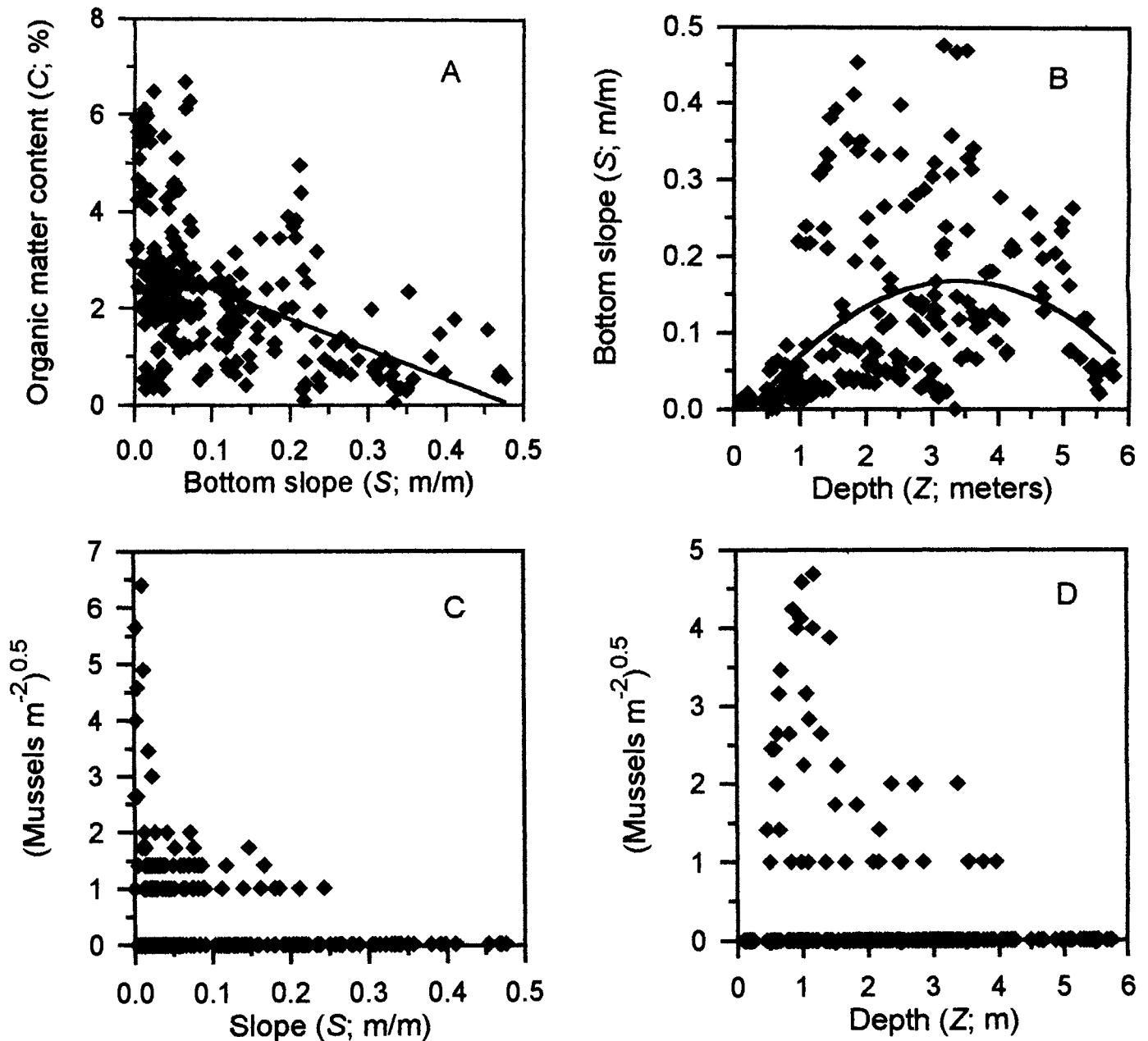


Fig. 2. (A) Relationship between slope and sediment organic matter content found at 27 sites and 243 sampling locations in Big Creek Lake. The line is the least squares regression of the relationship ($r^2 = 0.21$; $P < 0.001$). (B) Relationship between water depth and slope found at 27 sites and 243 sampling locations in Big Creek Lake. The line represents a parabolic fit ($r^2 = 0.12$; $t = 5.59$; $P < 0.0001$). (C) Relationship between the abundance of *Potamilus alatus* and slope at 27 sites and 239 sampling locations at Big Creek Lake ($r^2 = 0.12$; $t = -3.091$; $P < 0.0001$). (D) Relationship between the abundance of *Lampsilis siliquoidea* and water depth at 27 sites and 239 sampling locations in Big Creek Lake ($r^2 = 0.07$; $t = -4.31$; $P < 0.0001$).

DISCUSSION

Although each of the three most abundant species co-occur throughout the lake, they reach their peak abundance in different habitats. *Pyganodon* dominated the mussel fauna at virtually every site, and was particularly abundant in the lower part of the lake while *Potamilus* and *Lampsilis* were most abundant in the upper lake. This agrees with other research which suggests that *Pyganodon* is widely distributed but has an affinity for deep areas with high or-

ganic content (Cvancara and Freeman 1978, Ghent et al. 1978). Some species' mobility may be impaired by mud, or their specific gravity may make them sink in mud and die, so mussels with light inflated shells, such as *Pyganodon*, may be able to inhabit muddy substrates where others are excluded (Hinch et al. 1986, Stern 1983).

Assuming that abundance is an indicator of suitable habitat, *Pyganodon grandis*' suitable habitat appeared to be at a depth of around three meters (Fig. 3A), with slope of less than 0.15 m/m

Table 3. Bivariate correlations between each mussel species abundance and environmental characteristic found in 239 sampling locations at 27 sites in Big Creek Lake. *t*-values represent tests to determine whether abundance and environmental characteristic distributions overlap. Each *r* represents correlation between mussel species abundance and the environmental characteristic. *P*-values are the probability of each correlation being found by chance alone. "ns" represent correlations that are not significant ($P < 0.05$).

Species	Independent Variables	<i>r</i>	<i>P</i>
<i>Pyganodon grandis</i>	depth	-0.045	ns
	slope	0.077	ns
	fetch	0.200	0.002
	organic	-0.245	<0.001
<i>Potamilus alatus</i>	depth	-0.316	<0.001
	slope	-0.346	<0.001
	fetch	-0.141	0.017
	organic	0.173	0.011
<i>Lampsilis siliquoidea</i>	depth	-0.265	<0.001
	slope	-0.224	0.001
	fetch	-0.200	0.001
	organic	0.010	ns
<i>Unio merus tetralasmus</i>	depth	-0.032	ns
	slope	-0.084	ns
	fetch	0.141	0.027
	organic	-0.084	ns

(Figs. 3A and B), at fetch of greater than one kilometer, and in substrate containing less than 3.5% organic matter (eq. 2). Intermediate depth and substrate organic matter content, low slope, and high fetch may be important to *Pyganodon* abundance for several reasons. Turbulence due to high fetch at low depth may cause mussels to become unstable or dislodged from their substrate and thus

become an important source of mortality. Therefore, at intermediate depth, mussels may be able to remain firmly anchored to the substrate. Because the turbulence due to wave action decreases with increasing depth (Håkanson and Jansson 1983), deposition of previously suspended sediments occurs which could bury mussels. This may be why *Pyganodon* were most abundant in substrates with intermediate organic matter content at intermediate depth. *Pyganodon* abundance may be dependent on high fetch to increase turbulence and therefore suspend food particles in the water column.

The majority of *Lampsilis siliquoidea* were found in the upper part of the lake. *Lampsilis* was most abundant at slope less than 0.10 m/m (Fig. 3C), depths less than 1.5 m, in areas of low fetch (<0.4 km), and in substrate containing between one and three percent organic matter (Fig. 3C and D, eq. 3). Generally, *Lampsilis* were found in parts of the lake that were calm, low slope, intermediate depth areas where substrate organic matter content was not very high. This is in contrast to *Pyganodon* that were found in high fetch areas. Low fetch in shallow water may result in increased deposition due to decreased turbulence. *Lampsilis* may be abundant in intermediate organic matter substrates because sediment deposition may provide a food source, if *Lampsilis* engages in a significant amount of deposit feeding. *Lampsilis* abundance may also depend upon stable substrate which results from low fetch and low slope.

Like *Pyganodon grandis*, *Potamilus alatus* was also distributed throughout the lake, however, *Potamilus* was most abundant upstream. Substrate organic matter content had little influence on *Potamilus* abundance agreeing with previous descriptions of *Potamilus* habitat preference as relatively cosmopolitan (Clarke 1981, Cummings and Mayer 1992). *Potamilus* occurred at a broad range of depths (0.3–5 m), but only at low slope (<0.01 m/m) and low fetch (<0.8 km). *Potamilus* appeared to require the flattest habitat compared to *Pyganodon* and *Lampsilis*.

Mussel densities found at Big Creek Lake were low (cf. Downing and Downing 1992) but appeared to be consistent with those in other young, eutrophic reservoirs. Downing and Downing (1992) report *Pyganodon grandis* densities in oligotrophic to mesotrophic lakes in northern Minnesota and southern Quebec to range from 0.2–

Table 4. Results of regression analyses examining the statistical influence of independent variables on the abundance of each species found in each of the 239–25 m² quadrats (eq. (2–4)). Partial *t*-values test the hypothesis that coefficients are zero and *P*-values represent the probability that each correlation could be obtained by chance.

	ANOVA summaries for each species					
	<i>Pyganodon</i>		<i>Lampsilis</i>		<i>Potamilus</i>	
<i>R</i> ²	0.234		0.211		0.311	
<i>F</i>	11.79		15.65		12.96	
<i>P</i>	0.001		<0.001		<0.001	
Partial Effects	<i>Pyganodon</i>		<i>Lampsilis</i>		<i>Potamilus</i>	
Predictor	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>
Constant	0.85	0.394	9.49	<0.001	10.76	<0.001
depth	3.07	0.002	-2.77	0.006	-5.06	<0.001
depth ²	-3.23	0.001	—	—	—	—
slope	2.38	0.018	-4.81	<0.001	-5.03	<0.001
organic ²	—	—	—	—	-6.42	<0.001
fetch	6.35	<0.001	-3.50	0.001	-7.04	<0.001
slope × fetch	-5.15	<0.001	2.81	0.005	4.50	<0.001
organic × fetch	-3.72	<0.001	—	—	2.14	0.034
depth × fetch	—	—	—	—	3.01	0.003
depth × organic	—	—	—	—	2.81	0.005

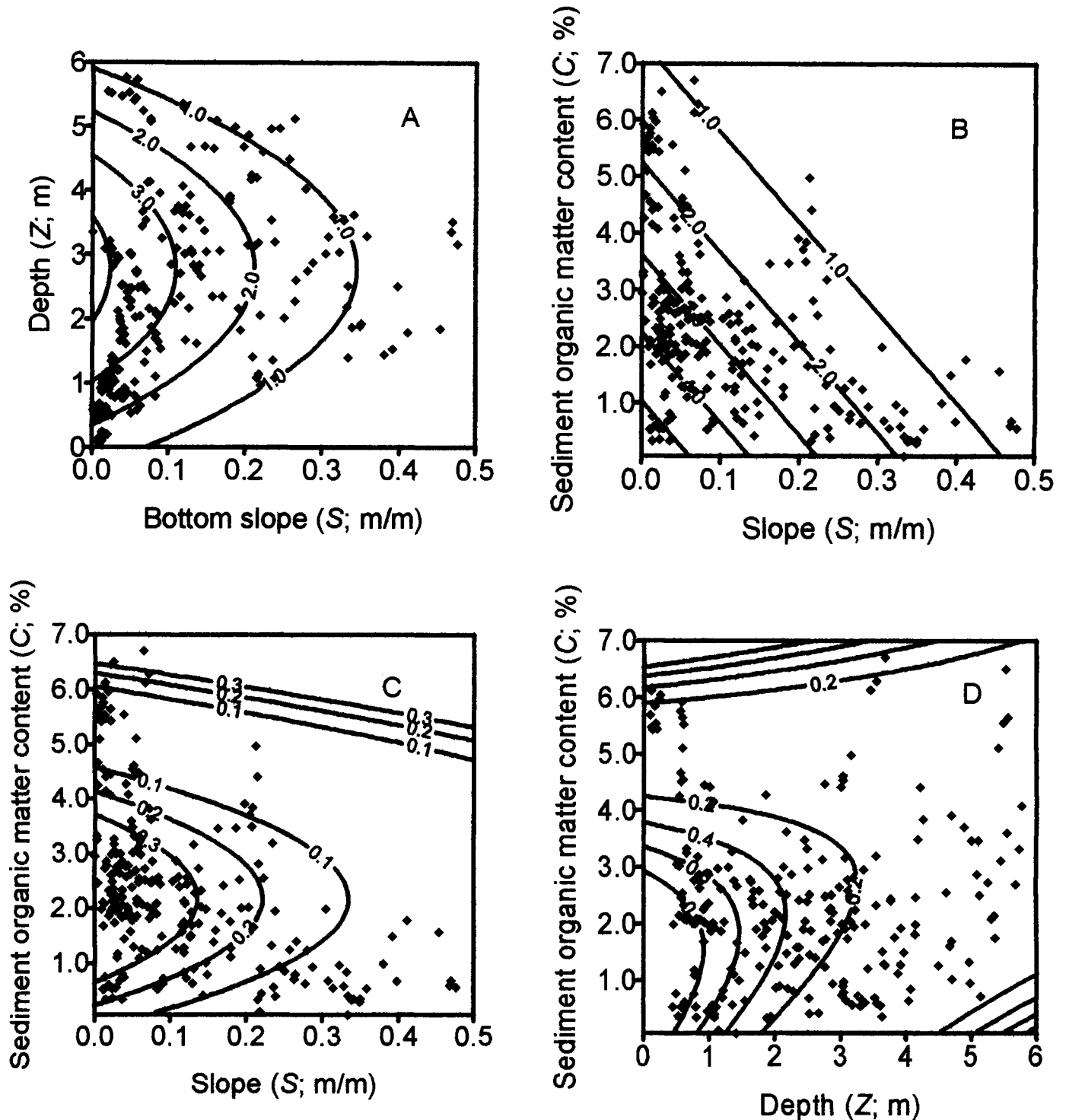


Fig. 3. (A) Mussel densities predicted from eq. (2) plotted as a function of depth and slope. Contours are predicted *Pyganodon grandis* abundance in a 25 m² quadrat. Predictions were made assuming average values of F (0.939) and C (2.09%). Posted dots indicate *Pyganodon* combinations of variables at which density observations in the 239 sampled quadrats were made. (B) Mussel densities predicted from eq. (2) plotted as a function of slope and sediment organic matter content. Contours are predicted *Pyganodon* abundance in a 25 m² quadrat. Predictions were made assuming average values of F (0.939 km) and Z (2.16 m). Posted dots indicate combinations of variables at which *Pyganodon* density observations were made in the 239 sampled quadrats. (C) Mussel densities predicted from eq. (3) plotted as a function of slope and sediment organic matter content. Contours are predicted *Lampsilis siliquoidea* abundance in a 25 m² quadrat. Predictions were made assuming average values of Z (2.16 m) and F (0.939 km). Posted dots indicate combinations of variables at which *Lampsilis* density observations were made in the 239 sampled quadrats. (D) Mussel densities predicted from eq. (3) plotted as a function of depth and sediment organic matter content. Contours are predicted *Lampsilis siliquoidea* abundance in a 25 m² quadrat. Predictions were made assuming average values of S (0.063) and F (0.939 km). Posted dots indicate combinations of variables at which *Lampsilis* density observations were made in the 239 sampled quadrats.

3.4 m⁻² (mean 0.96 m⁻²), while densities of *Lampsilis* generally ranged from 0.1–30 m⁻² (mean 6.3 m⁻²). In Big Creek Lake, however, the mean density of *Pyganodon* was 0.20 m⁻², near to the minimum seen elsewhere, while the mean density of *Lampsilis* was 0.04 m⁻² which is more than 100-fold less than the average density at other sites. Densities of *Pyganodon grandis* and *Lampsilis siliquoidea* in Big Creek Lake were similar to those found by Cvancara and Freeman (1978) in another eutrophic reservoir. They found *Pyganodon* at mean density 0.27 m⁻² and *Lampsilis* at mean density 0.05 m⁻². Such low densities may result from either the influences of the highly agricultural drainage basin (>95% cropland and pasture), the impacts of reservoir life on mussel populations, or the short lifetime (20–30 years) of these reservoirs.

This study indicates that several environmental factors influence the abundance of *Pyganodon*, *Potamilus*, and *Lampsilis*. *Potamilus* and *Lampsilis* appear to live within fairly narrowly defined habitats in this man-made reservoir. Alteration of environmental characteristics may therefore have a great impact on mussel abundance. In particular, sediment organic matter content may change rapidly through time. High levels of substrate organic matter content may be unsuitable for species such as *Pyganodon grandis* and *Unio merus tetralasmus* (Table 3). Increased organic matter deposition may occur as a result of increased erosion of agricultural soils. This could impact all species of freshwater mussel found in Big Creek Lake because increased siltation may bury mussel beds (Coker et al. 1921, Hartfield 1993, Mehlhop and Vaughn 1994). One of us (JRS) has observed extensive dead mussel beds buried in silt in inflows to lakes in agricultural areas of Iowa.

The results of this study agree with previous studies with one important exception. Abundance of *Pyganodon grandis* was found to be negatively correlated with increasing substrate organic matter content (Table 3). This result stands in contrast to Cvancara and Freeman (1978) and Ghent et al. (1978) who suggested that abundance of *Pyganodon grandis* was positively correlated with substrate organic matter content. This may result from inter-population differences or perhaps from more specific characteristics of substrates in these systems.

This study suggests that some confusion in the literature may have resulted from the simplistic bivariate approach used in previous studies. The resulting low *r*-values (<0.35) from the bivariate correlations may indicate that environmental characteristics in addition to water depth, bottom slope, sediment organic matter content, and maximum effective fetch determine mussel abundance and distribution. Additional factors that are likely to influence mussel abundance and distribution at some level include biological variables, climatic factors, physical characteristics, the impact of various human activities, and the potential impact of fish-host populations and behavior. These factors may combine in unexpected and interacting ways. For example, the significant interaction terms in eq. (2) suggest that *Pyganodon's* response to slope and sediment composition may vary with fetch-induced turbulence.

Freshwater mussels are thought to be disappearing rapidly, due principally to habitat destruction (Bogan 1993). This research has shown that some species of unionids in Big Creek Lake have specific, divergent habitat requirements. It has also shown a general need for habitat with stable substrates and moderate levels of turbulence. Turbulence is presumably necessary to provide food, oxygen, and to prevent siltation of mussel beds. This study has indicated several specific habitat characteristics that represent suitable habitat requirements for *Pyganodon grandis*, *Potamilus alatus*, and *Lampsilis siliquoidea*. Alteration of these habitat characteristics may cause mussel abundance to decline or increase, depending upon the direction of change.

The suitable habitat characteristics implied in this study indicate

that several kinds of habitat changes may negatively affect species abundances. For example, dredging, channel modification, and riparian management schemes can alter lake basin morphometry, increasing or decreasing bottom slopes, and altering depth profiles. In fact, construction of bulkheads, revetments, groins, breakwaters, and jetties are frequently applied methods that attempt to directly manipulate depth, slope and sediment mobility (Coastal Engineering 1984). Increased slope would likely negatively affect abundance of *Pyganodon grandis*, *Potamilus alatus*, and *Lampsilis siliquoidea*. Decreased slopes could encourage increased siltation which would negatively affect mussel abundance. Decreased water level, for extended periods of time, might cause mussel die-offs at shallower depths and increased turbulence at deeper sites. Increased siltation from nutrient and sediment loading in agricultural landscapes may bury and suffocate mussel beds in highly organic sediments (Coker et al. 1921, Hartfield 1993, Mehlhop and Vaughn 1994). Modifications of the lake to enhance recreational fishing, such as the addition of submerged structure, may cover mussel beds, result in decreased turbulence, and cause increased siltation, all of which may negatively impact mussel abundances. This study suggests that alteration of mussels' physical habitat must be done with extreme caution if these important components of aquatic biodiversity are to be preserved.

Understanding the factors that affect freshwater mussel distribution may make it possible to efficiently conserve remaining populations. Knowledge of suitable habitat characteristics can help to locate mussels so they can be efficiently documented and monitored to determine changes in status, whether they are growing, stable, or declining. Future conservation efforts may necessitate habitat modification to provide suitable mussel habitat.

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