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A calcium-based invasion risk assessment for zebra and quagga mussels (*Dreissena* spp)

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We used calcium concentration data from over 3000 stream and river sites across the contiguous United States to classify ecoregions relative to their risk for *Dreissena* species invasion. We defined risk based on calcium concentrations as: very low (< 12 mg L^{-1}), low (12–20 mg L^{-1}), moderate (20–28 mg L^{-1}), and high (> 28 mg L^{-1}). Ecoregions comprising 9.4% and 11.3% of land area were classified as very low risk and low risk, respectively. These areas included New England, most of the southeast, and western portions of the Pacific Northwest. High-risk ecoregions comprised 58.9% of land area. Ecoregions with highly variable calcium concentrations comprised 19.8% of land area; none could be classified as moderate risk. The majority of *Dreissena* occurrences (excluding the Great Lakes) were located in high-risk ecoregions, and most exceptions occurred in highly variable ecoregions. In low-risk ecoregions, mussels occurred in large rivers flowing from high-calcium regions. Our map provides guidance for the allocation of management resources.

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When an alien species is invasive and has clear negative ecological and economic impacts, there is considerable interest in determining its potential distribution. Soon after the zebra mussel (*Dreissena polymorpha*) was discovered in the Great Lakes in 1988, its potential for rapid invasion and for major impacts on infrastructure and ecosystems was recognized. Not unexpectedly, this triggered a flurry of studies aimed at describing the species' potential range and identifying possible limiting factors (eg Strayer 1991; Neary and Leach 1992; Ramcharan *et al*. 1992; Mellina and Rasmussen 1994). These studies and others proposed a variety of factors that could limit the distribution of zebra mussels, including pH, calcium, temperature, salinity, substrate size, and nutrients.

The zebra mussel's early range expansion was so rapid that Ludyanskiy *et al*. (1993) projected that "...by the year 2000, the zebra mussel can be expected to have colonized all North American rivers, lakes, and reservoirs that fit its broad ecological requirements". One need only view the annual maps of zebra mussel distribution (eg US Geological Survey's Non-indigenous Aquatic Species) for the first decade after its introduction to understand this concern. However, the rate of zebra mussel expansion slowed considerably after ca 1994, such that the extent of the zebra mussel's range shown on the 1995 and 2006 distribution maps are not very different. From 1995 to 2006, there was continued spread within the Great Lakes and additional inland locations in the Upper Midwest and New York State, and slow extension up the Arkansas and Missouri Rivers. However, there was no invasion of New England, the mid-Atlantic Piedmont and Coastal Plains, the southeast, or areas west of the 100th meridian.

Meanwhile, a second non-native *Dreissena* species, the quagga mussel (*D bugensis*), was identified in the Great Lakes in 1989. This species received less attention, primarily because it appeared to be confined to deeper waters, and was only slowly expanding its range. Thus, laboratory and field studies focused on zebra mussels. However, as the quagga mussel spread within the Great Lakes and the St Lawrence River, it began to invade and dominate shallower waters previously occupied only by zebra mussels (Stoeckmann 2003; Jones and Ricciardi 2005). This picture of a slow replacement of zebra mussels by quagga mussels, limited to the Great Lakes, changed suddenly with the discovery, in January 2007, of well-established quagga mussel populations in Lake Mead, Nevada, and downstream, in Lake Havasu and Lake Mojave (100th Meridian Initiative nd). As of September 2007, quagga mussels have also been found in several reservoirs in San Diego and Riverside Counties in California, in Lake Powell, Arizona, and near Phoenix, Arizona.

Given this recent *Dreissena* incursion into the western states, and continued uncertainty regarding non-invaded areas in the eastern US, we believe that there is a need for a national-scale map of *Dreissena* invasion risk. We know of two studies that developed such maps for zebra mussel. In 1991, Strayer used air temperature to model the species' potential distribution (Strayer 1991); however, zebra mussels currently occupy sites south of Strayer's proposed southern limit. More recently, Drake and Bossenbroek (2004) used a genetic algorithm for rule-set production (GARP, a type of machine-learning algorithm), with 11 mapped climate, geological, and topographic variables as inputs, producing three maps (models) of the potential range of zebra mussels for the 48 contiguous states. However, while calcium concentrations have been noted

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as a limiting factor (Hincks and Mackie 1997; Cohen and Weinstein 2001; Jones and Ricciardi 2005), it was not an explicit input variable in their models. Calcium is considered to be a key limiting factor, required for basic metabolic function as well as shell building. *Dreissena* appear to have higher calcium requirements than do many other freshwater mussels (USEPA EMAP unpublished). We were also skeptical of the Drake and Bossenbroek (2004) models because they indicated high likelihood of mussel invasion in areas known to have low calcium concentrations (eg New England; Whittier *et al*. 1995), and because two of the models showed very low likelihood for the Colorado River basin and the Lake Mead area; the third showed very scattered areas of high likelihood in parts of the basin, but not around Lake Mead.

Our preliminary assessments suggested that current mussel distributions in North America appear to be associated with calcium concentrations in surface waters. In this paper, we develop and evaluate a national-scale map of *Dreissena* spp invasion risk, based on calcium concentrations in streams and rivers. Our work is based primarily on published studies of zebra mussel and its distribution; however, the few studies of calcium requirements in quagga mussel suggest that its requirements do not differ greatly from those of zebra mussels.

Methods

Our primary water chemistry data were taken from several large-scale probability surveys made by the US Environmental Protection Agency's Environmental Monitoring and Assessment Program (USEPA EMAP), including the Western Pilot survey (in 12 western states) and two surveys in the mid-Atlantic region. We also used data from the Wadeable Streams Assessment (USEPA WSA 2006), a survey that included 739 sites in the 36 states not sampled by the Western Pilot survey. The field collection and water chemistry protocols were consistent for all of our 3091 stream and river sites.

We used Omernik's (1987) Level III ecoregions as a geographic framework, to delineate areas with similar ranges of surface-water calcium concentrations. Twenty-three of the 82 ecoregions had fewer than 10 data sites and were combined with neighboring ecoregions we judged to have similar geologies and similar distributions of calcium values. Two wetland-dominated ecoregions, the Southern Florida Coastal Plains and the Northern Minnesota Wetlands, had zero and one site, respectively, and were consequently excluded from further assessments.

We defined *Dreissena* invasion risk based on calcium concentrations as: very low (< 12 mg L^{-1}), low (12–20 mg L^{-1}), moderate (20–28 mg L^{-1}), and high (> 28 mg L^{-1}). We based these ranges on values taken from the literature as follows: in the early 1990s, based primarily on European studies, 28 mg L^{-1} of calcium was proposed as a minimum concentration needed for zebra mussels to become established (Ramcharan *et al*. 1992). Other studies suggested that calcium concentrations as low as 12 mg L^{-1} could maintain zebra mussels, and *D polymorpha* has been found in North American waters at concentrations as low as 20 mg L^{-1} or less (Cohen and Weinstein 2001). In a meta-analysis of laboratory and field studies, Cohen and Weinstein (2001) concluded that 20 mg L^{-1} Ca was a functional lower calcium concentration needed for zebra mussels to establish reproducing colonies. Zebra mussel occurrences in water bodies with calcium concentrations < 20 mg L^{-1} had relatively low abundances (but see Jones and Ricciardi 2005) or are likely to be population sinks (sensu Pulliam 1988).

We classified ecoregions into invasion risk categories, following the rules outlined in Table 1. Some ecoregions are quite heterogeneous geologically, with widely varying water chemistry in different streams. Thus, we designated a highly variable class for ecoregions which included a substantial proportion of sites with both very low calcium concentrations and high concentrations (Table 1).

We compared the Omernik *et al*. (1988; WebFigure 1) alkalinity map to our ecoregion classifications. Generally, the predominant acid anion in alkaline systems is bicarbonate, which is primarily derived from weathering of calcium and magnesium carbonate bedrock. The alkalinity map was developed to delineate areas where surface waters could potentially be sensitive to acidic deposition. The map had four low-alkalinity classes (up to 400 μeq L^{-1}), which we combined into one class. For lakes in the northeastern US, Whittier *et al*. (1995) showed that alkalinity of 400 μeq L^{-1} was equivalent to a calcium concentration range of 6 to 9 mg L^{-1}. In the WSA data, only eight out of 180 sites with < 400 μeq L^{-1} alkalinity had calcium concentrations $\geq$ 12 mg L^{-1} (USEPA WSA 2006). Two of these were acidified by acid mine drainage (pH = 3.7 and 5.0), while the pH at the remaining six sites ranged from pH 6.3 to 6.9, generally considered too acidic for zebra mussels (eg Neary and Leach 1992; Ramcharan *et al*. 1992).

Calcium is usually conserved in aquatic ecosystems; that is, it is not greatly depleted by natural processes. Thus, large rivers originating in high-calcium regions and flowing through low-cal-

Table 1. Ecoregional risk classifications based on calcium concentration sample statistics in US streams and rivers (USEPA EMAP unpublished; USEPA WSA 2006)

Risk class	*Distribution of calcium concentrations at sites*
Very low	75th percentile <12 mg L^{-1}
Low	12 mg L^{-1} $\leq$ 75th percentile < 20 mg L^{-1} or 75th percentile < 21 mg L^{-1} and maximum < 28 mg L^{-1}
High	mean $\geq$ 28 mg L^{-1} and 25th percentile > 12 mg L^{-1}
Highly variable	$\geq$ 15% of sites with Ca < 12 mg L^{-1} AND $\geq$ 15% of sites with Ca $\geq$ 28 mg L^{-1}

cium regions carry high calcium concentrations considerable distances downstream. Because many reported zebra mussel occurrences were in large rivers (USGS NAS nd), we also examined calcium concentrations from 48 large river sites in the USGS's National Stream Quality Accounting Network (USGS NASQAN nd). Water samples were generally taken monthly for 5 to 10 years.

Finally, we plotted locations of *Dreissena* spp occurrences onto these maps, based on the USGS Non-indigenous Aquatic Species Database (USGS NAS nd). We examined the specific location information for occurrences that appeared to be in "very low-risk", "low-risk", and "highly variable" ecoregions.

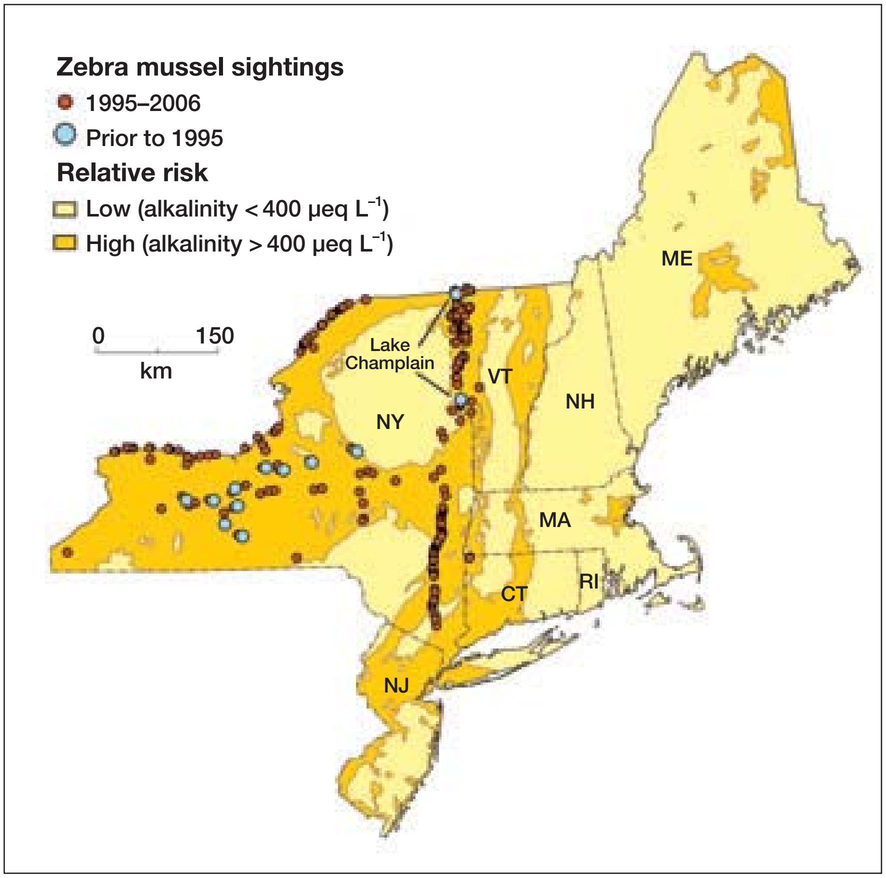

Figure 1. *Eight states in the northeastern US showing low-alkalinity areas (pale yellow), where calcium concentrations were expected to be too low to support zebra mussels. Blue dots indicate zebra mussel occurrences in inland lakes, known through 1994, when Whittier* et al. *(1995) proposed this risk model. Red dots indicate known* Dreissena *occurrences since that time.*

Results

We initially evaluated our hypothesis that low-alkalinity/low-calcium regions would resist *Dreissena* invasion by plotting zebra mussel occurrences (through 2006) in the eight-state area originally assessed by Whittier *et al*. (1995; Figure 1). Despite close proximity to multiple potential sources of *Dreissena*, the low-alkalinity (very low-calcium) areas have not been invaded since the 1995 study. To date, outside of the Great Lakes and the St Lawrence River, zebra mussels have been reported (USGS NAS nd) in two lakes in Connecticut (among the highest calcium values in the state; Cohen and Weinstein 2001), four in Vermont (including Lake Champlain), and 25 in New York State (including Lake Champlain), as well as the Erie Canal/Mohawk River system, the Hudson River, and the Susquehanna River. The only mussel occurrences in low-alkalinity areas were in the Hudson River (flowing from higher alkalinity areas) and in two lakes at the edge of the low-alkalinity area, Lake George (which has not been fully colonized) and Glen Lake.

For the 48 contiguous states, ecoregions comprising 9.4% and 11.3% of land area were classified as very low risk and low risk, respectively. These areas included New England, most of the southeast, and western portions of the Pacific Northwest (Table 1; Figure 2; WebTable 1). High-risk ecoregions comprised 58.9% of land area. Ecoregions with highly variable calcium concentrations comprised 19.8% of land area. We originally tried to define a moderate risk category, but all ecoregions not classified as either very low risk, low risk, or high risk were highly variable. Large portions of the very low- and low-risk ecoregions were in low-alkalinity areas. Some variability existed within our classification framework; five of the high risk ecoregions had > 10% of sites with very low calcium, while two of the low-risk ecoregions had > 10% of sites with high calcium concentrations. The Central Basin and Range ecoregion (mapped as high risk) met the criteria for both high risk and highly variable, while the Northern Appalachians and Uplands (mapped as highly variable) met the criteria for both low risk and highly variable.

The majority of reported *Dreissena* occurrences (excluding the Great Lakes) were in high-risk ecoregions (Figure 2). Most exceptions were in highly variable ecoregions, primarily the Northern Lakes and Forests ecoregion in northern Michigan, Wisconsin, and Minnesota, the Mississippi Alluvial Plain ecoregion, and several Appalachian ecoregions. The Tennessee River, with zebra mussels reported in multiple locations, drains portions of at least three highly variable ecoregions, one high-risk, one low-risk, and one very low-risk ecoregion. It also carries barge traffic from the highly invaded Ohio and Mississippi Rivers

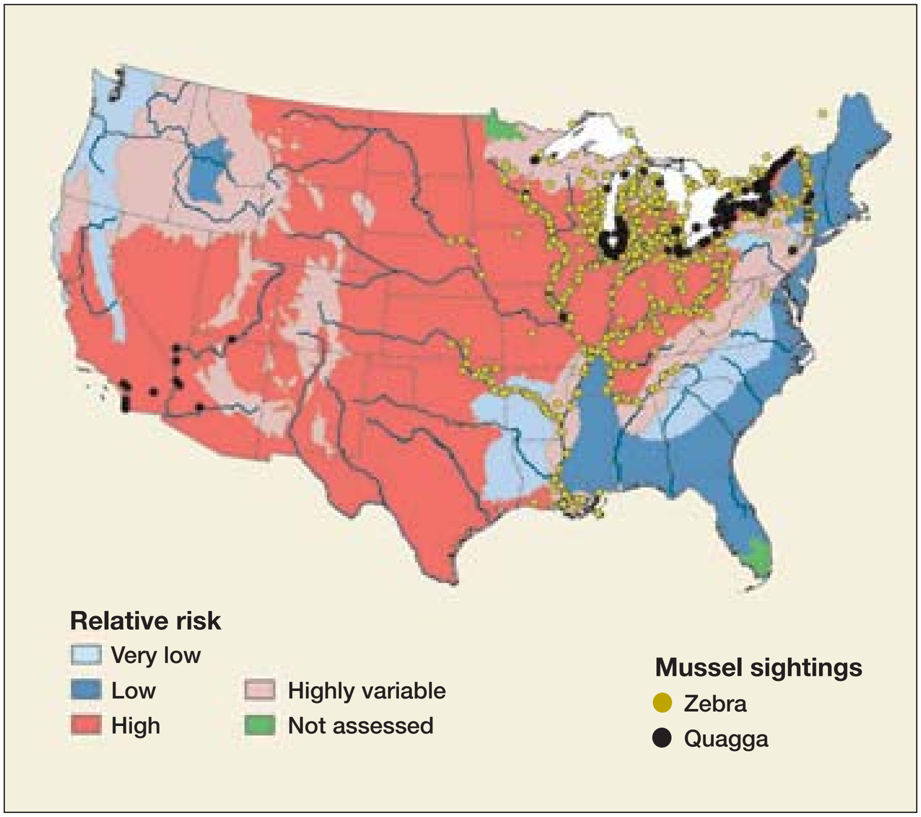

Figure 2. Dreissena *invasion risk classes for ecoregions of the contiguous US based on calcium concentrations in streams and rivers. Depending on watershed characteristics, some portions of the highly variable ecoregions will be at high risk, while others will be at very low risk. Dots indicate zebra mussel and quagga mussel observations through October 2007.*

(WebTable 2). At the mouth of the Tennessee River, the median calcium concentration was 19 mg L^{-1} (USGS NASQAN nd).

The only *Dreissena* occurrences well within low-risk or very low-risk ecoregions were found in the Arkansas River, which drains large, high-calcium areas before flowing into the very low-calcium regions of Arkansas and southeastern Oklahoma. The median and 25th percentile of calcium concentrations in the Arkansas River were 36.2 mg L^{-1} and 30 mg L^{-1}, respectively, downstream from Little Rock, Arkansas.

Discussion

We believe that our ecoregional map of surface-water calcium concentrations is a useful, broad-scale depiction of the relative risk for *Dreissena* invasion. The calcium classifications are consistent with the fact that most of New England, the Piedmont, and Coastal Plains ecoregions along the Atlantic, and much of the southeast have not been invaded by zebra mussel, despite nearby source populations, and apparently appropriate climate, geology, and topography (Drake and Bossenbroek 2004). We note that all new locations recorded since 2003 that have extended *Dreissena*'s geographic range have been in the high-risk ecoregions, as have those within the existing range.

The apparent contradictions between our map and some zebra mussel sites (primarily on large rivers) emphasize that a useful risk model for any specific water body will need to include additional information about the watershed, as well as on *Dreissena* autecology. In the case of the portion of the Arkansas River within the very low-risk areas, one must know that most of the upstream river drains high-calcium areas, and high-calcium concentrations in the lower mainstem of the river reflect that water source rather than local conditions. The other key requirement for *Dreissena* in river systems is the presence of an invaded upstream lake or reservoir to maintain a supply of larvae (Horvath *et al.* 1996; Allen and Ramcharan 2001). The Arkansas River system has invaded reservoirs, as well as a series of locks and dams on the mainstem. On the other hand, the lower Missouri River is not dammed and currently does not support mussels (Allen and Ramcharan 2001), despite more than adequate calcium levels and regular barge traffic. However, the lower Missouri River may be colonized in the future, if nearby lakes are invaded.

The Tennessee River provides an opportunity to examine whether 20 mg L^{-1} calcium marks the approximate minimum concentration needed to support zebra mussels over time (Cohen and Weinstein 2001). At the river mouth, about 75% of monthly calcium measurements were $\leq$ 20 mg L^{-1}, yet there were numerous zebra mussel sites in upstream reservoirs. Recall that the Tennessee River watershed drains portions of ecoregions in all four risk classes. Calcium concentrations within and among the reservoirs and inflowing streams ranged from as low as 1.1 mg L^{-1} to as high as 37 mg L^{-1} (T Baker unpublished). Thus, some portions of the river/reservoir system have sufficient calcium to support mussel colonies that can provide larvae to recolonize areas with marginal calcium levels. While detailed data were not available, zebra mussel presence and abundance in Tennessee River reservoirs are known to be quite variable, with some dense colonies disappearing, and the highest abundances shifting from upstream to downstream locations in recent years (C Saylor and D Baxter pers comm).

Finally, two important points about our model should be noted. First, we assessed calcium only in flowing waters. It seems reasonable to assume that lakes will have calcium levels similar to those in streams in the same ecoregion, but we have not tested this assumption. Second, our work was based primarily on studies of zebra mussels. Much less is known about the ecology of the quagga mussel, and the zebra mussel may not always be a good analog. Some differences are clear; quagga mussels can spawn in colder water, become abundant in much deeper water, and spread more slowly than zebra mussels, but appear able to eventually become the dominant species (Stoeckmann 2003; Jones and Ricciardi 2005). There is conflicting evidence about the quagga mussel's calcium requirements, and a clear need for additional studies. This is especially important for resource managers in western states. We believe that our map provides guidance for the allocation of management resources.

Acknowledgements

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WebTable 1. Ecoregions (Omernik 1987) grouped by *Dreissena* spp invasion risk classes (calcium concentrations in mg L^{-1})

Ecoregion	*Median Ca (interquartile range)*
Very low-risk	
Ouachita Mountains and Boston Mountains	2.3 (1.4–5.0)
Blue Ridge	3.2 (1.7–5.4)
Cascades	4.8 (3.0–6.7)
North Central Appalachians	4.8 (3.1–7.8)
Piedmont	5.8 (4.1–8.6)
Puget Lowland and Willamette Valley	5.7 (4.5–9.1)
Eastern Cascades Slopes and Foothills	7.8 (4.4–9.7)
South Central Plains and Arkansas Valley	5.5 (3.6–9.8)
North Cascades	4.3 (2.7–10.4)
Sierra Nevada	7.0 (3.5–11.5)
Coast Range	6.2 (3.6–11.6)
Low-risk	
Middle Atlantic Coastal Plain and Atlantic Coastal Pine Barrens	8.8 (5.9–12.6)
Southeastern Plains and Mississippi Valley Loess Plains and Southern Coastal Plains	5.9 (2.3–13.9)
Northeastern Highlands	6.8 (3.9–14.9)
Idaho Batholith	5.9 (2.6–15.6)
Laurentian Plains	11.3 (7.1–19.4)
Northeastern Coastal Zone	10.8 (4.9–20.9)
Highly variable	
Southwestern Appalachians and Central Appalachians	11.0 (4.6–30.3)
Klamath Mountains	13.2 (8.5–23.7)
Snake River Plain and Northern Basin and Range	13.9 (6.0–29.2)
Blue Mountains	14.3 (7.4–27.5)
Northern Rockies and Canadian Rockies	15.1 (3.6–28.3)
Ridge and Valley	15.2 (4.8–40.8)
Northern Appalachian Plateau and Uplands	15.4 (8.7–20.5)
Southern Rockies	15.6 (7.7–29.3)

(Continued)

WebTable 1. *Continued*

Ecoregion	*Median Ca (interquartile range)*
Northern Piedmont	15.8 (7.2–27.9)
Columbia Plateau	18.3 (9.7–30.2)
Middle Rockies	18.9 (7.7–35.2)
Northern Lakes and Forests	19.9 (12.9–33.8)
Mississippi Alluvial Plain	25.6 (10.7–48.2)
Wasatch and Uinta Mountains	29.4 (2.9–54.4)
Arizona/New Mexico Mountains	39.2 (12.8–50.9)
High-risk	
Western Allegheny Plateau	28.4 (15.5–57.6)
Western Gulf Coast Plains	34.5 (26.5–40.9)
Central Basin and Range	36.9 (14.2–53.5)
Ozark Highlands	40.2 (37.0–48.4)
Chihuahuan Desert and Madrean Archipelago	41.1 (33.4–64.3)
Southern California Mountains	42.3 (26.4–87.6)
Northwestern Glaciated Plains	42.9 (29.6–165.5)
Erie Drift Plains	43.3 (31.8–57.6)
Eastern Great Lakes and Hudson Lowlands	47.8 (34.1–71.4)
Northwestern Great Plains and Nebraska Sand Hills	48.4 (35.9–93.5)
North Central Hardwood Forests and Driftless Area	49.2 (19.0–69.3)
High Plains	49.9 (39.5–87.8)
Wyoming Basin	51.4 (35.7–88.2)
Colorado Plateaus and Arizona/New Mexico Plateau	54.8 (42.1–81.0)
Interior Plateau	56.4 (32.6–67.2)
Flint Hills and Central Irregular Plains	58.4 (39.0–68.3)
Central Oklahoma/Texas Plains and Edwards Plateau and Texas Blackland Prairies and East Central Texas Plains	58.9 (23.8–70.1)

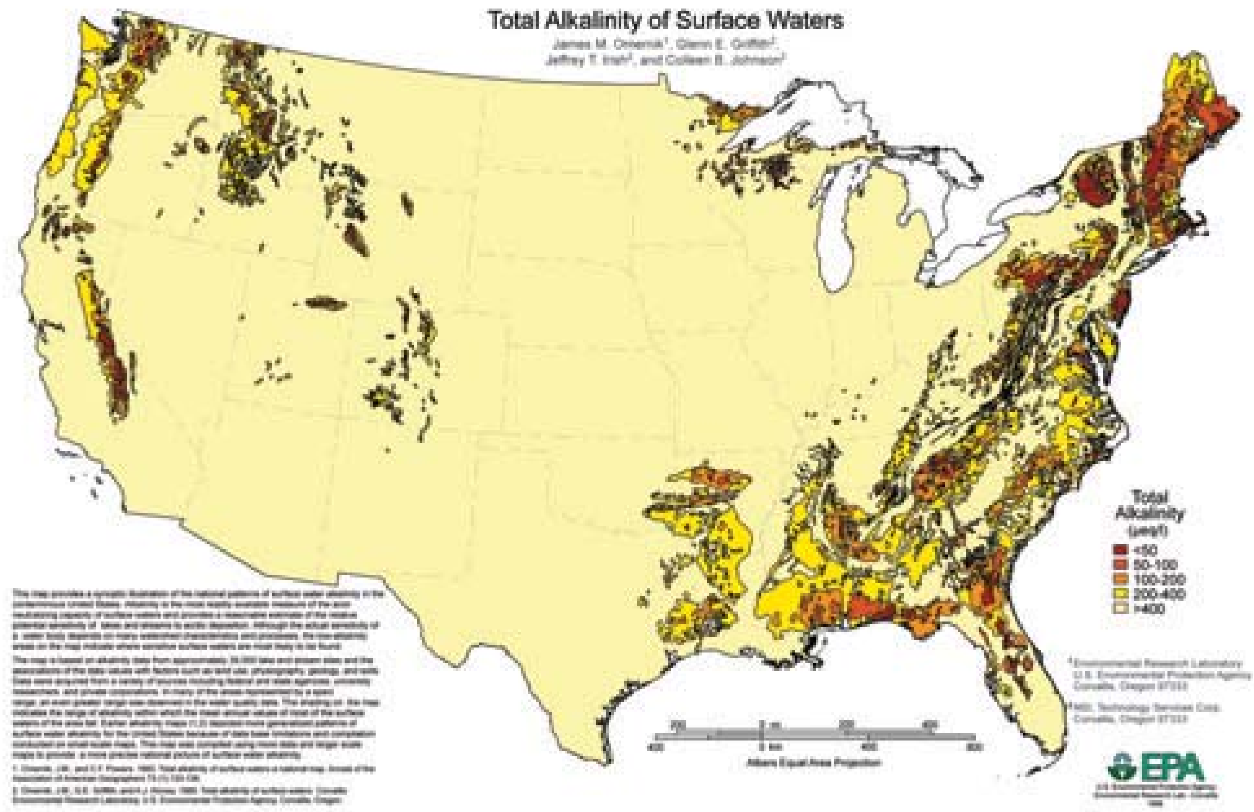
(Continued)

WebTable 1. ***Continued***

Ecoregion	*Median Ca (interquartile range)*
Interior River Valleys and Hills	59.0 (49.2–67.9)
Southern and Central California Chaparral and Oak Woodlands and Central California Valley	62.8 (27.0–104.3)
Mojave Basin and Range and Sonoran Basin and Range	62.9 (40.2–107.5)
Southwestern Tablelands	68.5 (40.4–160.9)
Eastern Corn Belt Plains and Southern Michigan/Northern Indiana Drift Plains and Huron/Erie Lake Plains	75.1 (64.1–88.3)
Western Corn Belt Plains	78.4 (66.9–90.4)
Southeastern Wisconsin Till Plains and Central Corn Belt Plains	80.9 (74.0–85.0)
Northern Glaciated Plains	82.3 (66.4–111.4)
Lake Agassiz Plain	98.1 (82.2–126.6)
Central Great Plains	140.0 (70.3–328.8)
Not assessed	
Northern Minnesota Wetlands	
Southern Florida Coastal Plain	

WebTable 2. Large rivers in the USGS National Stream Water Quality Network (NASQAN), median calcium concentrations and reported *Dreissena* spp presence (USGS NAS)

River	*Median Ca (mg L^{-1}) (stations)*	*Reported* Dreissena *occurences (zebra mussel except in Colorado R)*
Ohio (mainstem)	29.4–38.3 (3)	Multiple locations, full length
Wabash	54.1	Four locations
Tennessee	19.1	Multiple locations
Cumberland	29.6	Multiple locations
Mississippi (mainstem)	38.5–63.1 (5)	Multiple locations, full length
Minnesota	91.6	
Arkansas	36.2	Multiple locations, Kansas/Oklahoma border to mouth
Atchafalaya	36.7	Several locations
Missouri (mainstem)	49.8–57.1 (5)	Three locations between Fort Randall Dam, SD and Omaha, NE
Yellowstone	45.7	None
Platte	56.0	None
Rio Grande (mainstem)	64.8–178.4 (7)	None
Pecos	140.0	None
Arroyo Colorado	200.0	None
Colorado (mainstem)	69.1–87.0 (6)	Quagga mussels, Lake Mead to Lake Havasu
Green	53.0	None
San Juan	60.9	None
Columbia (mainstem)	14.0–18.6 (4)	None
Snake	14.8	None (possible quagga mussel introduction to headwater reservoir)
Willamette	5.9	None
St Lawrence	32.0	Multiple locations from Lake Ontario to past Montreal
Susquehanna	17.0	Four locations
Alabama	12.5	None
Tombigbee	15.5	None



WebFigure 1. *Total alkalinity of surface water (Omernik* et al. *1998). This map provides a synoptic illustration of the national patterns of surface-water alkalinity in the conterminous United States and is based on alkalinity data from approximately 39 000 lake and stream sites, and the associations of the values with factors such as land use, physiography, geology, and soils. For the* Dreissena *spp study, we considered all areas with alkalinity < 400 μeq L^{-1} as one low-alkalinity class, expected to have calcium concentrations < 12 mg L^{-1} in surface waters.*