SECOND EDITION

Quagga
and
Zebra Mussels

Biology, Impacts, and Control

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Don W. Schloesser

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Cover Image Credit: Chris Houghton, Rob Paddock, and John Janssen, University of Wisconsin-Milwaukee, School of Freshwater Sciences. This image of quagga mussels (profunda/deepwater morph) presents a composite of photos taken on the southern slope of Northeast Reef in Lake Michigan (43° 45.11′N, 87° 34.70′W) on April 25, 2012. Image photos were taken at a depth of 52 m with a deepwater ROV and clearly show the elongated siphons of the profunda morph.

Zebra Mussel Impacts on Unionids
A Synthesis of Trends in North America and Europe

Frances E. Lucy, Lyubov E. Burlakova, Alexander Y. Karatayev, Sergey E. Mastitsky, and David T. Zanatta

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ABSTRACT

This chapter examines impacts of exotic zebra mussel (*Dreissena polymorpha*) infestation on unionids from water bodies in North America, Belarus, and Ireland over the past two centuries. A variety of methods were used to assess impacts ranging from short-term studies of multiple water bodies to extensive multi-year studies of a single water body. In general, there was a strong positive linear relationship between numbers of zebra mussels per unionid and zebra mussel density. However, datasets indicated that a high percentage of unionids may be infested with zebra mussels even when zebra mussel density in a water body was low. During the first 10 years subsequent to a zebra mussel invasion, there was an overall trend for increased weight of zebra mussels per unionid with increased unionid size, but this trend decreased 10 years after the initial invasion. We discuss possible mechanisms for coexistence of zebra mussels and unionids and make recommendations for management options and unification of research methods. Finally, we identify research priorities that will provide a better understanding of zebra mussel–unionid coexistence and hence aid in the development of unionid survival and management strategies during the initial stages of invasion by dreissenids or other byssate exotic bivalves.

INTRODUCTION

Continued invasion and spread of zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena rostriformis bugensis*) has threatened survival of native unionid mussels in North America and Europe. Members of the family Unionidae are a major component of freshwater systems, representing the largest and most long-lived (i.e., beyond 100 years) freshwater invertebrate species (Lydeard et al. 2004, Strayer et al. 2004). These bivalves are very important components of aquatic ecosystems, often dominating benthic biomass and production (Negus 1966, Hanson et al. 1989), impacting clarity and quality of water and plankton primary production by removing phytoplankton as well as suspended matter by filtration, affecting nutrient dynamics through excretion and biodeposition of feces and pseudofeces, releasing nutrients from the sediment to the water column, and increasing water and oxygen content in sediments through bioturbation (reviewed in McMahon and Bogan 2001, Vaughn and Hakenkamp 2001, Strayer et al. 2004, Vaughn et al. 2004, 2009, Vaughn and Spooner 2009). Order Unionoida represents the largest freshwater bivalve radiation, with 6 families, 181 genera, and over 800 species distributed across 6 of the 7 continents (Bogan and Roe 2008). Of the six families, Unionidae has the greatest number of species (297) found in North America (Graf and Cummings 2007, Bogan 2008). Unionids are also the most endangered group of freshwater animals, particularly in North America (Bogan 1993, 2008, Stein and Flack 1997, Lydeard et al. 2004, Graf and Cummings 2006). Due to their sensitivity to water and habitat quality, sedentary lifestyle, long life span, complex life cycles with parasitic larvae that require specific host fish, slow growth, and low reproductive rates, over 76% of the North American Unionidae and Margaritiferidae are presumed extinct, threatened, endangered, or of special concern (Williams et al. 1993). In contrast to the high diversity of unionids in North America, only 14 species of the order Unionoida are recognized in Europe (Jaeckel 1967), including 9 species in Belarus. Three species of Unionoida occur in Ireland: *Margaritifera margaritifera* (L., 1758) (pearl mussel), *Anodonta anatina* (L., 1758) (duck mussel), and *Anodonta cygnea* (L., 1758) (swan mussel). Ross (1984, 1988) and Lucey (1995) have noted difficulties in distinguishing between the two common species of *Anodonta* (Kerney 1999), and until molecular phylogenetic investigations are undertaken, there is a distinct possibility that only one true species exists. Therefore, in the present study *A. anatina* and *A. cygnea* will not be distinguished and considered only as *Anodonta*.

The decline of unionids by anthropogenic drivers is well-documented (Bogan 1993, Williams et al. 1993, Richter et al. 1997, Lydeard et al. 2004, Strayer et al. 2004, Strayer and Dudgeon 2010). In addition to impacts due to habitat destruction and loss of water quality, dreissenid mussels have escalated this decline as they settle and attach, often in very large numbers, to the exposed posterior end of the unionid shell,

Table 40.1   Geographic Coordinates of the Water Bodies Studied

Water Body	Latitude	Longitude
USA		
Lake Clark	42°07′13 N	84°19′08 W
Lake St. Clair	42°26′55 N	82°40′35 W
Lake Vineyard	42°05′02 N	84°12′35 W
Belarus		
Lake Batorino	54°50′52 N	26°57′19 E
Lake Bolduk	54°58′27 N	26°25′09 E
Lake Bolshie Shvakshty	54°58′12 N	26°35′09 E
Lake Dolzha	55°27′42 N	26°46′40 E
Lake Drisvyaty	55°36′55 N	27°01′40 E
Lake Lepelskoe	54°54′20 N	28°41′24 E
Lake Malye Shvakshty	54°59′37 N	26°33′02 E
Lake Naroch	54°51′22 N	26°46′57 E
Lake Spory	55°04′11 N	26°47′14 E
Lake Svir	54°48′06 N	26°29′09 E
Lake Volchin	55°00′04 N	26°52′23 E
Lake Volos	55°43′50 N	27°08′18 E
Ireland		
Lough Key	54°00′05 N	08°14′41 W

hampering filter feeding, respiration, locomotion, and reproduction (Mackie 1991, Schloesser et al. 1996, Karatayev et al. 1997, Strayer 1999). Zebra mussels may directly compete with unionids for food (Haag et al. 1993, Strayer and Smith 1996, Caraco et al. 1997), occupy available substrate (Tucker 1994), and induce shell deformities (Lewandowski 1976a, Hunter and Bailey 1992). In most of pre-glaciated Europe, zebra mussels and unionids coexisted (Karatayev et al. 1997), although there is no known zebra mussel fossil record for Ireland. In contrast, unionids in North America have evolved with no adaptive mechanism to deal with epizootic colonization by dreissenids (Haag et al. 1993); consequently, many studies have either forecasted or reported high mortality or extirpation of unionids within the first decade of invasion (Ricciardi et al. 1995, 1998, Nalepa et al. 1996).

In this chapter, we examine three detailed case studies of dreissenid impacts on unionids in different regions of Europe and North America (Table 40.1), analyze data from multiple water bodies across both continents to find general trends, discuss possible mechanisms for coexistence, and make recommendations for future studies.

CASE STUDY SITES

Lake St. Clair, United States/Canada

Lake St. Clair is located in the Laurentian Great Lakes system within central North America. This lake receives water from the St. Clair River through a large delta at the river mouth and drains into Lake Erie via the Detroit River. Other

important tributaries include the Clinton River in Michigan and the Sydenham and Thames Rivers in Ontario. Lake St. Clair is heart shaped, with a maximum natural depth of 6.5 m and a surface area of 1115 km^2. A navigation channel dredged to a depth of 8.3 m bisects the lake approximately along the Canada/U.S. border to accommodate commercial shipping traffic between Lake Erie and Lake Huron (Edsall et al. 1988). The southern and western/northwestern shores of the lake are heavily urbanized, while the northeastern shore consists of a large delta with vast natural marshlands. The eastern shore of the lake is mainly rural farmland and wetland. Leach (1991) described the substrate of Lake St. Clair as muddy sand in the central part and gravel or sand close to shore. Prior to the first report of zebra mussels in 1988 (Hebert et al. 1989), unionids provided the only hard substrate in many areas (Nalepa and Gauvin 1988). At present, most hard substrate in offshore areas consists of unionid shells and druses of live and dead *Dreissena* (Hunter and Bailey 1992, Nalepa et al. 1996).

Various Water Bodies, Belarus

Belarus is a relatively small country located in the geographical center of Europe. Around the turn of the nineteenth century, three interbasin canals were constructed to connect the Black and Baltic Sea basins and thus expand shipping.

These canals provided invasion corridors for the introduction of numerous Pontocaspian species from the Black Sea to the Baltic Sea basin (Mordukhai-Boltovskoi 1964, bij de Vaate et al. 2002, Karatayev et al. 2003, 2008b). There are 1040 glacial lakes in Belarus, and these lakes have very different morphology, water chemistry, trophic status, and land use patterns (Karatayev et al. 2005, 2008a). As of 2000, zebra mussels have been found in only 21.2% of the 553 lakes surveyed despite the presence of mussels in this region for almost 200 years (Karatayev et al. 2003, 2010). These lakes, along with several reservoirs, vary in time since zebra mussel colonization (from less than 5 to over 100 years ago) and therefore provide valuable models to study zebra mussel–unionid relationships (Karatayev et al. 2003, 2010) (Table 40.2).

Lough Key, Ireland

Lough Key is a small lake (9 km^2) located in the Upper Shannon River basin district in Ireland. Prior to the invasion of zebra mussels in Lough Key, *Anodonta* was described as being "common" in the lake (Ross 1984). Zebra mussels in low densities were discovered in Lough Key in early 1998 (D. Minchin, personal communication), and a rapid expansion occurred in 1999 as densities reached 148,000 m^{-2} on stony substrates (Lucy and Sullivan 2001). This small lake

Table 40.2   Unionid Sampling Techniques Employed by Surveys in Lake St. Clair, United States, Water Bodies in Belarus, and in Lough Key, Ireland

Unionid Sampling Technique	Lake St. Clair	Belarus	Lough Key, Ireland
SCUBA: 0.25 m^2 quadrat, 10 replicates	1986, 1990, 1992, 1994	Lakes Naroch (1990, 1993–1995, 1997), Lukomskoe (1978), Myastro, and Batorino (1993, 1995); reservoirs Drozdy and Chizhovskoe (1995)	
SCUBA: 1 m^2 quadrat, 20 replicates	1994		
SCUBA: timed searches	1994, 2001		
SCUBA: timed searches and "stake and rope"	2002, 2009		
SCUBA: 0.75 h "loss" survey	2010		
SCUBA: density estimate, no quadrat, not timed			1998, 1999
SCUBA transect, 0.06 m^2 quadrat, three replicates			2002
Snorkel not timed			2000, 2001, 2003
Snorkel, transect		Lake Lepelskoe (1997); lakes Volchin, Bolshiye Shvakshty, Malye Shvakshty, Bolduk, Dolzha, Myadel, Spory, Svir, and Naroch (1998); Lakes Yuzhny Volos and Drisvyaty (1999)	
Rake			1998
Ekman grab	1994	At depths >2 m in lakes Naroch (1990, 1993–1995), Myastro, and Batorino (1993, 1995); reservoirs Drozdy and Chizhovskoe (1995)	2001
ROV camera			2001

has a maximum depth of 25 m and has one inflow and out-flow, the Boyle River. Underlying geology of the lake is composed of sandstone, shale, and limestone that results in calcium-rich waters (Bowman 1998) and therefore highly suitable for zebra mussel colonization. The primary substrate in the lake is mud (>70% of total area), which is present in deeper areas (>3 m) and accounts for between 5% and 100% of the heterogeneous substrate in many littoral areas (Lucy et al. 2005). Other common substrates found in littoral areas are comprised of boulders, cobble, and gravel, and these hard-bottom types provide the main substrate for zebra mussel attachment in the littoral. *Anodonta* and its empty shells were also found to be an important substrate for zebra mussel attachment in the period soon after colonization (Lucy and Sullivan 2001).

SAMPLING PROTOCOLS

A variety of sampling methods have been used in these water bodies (Table 40.2). Methods were developed over a period of time to best document changes in zebra mussel and unionid densities. SCUBA and snorkeling were the most common collection methods used in all three case studies. The depth of sampling sites across all studies varied from 1.0 to 6.5 m (Lake St. Clair), 0.5 to 2.5 m (Belarus), and 1.0 to 5.0 m (Lough Key). Substrate was identified and recorded in situ.

Field surveys in Lake St. Clair were initially performed by SCUBA divers that collected samples in defined quadrats at 29 stations repeatedly sampled across the lake (all in water >2 m) in 1986, 1990, 1992, and 1994 (Nalepa et al. 1996). These same methods were used to survey unionids and zebra mussels at 12 of these stations in 2001 (Hunter and Simons 2004). Additional surveys incorporated timed searches (Nalepa et al. 2001), which were then combined with a semiquantitative "stake and rope" technique (Zanatta et al. 2002, McGoldrick et al. 2009). In 2010, a 0.75 h/diver-snorkel survey was also used in advance of the "stake and rope" technique to sample unionids (Zanatta, this study). In Belarus, unionids were collected while snorkeling within a 1 m wide transect (100 or 500 m, depending on unionid density); however, untimed searches were used at very low densities. Zebra mussels and unionids were collected using replicate 0.25 m² quadrats along 8 permanent transects in Lake Naroch, 5 permanent transects in Lake Myastro and Lake Batorino, 6 transects in reservoirs Drozdy and Chizhovskoe, and 14 transects in Lake Lukomskoe (see details in Table 40.2 and Burlakova et al. 2006).

Ekman grabs were also used for sample collection in one Lake St. Clair survey (Gillis and Mackie 1994) and in transect surveys in Belarus and Lough Key. In Belarus, where lake transect surveys were not carried out, zebra mussel density was determined from 10 to 32 Ekman grabs collected from 5 to 16 sites in each lake, depending on lake size. Other methods were also used in Lough Key, namely, raking and

filming with an underwater remotely operated vehicle (ROV) camera. Except for the latter method, collected unionids were identified and measured to the nearest millimeter (using calipers or a ruler), and the number of attached zebra mussels counted. In Lake St. Clair and Belarus, unionids were identified to species in most cases. In Lough Key, this was not necessary as only one genus (*Anodonta*) was present. Zebra mussels were removed from the unionids and counted, and in some cases shell lengths measured as mentioned.

In Lake St. Clair, all unionids collected in 2003 (McGoldrick et al. 2009) and 2010 (this study) were returned to the lake. For studies in Belarus, both zebra mussels and some unionids were opened to remove water from mantle cavities and then weighed to the nearest gram after being blotted dry on absorbent paper (wet weight, soft tissue plus shell). For other unionids, weight weights were derived from length–weight relationships for each species. Live unionids were then carefully replaced into the substrate from the water body where they were collected. At Lough Key, weights of both zebra mussels and unionids were determined after they were blotted dry. Unlike studies in Belarus, however, water was not removed from mantle cavities.

STATISTICAL MODELING

Several statistical models were used to describe relationships between the number and total weight of dreissenids per unionid host and the parameters of interest. A *linear regression* model was applied to relate (1) the number of dreissenids per unionid in European and North American water bodies and corresponding densities of dreissenids on other substrates and (2) total weight of dreissenids attached to the unionid and unionid shell length (Lough Key only). A negative binomial distribution-based *generalized additive model* was used to determine whether dreissenid density in Lake St. Clair changed significantly over time (Wood 2006). The model was defined as $Density = \alpha + s(YSI) + \varepsilon$, where α was the average zebra mussel density over all samples, $s(YSI)$ was a smooth function for the year since invasion (calculated as a cubic regression spline), and ε were the model residuals that were assumed to be normally distributed around the mean 0. Data used in this model were repeatedly collected from 12 stations over a span of 11 years (Hunter and Simons 2004). To account for temporal correlation between successive density measurements, an autoregressive component was incorporated into the residual variance of the model (Zuur et al. 2009). We did not incorporate the random effect of sampling station into the model as a preliminary analysis showed it was not necessary.

A *generalized least squares model* was used to examine the relationship between the total weight of attached zebra mussels to the shell length of the corresponding unionid host. In this analysis, we used our original data collected in 15 water bodies: 12 in Belarus, 1 in Ireland, and 2 in

the United States. Representatives of seven unionid genera were examined, that is, *Anodonta* (*n* = 158), *Anodontoides* (*n* = 4), *Elliptio* (*n* = 14), *Lampsilis* (*n* = 8), *Pyganodon* (*n* = 3), *Unio* (*n* = 219), and *Villosa* (*n* = 5). A preliminary exploratory analysis suggested that this dataset could be sufficiently fitted with the following model: *Weight* = $\alpha + \beta_1 L + \beta_2 TSRI + \varepsilon$, where α is the intercept and β_1 and β_2 are the coefficients reflecting the effects of the unionid shell length (*L*) and the time since recognized invasion (*TSRI*) of *Dreissena*, respectively. *TSRI* is considered as a nominal variable that takes a value of 0 if <10 years and 1 if ≥10 years. We used the *TSRI* (= initial detection) rather than the time since actual initial invasion as the latter is rarely known (Burlakova et al. 2006). ε are the residuals, which are approximately normally distributed around the mean 0, and have a variance that was allowed to vary with host length within water body/unionid genus combinations (see Zuur et al. [2009] for more details on this type of parameterization). A preliminary analysis suggested that there was no need to include the random effect of the sampling water body into the model.

Statistical analyses were carried out in the R v2.11.1 computing environment (R Development Core Team 2010) with the help of base R functions as well as an *nlme* package (Pinheiro and Bates 2000). Selection of the optimal model at intermediate steps of analysis was based on the combined use of Akaike's information criterion and analysis of variance (ANOVA) of competing models. Model validation was performed via visual examination of residuals plotted against fitted values and observed values of explanatory variables (Zuur et al. 2009).

RESULTS

Case Studies

Lake St. Clair, United States/Canada

A total of 37 unionid species are known from Lake St. Clair and its tributaries (La Rocque and Oughton 1937, Graf 2002). In 1986, immediately prior to the invasion of the lake by zebra mussels, unionids were abundant throughout the lake with mean densities of 1.9 m^{-2} (Nalepa and Gauvin 1988) (Figure 40.1a). *Lampsilis siliquoidea* was by far the most abundant unionid species. It accounted for 45% of the total unionid community and had a population age structure indicating that the population size was stable (Nalepa and Gauvin 1988). In contrast, the second most abundant unionid in 1986, *Leptodea fragilis*, showed a great deal of variation in recruitment on a yearly basis. Nalepa and Gauvin (1988) noted that while the diversity and community composition of the total unionid community in Lake St. Clair had not changed greatly since the early twentieth century, there were some indications that a few species may have declined.

Lake St. Clair and western Lake Erie were "ground zero" for the invasion of the zebra mussel in North America as these areas were the first colonized on the continent (Hebert et al. 1989, Carlton 2008). Based on size classes present (Hebert et al. 1989, Griffiths et al. 1991) and anecdotal reports (Carlton 2008), it was believed that the zebra mussel had been present since at least 1986. Densities of zebra mussels in Lake St. Clair quickly increased after first detection in 1988 and spread through the lake occurring in two stages: fi rst in the southeast basin (Figure 40.2a) and then into the northwest basin (Figure 40.2b) (Nalepa et al. 1996). In 1990, zebra mussels had a mean density of 1,663 m^{-2}, with a maximum density of 10,389 m^{-2} in the southeast. By 1994, mean density had increased to 3,241 m^{-2}, peaking at 23,037 m^{-2} in the northwest side of the lake (Figure 40.2c). Zebra mussel densities appeared to decline after 1994, with mean densities of 1237 and 1824 m^{-2} recorded in more limited sampling in 1997 and 2001, respectively (Nalepa et al. 2001, Hunter and Simons 2004; Figure 40.3). Trends in population densities in Lake St. Clair varied among sites; densities at some sites increased steadily over time, but densities at other sites gradually or rather abruptly decreased (Figure 40.4). However, the overall trend of increase during the first 8–9 years of colonization was followed by a subsequent decline. This conclusion is supported by the (marginally) significant time smoother term of the generalized additive model fitted to density data from Hunter and Simons (2004) (Figure 40.5).

Following the establishment and spread of zebra mussels, unionid densities and diversity in Lake St. Clair declined massively (Figures 40.1b,c and 40.3). Paralleling spatial patterns of zebra mussel densities, unionids in the southeast part of the lake were affected first, with severe declines between 1986 and 1990 (Nalepa et al. 1996). Unionids in the northwestern side of the lake, with the bulk of its water emanating from the St. Clair River (and Lake Huron), took longer to show impacts by zebra mussels, but massive declines were evident throughout the lake by 1994. Loss of unionid diversity took longer to become evident: 18 species were present in 1986, 17 species in 1990, and 12 species in 1992, and none were found live in 1994.

Additional survey work in 1997 (Nalepa et al. 2001) and 2001 (Hunter and Simons 2004) failed to recover any live unionids from open waters of the lake despite the apparent decline in zebra mussel density. Areas sampled previously by Gillis and Mackie (1994) were exhaustively sampled in 1998 and 1999 but no live unionids were found (Zanatta et al. 2002). Declines in unionid densities in Lake St. Clair mirror those resulting from zebra mussel competition and infestation in the Hudson River (Strayer and Malcom 2007), with mean unionid densities declining to levels two orders of magnitude lower than present pre-*Dreissena*.

After the loss of unionids in the open waters of both Lake St. Clair and western Lake Erie (Schloesser and Nalepa 1994), further surveys documented an apparent refuge for
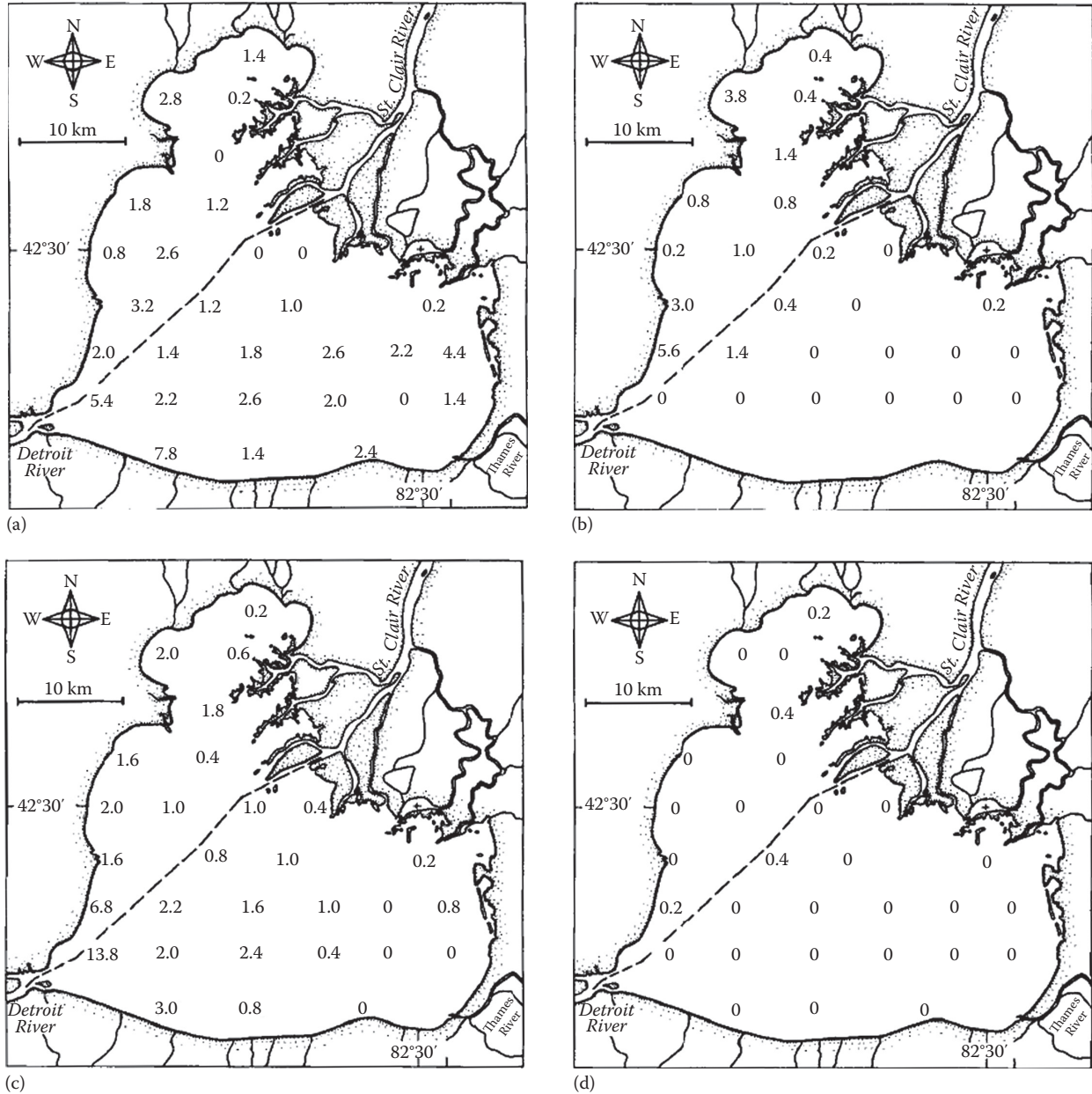
Figure 40.1 Mean density (m^{-2}) of Unionidae at 29 sampling sites in Lake St. Clair in (a) 1986, (b) 1990, (c) 1992, and (d) 1994. (From Nalepa, T.F. et al., *Great Lakes Res.*, 22, 354, 1996.)

unionids from the effects of zebra mussels in a shallow wetland area in western Lake Erie (Metzger Marsh; Nichols and Wilcox 1997). To determine if similar refuges occurred in Lake St. Clair, shallow bays and wetlands of the St. Clair delta (Figure 40.6) were first examined in 1999 (Zanatta et al. 2002). Surveys of both habitats by Zanatta et al. (2002) and McGoldrick et al. (2009) documented the unionid community (densities, diversity, and health) along with densities of the zebra mussel population (adults and larvae). Virtually all unionids found live in the delta were found in shallow water (<1 m) on sand substrates. The unionid community was diverse with 22 species being present (including

several species of conservation concern in Michigan and Ontario, Canada; COSEWIC 2010; Government of Canada 2010; Michigan Department of Natural Resources 2011; Table 40.2); however, densities were very low (0.05 m^{-2}) in comparison to densities in the open lake prior to the zebra mussel invasion (1.9 m^{-2}). Unfortunately, unionid densities in the St. Clair delta in the period before zebra mussels became established are unknown. Open-water sites closest to the delta had low unionid densities in 1986 (<1 m^{-2}, Figure 40.1). Relative frequencies of unionid species in the delta (and higher-level taxonomic groups: Anodontinae, Ambleminae, Lampsilini) were similar to the pre-zebra
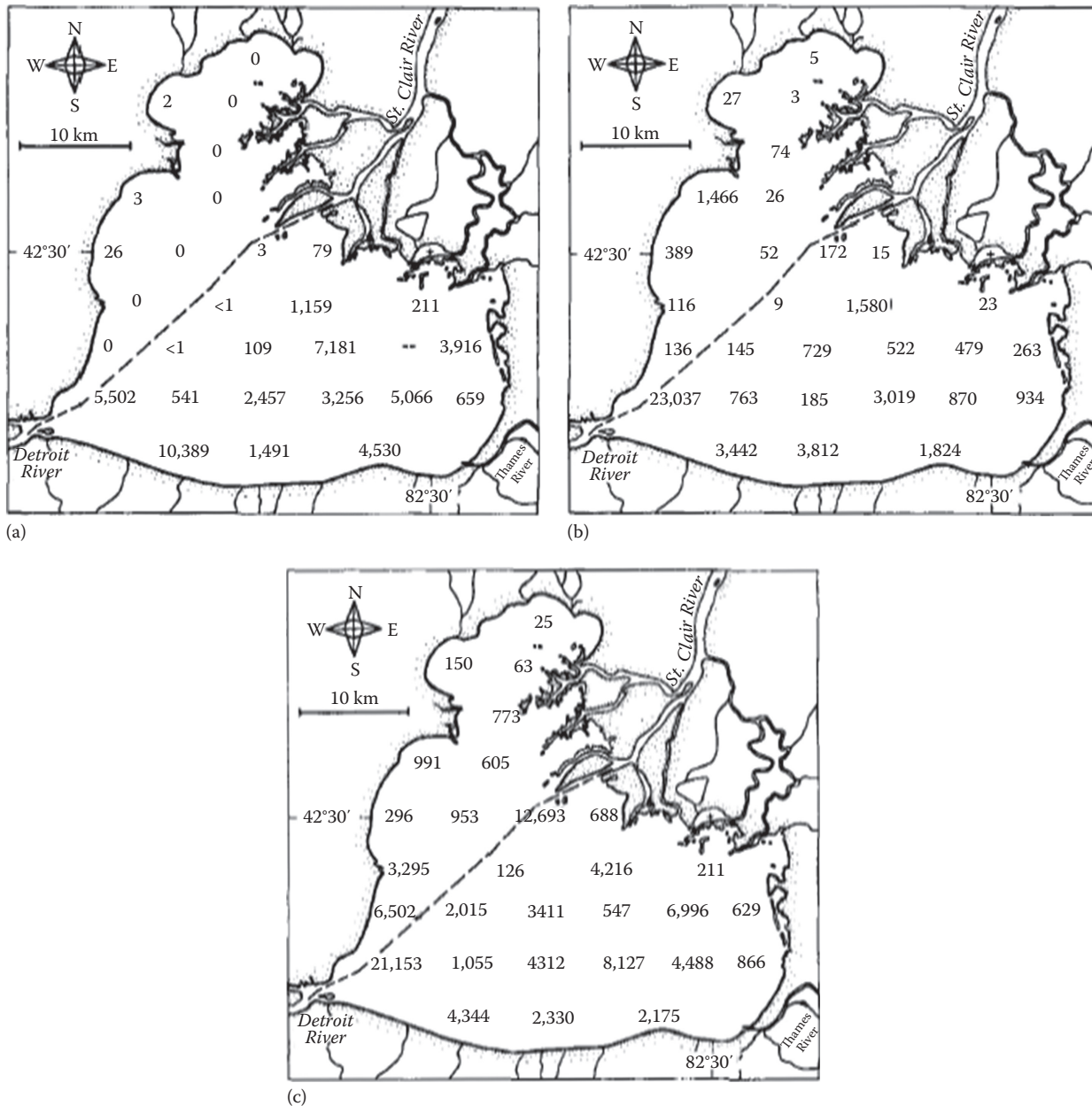
Figure 40.2 Mean density (m⁻²) of zebra mussels at 29 sampling sites in Lake St. Clair in (a) 1990, (b) 1992, and (c) 1994. (From Nalepa, T.F. et al., *Great Lakes Res.*, 22, 354, 1996.)

mussel community in the open lake. As lampsiline and ano-dontine mussels were more affected by zebra mussels than other unionid taxa (Schloesser et al. 1998), the dominance of lampsilines in the unionid community of the delta suggests that this community was sheltered from the most severe effects of zebra mussels (McGoldrick et al. 2009). While the delta remains a unionid refugia even though zebra mussels have been abundant in nearby offshore waters for nearly 25 years, the long-term survival of the unionid community in this region remains in question.

In order to assess trends in the unionid community in the delta, the area on the U.S. side of the delta was resurveyed in 2010. Results indicated the unionid community remained in a state of flux. Of the nine sites resurveyed using the same "stake and rope" technique as in 2003 (Zanatta et al. 2002, McGoldrick et al. 2009), unionid densities declined below detectable levels at three sites, declined significantly at two sites (two-tailed t-tests, $P < 0.05$), did not change at three sites ($P > 0.05$), and increased at one site ($P < 0.01$) (Figure 40.7). Data used for the t-tests were normally distributed (Kolmogorov–Smirnov test) and group variances were not different, thus appropriate for t-tests (Zar 1996). Densities at some of the sites sampled with the "stake and rope" method in 2010 but previously sampled with only
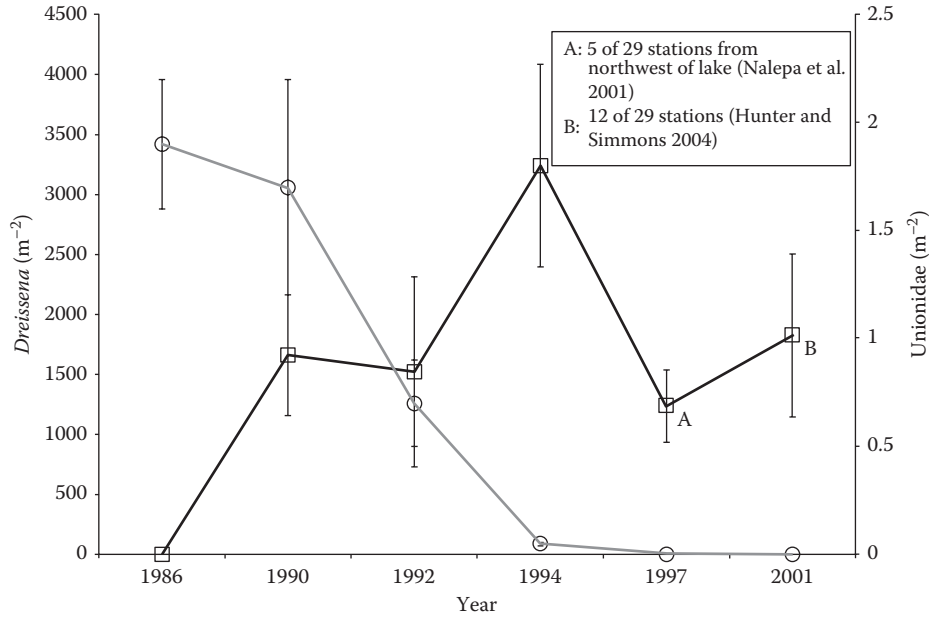
Figure 40.3 Mean (± SE) density (m^{-2}) of *Dreissena* (zebra mussel) and Unionidae in Lake St. Clair (note different scales). Densities in 1986, 1990, 1992, and 1994 were taken from Nalepa et al. (1996), densities in 1997 were taken from Nalepa et al. (2001), and densities in 2001 were taken from Hunter and Simons (2004). *Dreissena* = square/black line; Unionidae = circle/gray line.
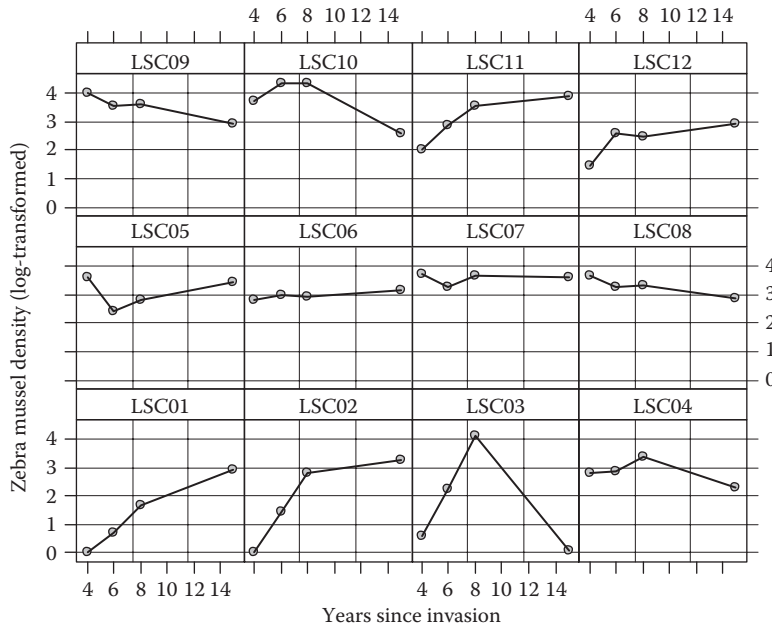

Figure 40.4 Density of *Dreissena* (zebra mussel) relative to time after initial invasion at 12 stations (LSC01 to LSC12) repeatedly sampled in Lake St. Clair. (From Hunter, R.D. and Simons, K.A., *J. Great Lakes Res.*, 30, 528, 2004.) Density was log$_{10}$(x + 1)-transformed to better depict trends.

timed searches in 2003 were among some of the highest found, especially at sites in Big Muscamoot Bay and Little Muscamoot Bay (Sites 23 and 24; Figure 40.7). Anecdotally, it appeared that densities at some sites that were surveyed using time search only in 2003 increased in 2010. Of note, population densities at sites in the outer bays of the delta (closest to open lake environments, i.e., Sites 9, 12, 13, 17) either declined with individuals still present or declined with individuals no longer found. In contrast, densities at sites further into the bays of the delta were stable or increased between 2003 and 2010. The relative composition of the community remained generally the same over this
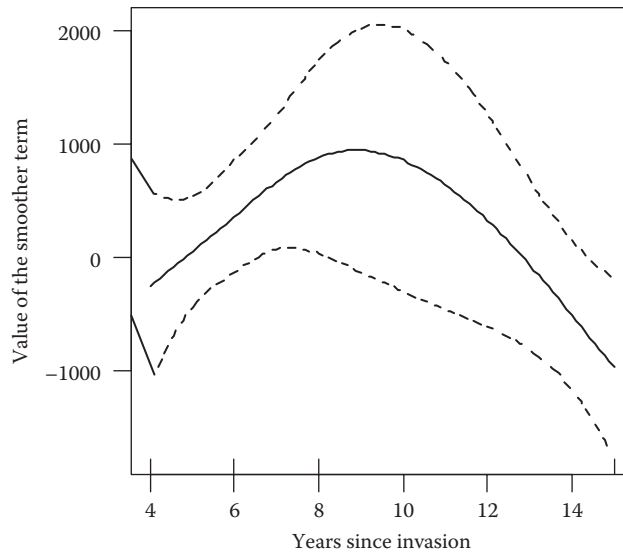
Figure 40.5 Estimated smoother term (*s*) for the generalized additive model that describes the change in zebra mussel density relative to the number of years after the initial invasion (*YSI*) at 12 stations in Lake St. Clair. *Density* = 2838 + *s*(*YSI*) (see "Statistical Modeling" for details). Both the intercept and the smoother of this model are significant ($P < 0.001$, *z*-test, and $P = 0.036$, χ^2-test, respectively). The solid line is the estimated smoother, and the dotted lines are 95% point-wise confidence bands.
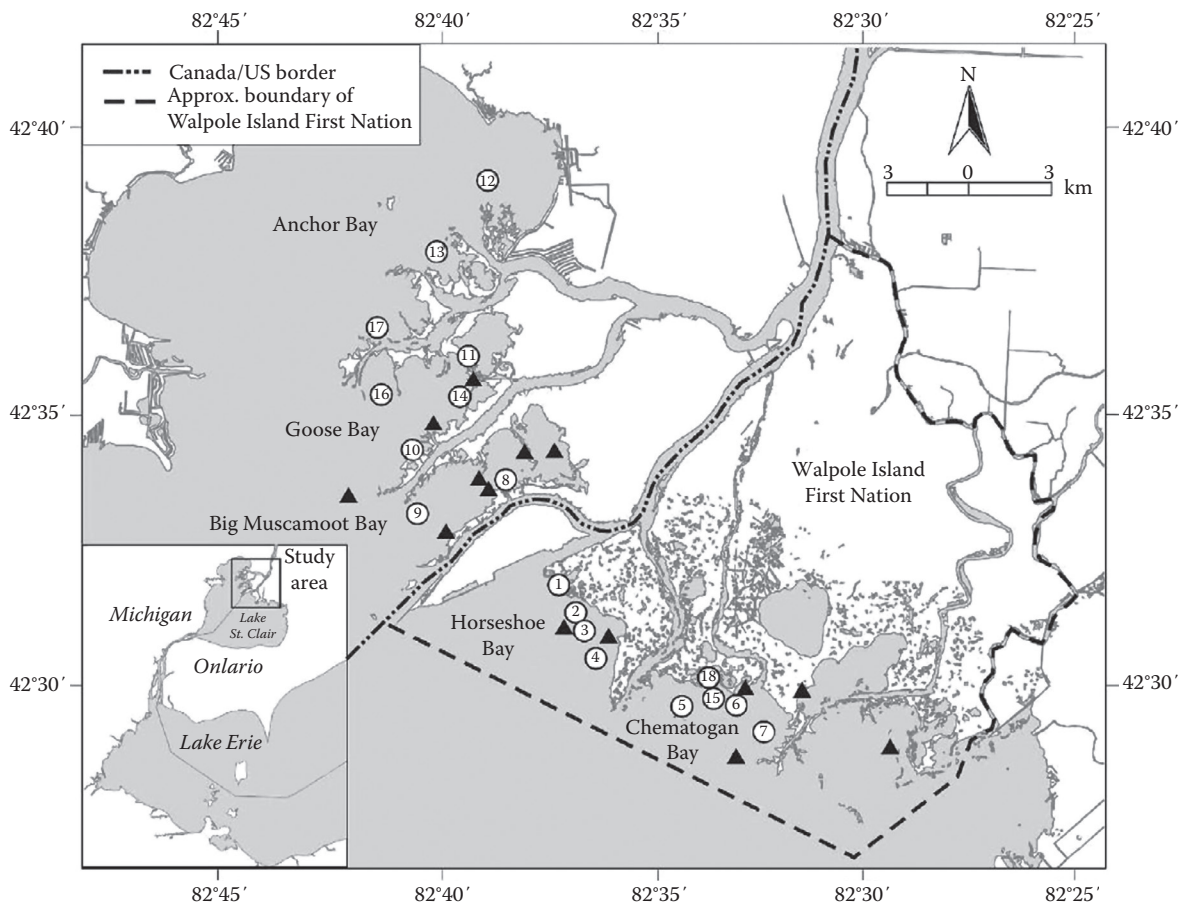
Figure 40.6 Locations of 32 sites surveyed for unionids in the Lake St. Clair delta in 2003, 2005, and 2010. Sites surveyed quantitatively in 2003 and 2005 (*n* = 18) are indicated by circles containing the site number; sites surveyed semiquantitatively (timed search) in 2003/2005 are indicated by black triangles. All sites on the U.S. side were sampled quantitatively in 2010 using the "stake and rope" technique. (From McGoldrick, D.J. et al., *J. Great Lakes Res.*, 35, 137, 2009; Zanatta, D.T. et al., *J. Great Lakes Res.*, 28, 479, 2002.)

Figure 40.7 Comparison of unionid densities (±SE) in 2003 and 2010 at sites in the St. Clair delta. Densities in both years were determined with the "stake and rope" technique (Zanatta et al. 2002). Differences between years for each site were determined with a two-tailed *t*-test. Asterisk = difference between years was significant; NS = differences between years were not significant.
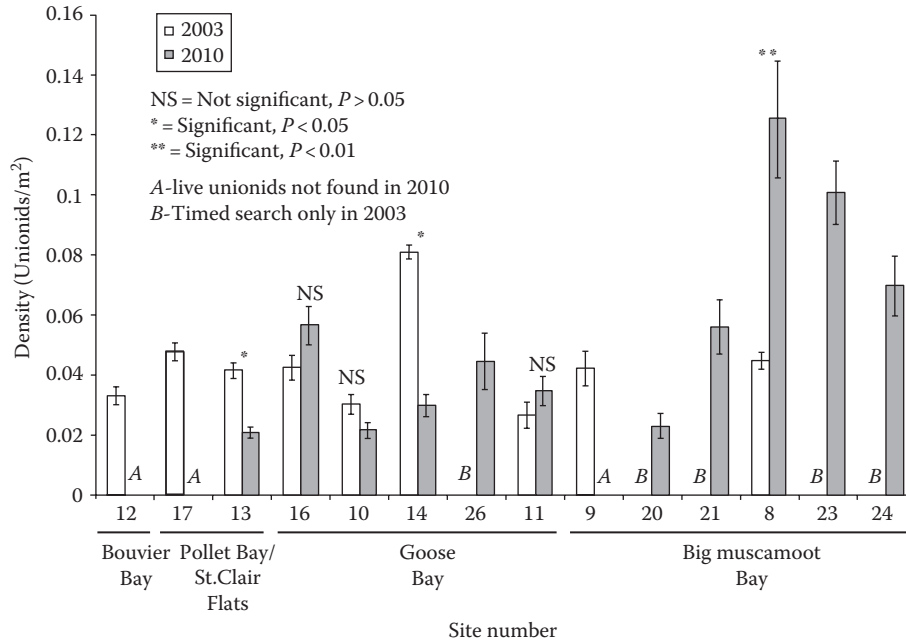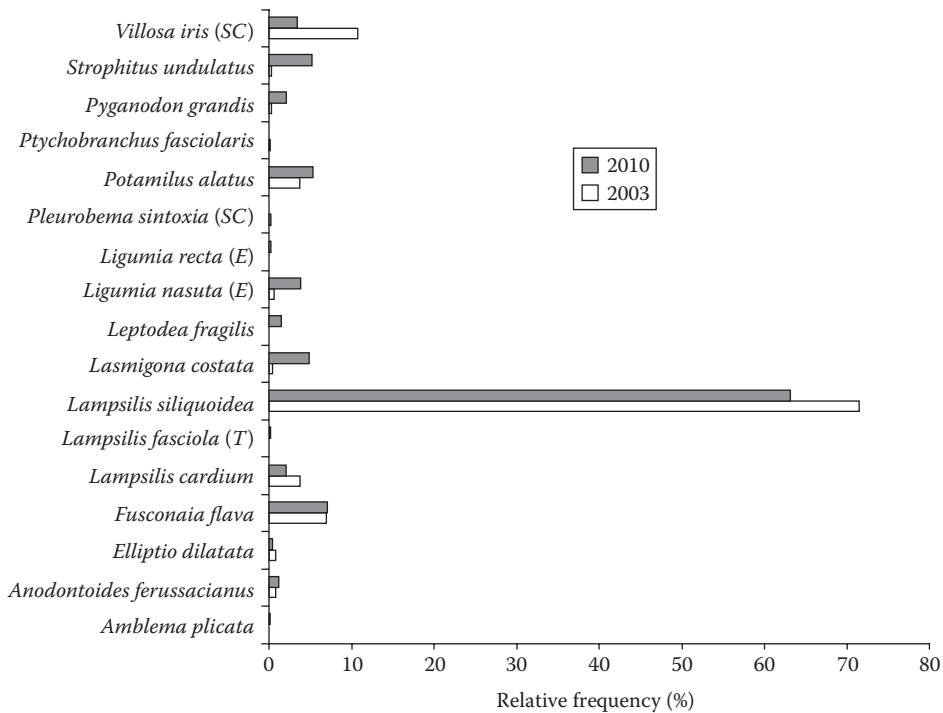

Figure 40.8 Relative abundances (percent frequency) of unionid species in 2003 and 2010 at sites on the U.S. side of the St. Clair delta. Species of conservation concern in Michigan are labeled (*E* = endangered, *T* = threatened, *SC* = special concern).

7-year period. However, there was an increase in frequency of *Ligumia nasuta* (endangered in Michigan and Canada), *Lasmigona costata*, and *Strophitus undulatus* and a decline in frequency of *Villosa iris* (special concern in Michigan, endangered in Canada) (Figure 40.8).

While mechanisms for observed changes in unionid communities in the St. Clair delta remain unclear, there have been significant declines in zebra mussel densities across all sites (Figure 40.9). Sampling in 2010 marked the first year that quagga mussels, *D. rostriformis bugensis*,

Figure 40.9 Mean number (±SE) of *Dreissena* (zebra mussel) found attached to unionids at sites in the St. Clair River delta in 2003 and 2010. Differences between years at each site were tested using two-tailed *t*-tests. NS = not significant ($P > 0.05$), *$P < 0.05$, **$P < 0.01$, and ***$P < 0.001$.
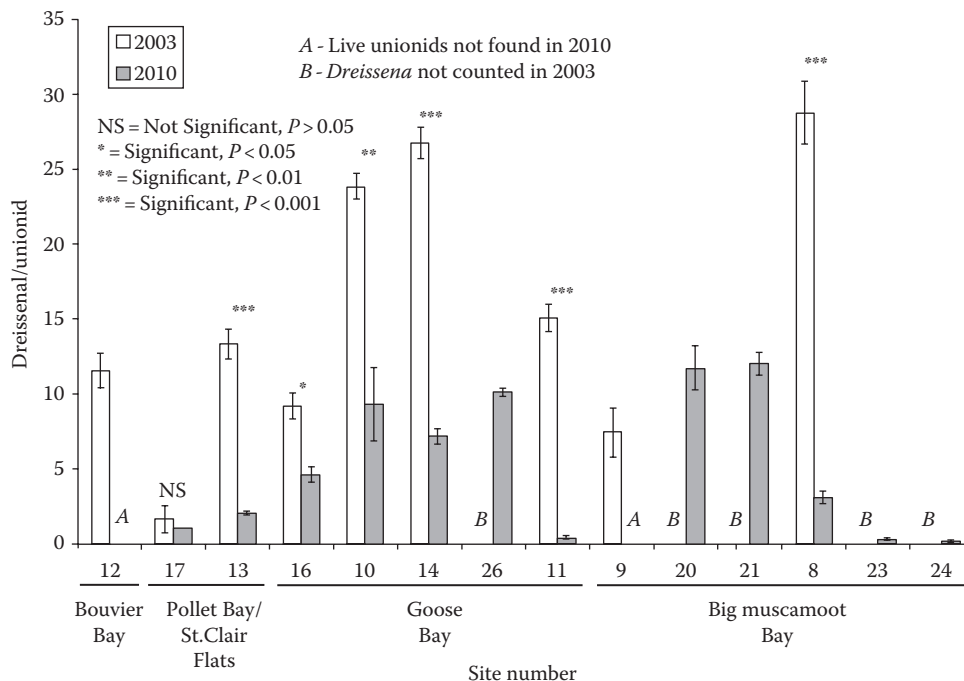
were detected in the delta. The proportion of quagga mussels to zebra mussels was not quantified, but the former species was very rare. Densities of *Dreissena* (both species), as estimated by the number per unionid, declined significantly (two-tailed *t*-test, $P < 0.05$) between 2003 and 2010 at all sites where unionids were still found alive. Of note, numbers of *Dreissena* per unionid were especially low in the inner bays of the delta, with significant declines ($P < 0.001$) at Sites 11 and 8 between 2003 and 2010, and very low numbers per unionid found at sites not previously documented in 2003 (Sites 23 and 24) (Figure 40.9). As with changes in unionid communities, mechanisms for lower infestation on unionids are unclear.

The unionid community on the U.S. side of the St. Clair delta has persisted since its discovery in 2001 (Zanatta et al. 2002), and findings in 2010 bode well for continued coexistence with *Dreissena*. Although unionid densities at some sites at the outer margins of the delta with relatively high densities in 2003 declined significantly, or declined to zero, densities in 2010 at majority of sites remained high, with unionids having a low number of attached *Dreissena*. Concern remains, however, for many of the rare unionid species (Table 40.3, Figure 40.9).

Several questions remain unanswered with respect to the long persistence of the St. Clair delta as a unionid refuge (many of these questions also apply to other refuges across

Table 40.3 Unionid Species of Greatest Conservation Need (Endangered, Threatened, Special Concern) in Michigan and Ontario That Have Been Found or Formerly Found in Lake St. Clair and/or Tributaries

Alasmidonta marginata	MI	*Quadrula quadrula*[a]	Ontario
Epioblasma t. rangiana[a,b]	MI, Ontario	*Pleurobema sintoxia*[a]	MI, Ontario
Epioblasma triquetra[a,c]	MI, Ontario	*Ptychobranchus fasciolaris*[a]	MI, Ontario
Lampsilis fasciola[a]	MI, Ontario	*Simpsonaias ambigua*[a]	MI, Ontario
Ligumia recta	MI	*Toxolasma parvus*[d]	MI, Ontario
Ligumia nasuta[a]	MI, Ontario	*Toxolasma parvus*[a]	MI, Ontario
Obovaria olivaria[d]	MI, Ontario	*Truncilla truncata*	MI
Obovaria subrotunda[a]	MI, Ontario	*Villosa fabalis*[a,c]	MI, Ontario
Obliquaria reflexa[d]	MI, Ontario	*Villosa iris*[a]	MI, Ontario

[a] Canada, listed by COSEWIC and/or under SARA (Government of Canada 2010).
[b] United States, federally endangered species.
[c] United States, federal candidate species.
[d] Canada, COSEWIC candidate species (COSEWIC 2010).

the lower Great Lakes). Future research on mechanisms for unionid persistence in the delta is critical. Why have zebra mussel populations declined precipitously throughout the delta (and possibly throughout the lake)? Monitoring of zebra mussel veliger densities, settlement rates, and water chemistry (nutrient levels) throughout the delta would provide valuable insights into this question. If the trajectories for *Dreissena* densities in Lake St. Clair continue as modeled (Figure 40.5), ultimately falling below threshold densities that induce unionid mortality (Ricciardi et al. 1995), it may be possible for unionids to recolonize and coexist with dreissenids in the open lake. Also, it is unclear if unionids still exist in the deepwater channels of the delta and the St. Clair River. If unionids still persist in these channels, they may be acting as source populations for unionids in the delta. Anecdotal evidence for this possibility comes from observations that numerous unionid shells were present in recent dredge spoils from channels in the St. Clair River (D. Dortman, Michigan Department Environmental Quality, personal communication). Finally, population genetics research (e.g., Krebs et al. 2003, Krebs 2004, Zanatta et al. 2007, Zanatta and Wilson 2011) can be used to measure genetic variation of unionid species within and among sites, bays, and tributary streams in the St. Clair delta, its tributaries, and other unionid refuges in the Great Lakes. Genetic research will provide valuable information that can be used to interpret source/sink dynamics among sites/bays in and among refuges and tributaries, determine if zebra mussel–induced unionid population crashes caused genetic bottlenecks, determine if gene flow exists among unionid populations in the region, and help predict where unionids are most likely to recolonize. Such studies can assist in prioritizing areas for conservation and give guidelines for managing the unionid communities of the St. Clair delta.

Various Water Bodies, Belarus

To determine the impact of dreissenids on unionid bivalves, 20 water bodies in Belarus were studied from 1990 to 2002. These water bodies had different limnological features and varied in time since zebra mussel colonization and in overall zebra mussel density (Burlakova et al. 2000, Karatayev et al. 2000, 2003, 2005, 2008a, 2010). The longest-established zebra mussel population occurred in Lake Lepelskoe, which was colonized shortly after construction of the Dnieper–Zapadnaya Dvina Canal in 1805 (Karatayev et al. 2008b). This canal was the route through which zebra mussels colonized water bodies in northern Belarus (Burlakova 1998, 1999, Karatayev et al. 2003, 2008b, 2010). The Svisloch River and its reservoirs Chizhovskoe and Drozdy were colonized with zebra mussels in the mid-1980s (Burlakova 1998, 1999). The Braslavskaya Lake system and Lake Lukomskoe were colonized in the late-1960s (Lyakhnovich et al. 1984), and lakes in the Naroch region were colonized in the late-1980s (Karatayev et al. 2003).

The relationship between zebra mussels and unionids was studied in Lake Naroch between 1990 and 2002. The first study in 1990 was conducted during the initial stages of zebra mussel colonization. In that year, the average density of zebra mussels across the whole lake was 7.4 m^{-2} and biomass was 1.5 g m^{-2}. Sixty percent of live unionids ($n = 93$) were colonized by zebra mussels. The average number of mussels per unionid was 9.5, and average biomass was 1.8 g. Unionids were most heavily infested with zebra mussels near a stream that flows into Lake Naroch from Lake Myastro. Lake Myastro was colonized before Lake Naroch, so this connecting stream likely provided a route for zebra mussel invasion into the latter lake (Burlakova et al. 2000). The number of unionids fouled with zebra mussels decreased with increased distance from stream inflow (Pearson $r = -0.82$, $P = 0.023$) (Burlakova et al. 2000).

Between 1990 and 1993, the density of zebra mussels in Lake Naroch increased over 100-fold, and biomass increased 68-fold (Karatayev and Burlakova 1995a, Burlakova et al. 2006). In 1993, all unionids in the littoral zone across the lake were heavily infested with zebra mussels and the majority of unionids were dead. Between 1993 and 1998, only a few live unionids were found during our lake-wide surveys, and in 2002, no live unionids were found.

In contrast, unionids were still abundant in Lake Lepelskoe in 1997, which was ca. 200 years after initial zebra mussel colonization. It was relatively easy for a diver to collect hundreds of unionids within an hour. Although 92% were infested with zebra mussels, the average weight ratio of zebra mussels to unionid was 0.73 ± 0.21 (mean $\pm$ SE), lower than that in Lake Naroch (0.91 ± 0.36, average for 1990, 1993–1995, 1998).

Extensive infestation and mass mortality of unionids is typical in the period soon after zebra mussels become established in a given water body and when population growth is rapid (Karatayev et al. 1997, 2002, Burlakova et al. 2000). In contrast to high unionid mortality observed in newly colonized Belarusian water bodies, unionids maintain relatively high densities in lakes where zebra mussels have been found for a long time period. In other cases, unionids appear to be abundant even after the period of initial zebra mussel colonization. Zebra mussels first colonized Lake Lukomskoe in the late 1960s and by 1978 obtained an average density of 758 ± 227 m^{-2} and a biomass of 124 ± 37 g m^{-2} (Karatayev 1983). In 1978, unionid density across the entire lake was 4.7 ± 1.9 m^{-2}, and 75% of the unionids (*Unio pictorum*, *Unio tumidus*, *A. anatina*, and *Anodonta piscinalis*) were fouled with zebra mussels. The maximum number of zebra mussels per unionid was 216, and the average was 30 ± 9. The average ratio of total weight of attached zebra mussels to unionid host weight was 1.20, and the range was 1.04–9.10. In the profundal zone of Lake Lukomskoe, which was dominated by silt, zebra mussels were found only on unionids. On average, about 20% of the total density and biomass of the population of zebra mussels in this lake were comprised of mussels attached to live unionids (Karatayev 1983).
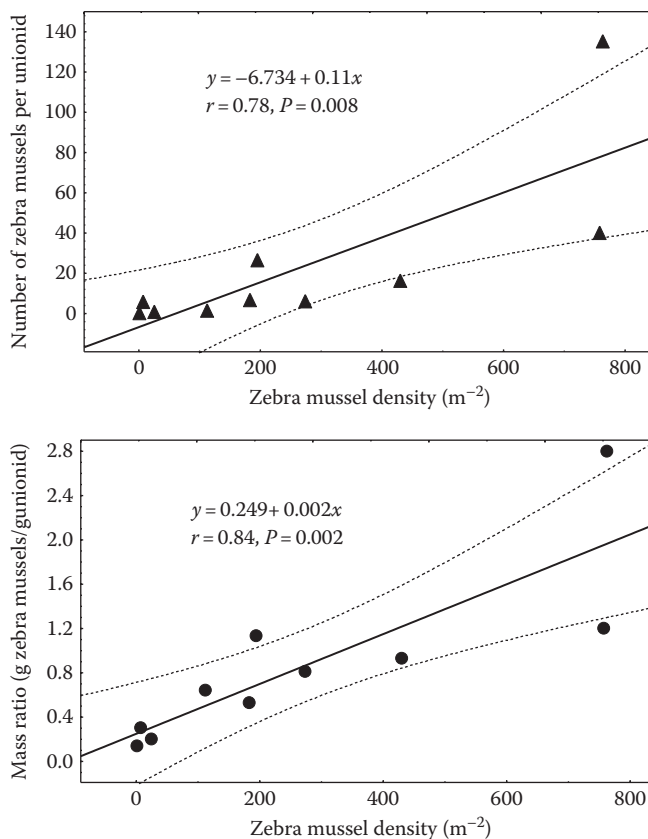
$$y = -6.734 + 0.11x$$
$$r = 0.78, P = 0.008$$

$$y = 0.249 + 0.002x$$
$$r = 0.84, P = 0.002$$

Figure 40.10 The number of attached zebra mussels per unionid relative to zebra mussel density (a) and the mass (weight) ratio of attached zebra mussels and unionid host relative to zebra mussel density (b) for water bodies in Belarus. Density given as number per m², and mass given as total wet weight (g). Each point represents a separate water body. Solid line was derived from the given regression and dotted lines represent 95% confidence limits of the regression line. (Modified from Burlakova, L.E. et al., *Int. Rev. Hydrobiol.*, 85, 529, 2000.)

To determine the relationship between zebra mussel density and unionid infestation, we examined data from Lake Naroch (collected in 1990 and 1993) and eight other lakes in the Naroch region (collected in 1998). We found a direct correlation between zebra mussel density and number of zebra mussels attached to unionids, as well as between zebra mussel density and the ratio of the total wet weight of attached mussels to the total wet weight of the unionid host (Pearson $r = 0.78$, $P = 0.008$, Pearson $r = 0.84$, $P = 0.002$, respectively) (Figure 40.10). From the perspective of the unionid, the weight of attached zebra mussels, or the weight ratio, is probably more important than density (Hebert et al. 1991, Karatayev et al. 1997).

Substrate type may impact the level of *Dreissena* infestation of unionids. In the Svisloch River, where sand and gravel alternate with silt, we found unionids in sand and gravel with high numbers of attached zebra mussels (up to 100 per unionid). In contrast, unionids completely buried in silt were free of zebra mussels, and at several of these silty sites, the density of unionids was around 100 m⁻². The average density of zebra mussels in the Drozdy Reservoir (Svisloch River) was 838 m⁻². All 54 unionids collected from this reservoir had zebra mussels attached, and 15 of

the unionids collected were alive. Densities of zebra mussels were much lower (81 m⁻²) in a downstream reservoir, Chizhovskoe, where silt substrates were prevalent. Unionids were abundant in this reservoir, and only 7 of total 107 unionids collected had attached zebra mussels. In Lake Volchin, unionids in sandy substrates were completely infested with zebra mussels, and the number of zebra mussels per unionid was 35.6 ± 8.3. In contrast, in the same lake the number of zebra mussels per unionid in silty substrates was only 13.4 ± 3.3. The difference in number of attached zebra mussels per unionid in the two substrates was significant ($P = 0.049$, ANOVA). The ratio of weight of zebra mussels to weight of host unionid was higher on sand (1.45 ± 0.29) than on silt (0.66 ± 0.17), but the difference was not significant ($P = 0.054$, ANOVA) (Burlakova et al. 2000). Similar results have been obtained in other European water bodies. For instance, in Lake Hallwil, Switzerland, Arter (1989) found that *U. tumidus* was usually buried in silty sediments and rarely overgrown by zebra mussels. However, *A. cygnea* was often only partly buried and was infested more often by zebra mussels relative to *U. tumidus*.

Our studies indicate that unionids may be capable of removing zebra mussels from their shell surface. Often in

water bodies where we found unionids heavily infested, we observed some individuals completely free of zebra mussels but had byssal threads attached to their shells. For example, in Lake Bolshiye Shvakshty, 40% of 147 unionids were infested with zebra mussels. Over 70% of these infested unionids had remains of byssal threads on their shells, indicating that more mussels were attached to them before collection. Moreover, 61% of uninfested unionids had zebra mussel byssal threads on their shells. Twenty-three percent of all unionids collected had neither zebra mussels nor byssal threads. Zebra mussel byssal threads were also found on uninfested unionids from other water bodies (e.g., lakes Dolzha, Spory, and Bolduk). In Lake Bolshiye Shvakshty, the average number of zebra mussels on unionids without remains of byssal threads was significantly higher ($P < 0.001$, t-test) than the average number on unionids with remains of byssal threads (7.2 ± 1.3 vs. 1.8 ± 0.2) (Burlakova et al. 2000).

Lough Key, Ireland

The initial introduction of the zebra mussel to Ireland occurred in the lower Shannon River basin in the early 1990s (McCarthy et al. 1998, Minchin and Moriarty 1998). The Shannon River is the largest navigable river system in Ireland, and the most likely vector of introduction was via imported leisure craft. Live zebra mussels were found on hulls of leisure craft that arrived in Ireland from Britain during the period between 1997 and 2001 (Minchin et al. 2002a). Further, zebra mussels in Ireland were genetically most similar to populations from the midlands of Britain (Pollux et al. 2003, Astanei et al. 2005). Once established, zebra mussels spread throughout Ireland via transport by recreational boats (Minchin et al. 2002b). Zebra mussels spread to most lakes in the Shannon River basin district, to heavily fished lakes in western Ireland, and to many other water bodies with moderate to high calcium concentrations (Lucy and Mastitsky, unpublished).

The unionid *Anodonta* was widely distributed in Lough Key (Figure 40.11), and the rest of the Shannon River system at the time zebra mussels arrived in the early 1990s. In April 1998, 23 live *Anodonta* were collected in Lough Key. Of these, 7 were free of attached zebra mussels, while the other 16 had only 1–5 attached mussels that were 3–13 mm in length. These small attached mussels likely settled the previous year. In contrast, *Anodonta* collected in November 1998 ($n = 72$) were more densely infested with mussels (mean = 78 mussels per unionid, range 0–314).

By July 1999, the mean number of zebra mussels found attached to individual *Anodonta* increased to 294 mussels per unionid (range 81–923), which was much higher than found in November 1998. In a limited sample of 12 dead *Anodonta* shells, the maximum number of attached zebra mussels was 1066.
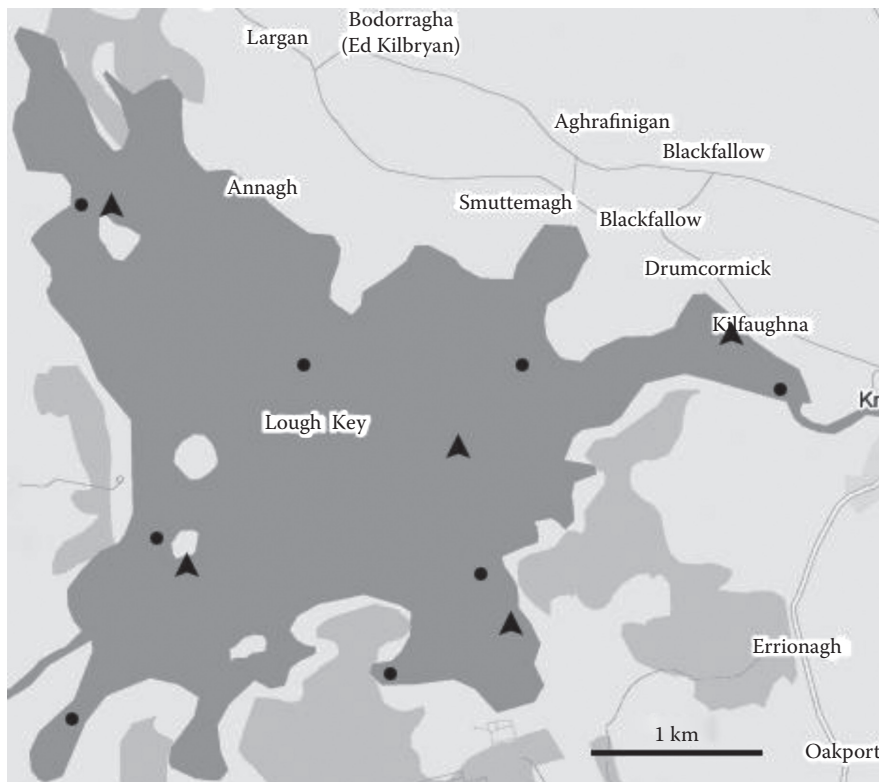

Figure 40.11 Sampling sites in Lough Key, Ireland. Solid circles, snorkel sites; solid triangles, monitoring sites. (From Lucy, F. et al., Nutrient levels and the zebra mussel population in Lough Key, ERTDI Report Series No. 34, Environmental Protection Agency, Wexford, Ireland, 2005; Map: © 2011 Google; Map data © 2011 Tele Atlas.)
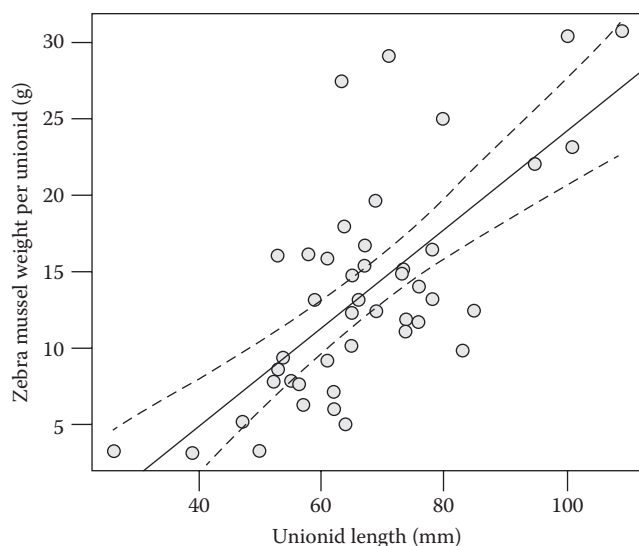
Figure 40.12 Relationship between weight (g) of attached zebra mussels on a unionid and shell length of the unionid (mm) in Lough Key, Ireland. The relationship was defined as *Weight = −7.80 + 0.32 × Length*. The model explained 62% of the variance and was highly significant (*P* < 0.001, *F*-test). Dotted lines represent 95% confidence limits of the regression line.

The total number of *Anodonta* collected in July 1999 was 58, and the live/dead ratio was 3.8 to 1 (Lucy and Sullivan 2001). It is not possible to ascertain how many of the dead unionids were attributed to biofouling because no decaying flesh was present to indicate whether shells were fouled prior to or after death, but they were all sampled from extant *Anodonta* beds. Attached zebra mussels were mainly young of the year (<3 mm) or age 1+ (3–19 mm), although age 2+ mussels (≥19 mm) were also found in low numbers. As zebra mussels became further established in Lough Key, it was common by 1999 to find small numbers of age 2+ or older (up to 36 mm) zebra mussels attached to *Anodonta* as well as to stone substrate.

Zebra mussels found on live *Anodonta* occurred mainly on the outside of the posterior end of the shell, but sometimes zebra mussels were found on the inside. The shell length of *Anodonta* collected live ranged from 26 to 85 mm, and the smallest individual collected was heavily infested on one half of its shell. In July 1999, the weight ratio of attached zebra mussels to corresponding live *Anodonta* ranged from 0.24 to 3.48 (mean 0.93).

In November 1999, 36 *Anodonta* were collected from one particular site but only 6 were live. The mean weight ratio of attached zebra mussels to live *Anodonta* was 0.45. Of the 30 dead *Anodonta* collected, 26 were mostly buried in the substrate and infested at the posterior end (4 were half shells only). This indicated that they had been fouled while live and had presumably died during 1999. Zebra mussels were found on 15 of the dead *Anodonta*, with an average of 745 individuals (range 334–1108) per shell and a biomass of 31.6 ± 13.3 g per shell. Collections in 1999 showed a strong positive linear relationship between total weight of attached zebra mussels and unionid shell length (*P* < 0.001, *F*-test) (Figure 40.12). In addition, the weight ratio of attached zebra mussel to unionid weight was significantly negatively associated with unionid shell length (*P* < 0.001, *F*-test).

In 2000, most *Anodonta* were found dead on their sides, with high densities of zebra mussels on the side exposed (outside and often inside) of shells. Zebra mussel colonization often extended from the shell outward onto the substrate. In 2001, a survey with an ROV around lakeshore and island perimeters revealed that the mean density of dead *Anodonta* shells was 2 m^{-2} (range 0–12). Byssal plaques were often noted at the posterior end of dead shells partially covered by substrate (Figure 40.13). By 2003, shells were observed to be primarily sunk in the soft substrate of the lake (Lucy et al. 2005). Mean lengths of dead shells were 8.4 ± 1 cm in 2000, 8.7 ± 1.1 cm in 2001, and 9.2 ± 8.1 cm in 2003, and all were significantly greater (*t*-test, *P* <0.001) than mean shell

(a)

(b)

Figure 40.13 Zebra mussels and byssal plaques on unionids collected from (a) Lake Naroch, Belarus, and (b) Lake St. Clair.

lengths of live *Anodonta* collected in 1999. This suggests that, at least in some cases, zebra mussels colonized empty *Anodonta* shells that resulted from individuals that had died of old age/natural causes prior to infestation. No shell deformities were noted on any *Anodonta* (live or dead) during the course of these surveys (1998–2003), indicating mortality was not due to physical damage to unionid shells.

From 2000 to 2003, no live *Anodonta* were recovered or viewed during grab sampling, snorkel, dive, transect, or video surveys. Hence, based on the evidence, the extirpation of *Anodonta* in all sampled areas occurred between November 1999 and August 2000. While it is quite possible that fish may reintroduce *Anodonta* to Lough Key from other parts of the Shannon River basin, without intensive sampling it may take years to detect whether this has happened. In such a case, the rapid extirpation of *Anodonta* following zebra mussel colonization could actually be reversed by a natural reintroduction to the lake. Since zebra mussel populations have subsequently stabilized in Lough Key, it is possible that reintroduction of unionids could result in sustained populations of *Anodonta* in the lake.

OVERALL IMPACTS

Based on these case studies, a high percentage of unionids will be infested even when zebra mussel density in a given water body is low, and infestation grows rapidly with increased zebra mussel density (Figure 40.14). When the average density of zebra mussels in a water body was
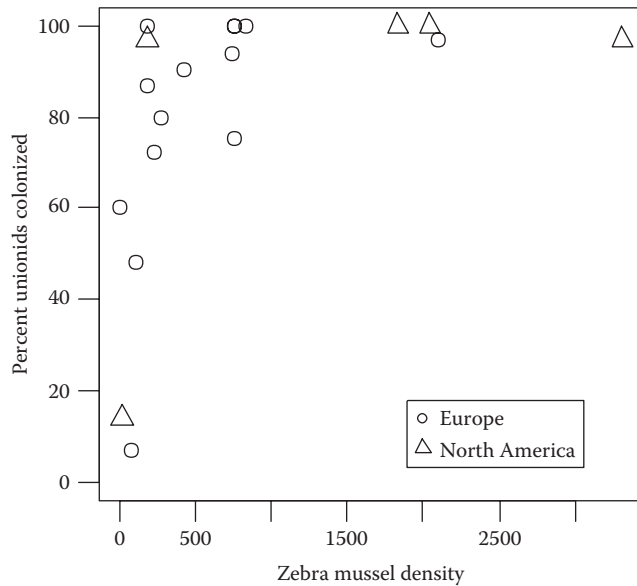

Figure 40.15 Relationship between mean number of zebra mussels per unionid and zebra mussel density (No. m⁻²) in water bodies in Europe and North America. The relationship was defined as *Number* = 0.081 × *Density*. The model explained 84.2% of the variance and is highly significant ($P < 0.001$, *F*-test). Dotted lines represent 95% confidence limits of the regression line. European data taken from Karatayev and Burlakova (1995), Burlakova et al. (2000), and Burlakova and Karatayev (unpublished); North American data taken from Nalepa et al. (1996).
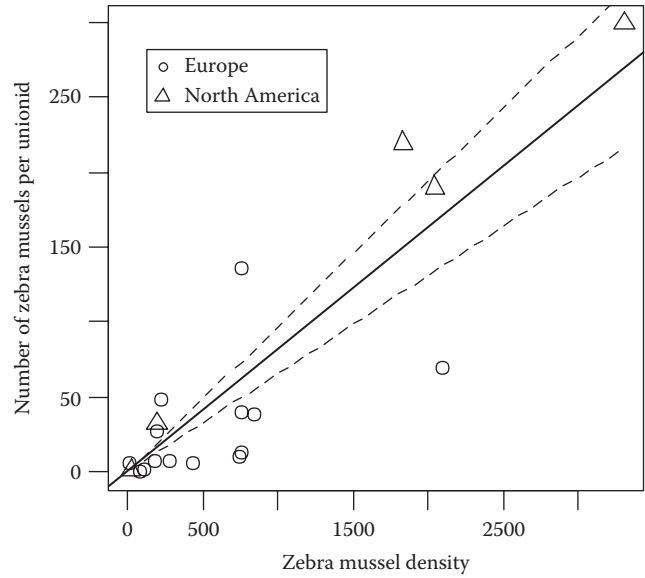
ca. >200 m⁻², up to 100% of unionids were found to be infested. There was no notable difference in infestation patterns between North American and European data (Figure 40.14). We found a strong positive linear relationship between the number of zebra mussels per unionid host and the zebra mussel density in a given water body (Figure 40.15). Interestingly, most North American observations occurred above the fitted regression line (Figure 40.15), suggesting that this relationship is stronger in North America than in Europe. However, as discussed later, this observation may be an artifact of sampling protocols.

The relationship between the weight of attached zebra mussels and the unionid shell length varied between the 15 international water bodies and also varied with the length of time after zebra mussels invaded (Figure 40.16). Overall, however, datasets were sufficiently fitted by the model: *Weight* = 3.28 + 0.17*L* − 6.58*TSRI*, where *L* is the unionid shell length and *TSRI* is the time since recognized invasion of zebra mussel (with value 0 if <10 years, and 1 if ≥10 years). All coefficients of the model were highly significant ($P < 0.001$, *t*-tests). For *TSRI* < 10 years, there was an overall trend for increase of zebra mussel weight with unionid host's size (Figure 40.17). For *TSRI* ≥ 10 years, such a pronounced trend was not observed (Figure 40.18), indicating that the infestation rate per unionid length declines. In addition, the weight of zebra mussels per unit of unionid length appeared to be significantly lower in water bodies

Figure 40.14 Relationship between the percentage of unionids infested with zebra mussels and the average density (No. m⁻²) of zebra mussels in a water body. European data taken from Karatayev and Burlakova (1995a), Burlakova et al. (2000), and Burlakova and Karatayev (unpublished); North American data taken from Nalepa et al. (1996).
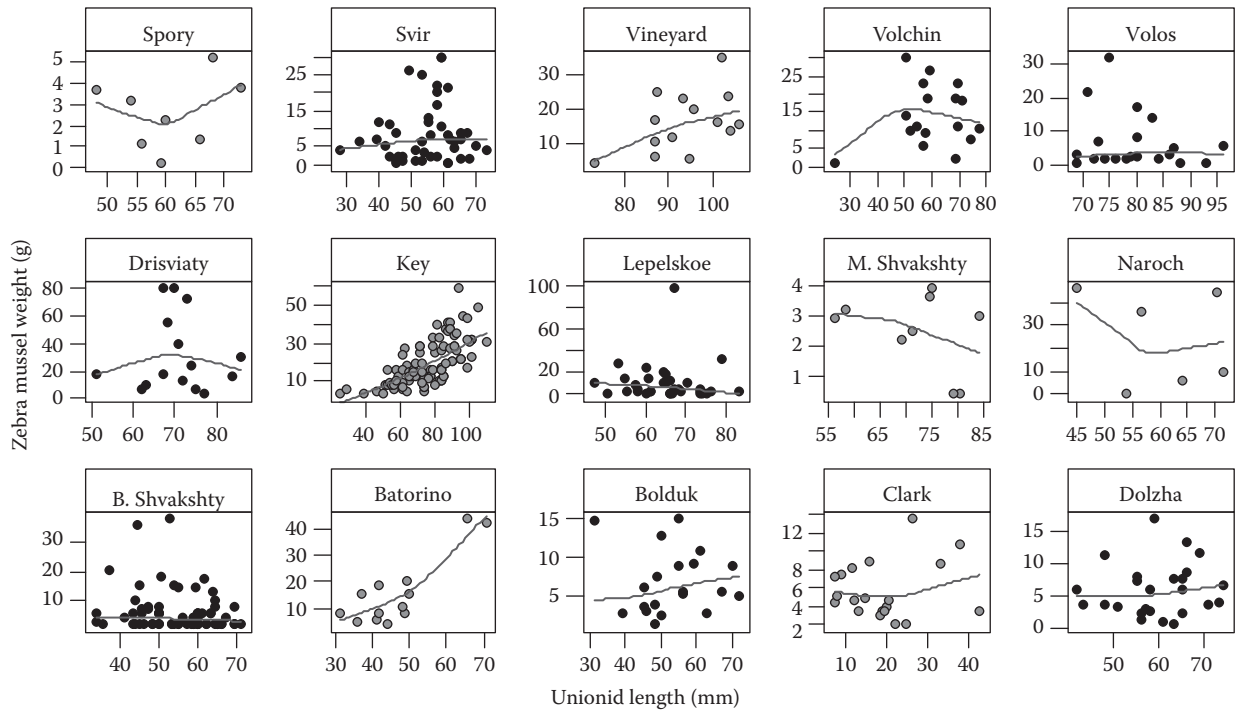
Figure 40.16 Relationship between weight (g) of zebra mussels attached to a unionid and shell length (mm) of the unionid for lakes in Belarus. Lakes were categorized by the *TSRI* of zebra mussel. A smoother was added to each panel to visualize the patterns in data. Gray points represent lakes with a *TSRI* < 10 years, and black points represent lakes with a *TSRI* ≥ 10 years. Data for Lakes Clark, Lepelskoe, Naroch, Volchin, and Vineyard are from Burlakova et al. (2000), data for Lough Key are from Lucy and Sullivan (2001), and data for all other lakes are from Karatayev and Burlakova (unpublished).
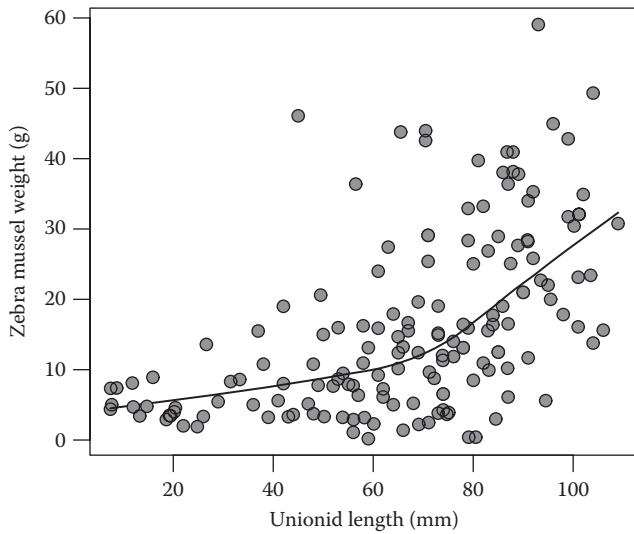

Figure 40.17 Relationship between weight (g) of attached zebra mussels and shell length (mm) of corresponding unionid for lakes with *TSRI* < 10 years (*n* = 162, data pooled for seven lakes). A smoother was added to visualize the pattern.
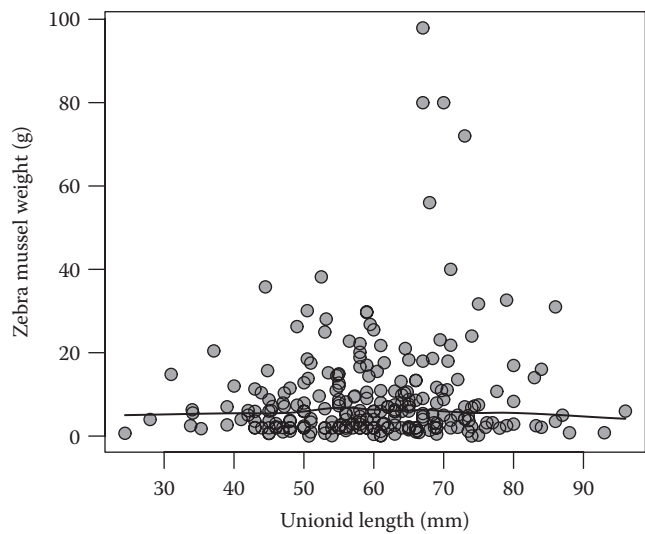

Figure 40.18 Relationship between weight (g) of attached zebra mussels and shell length (mm) of corresponding unionid for lakes with *TSRI* ≥ 10 years (*n* = 249, data pooled for eight lakes). A smoother was added to visualize the pattern.

colonized for over 10 years (median 0.096 vs. median 0.209; *P* < 0.001, Mann–Whitney test). The negative value of the regression coefficient of *TSRI* suggested that overall zebra mussel weight per unionid weight decreased with time in water bodies colonized by zebra mussels for over 10 years.

As an additional support of this finding, we observed that the ratio of zebra mussel weight to unionid weight was significantly lower when *TSRI* was ≥10 years compared to the ratio when *TSRI* was <10 years (*P* < 0.007, Mann–Whitney test; Figure 40.19). For all water bodies, the median ratio
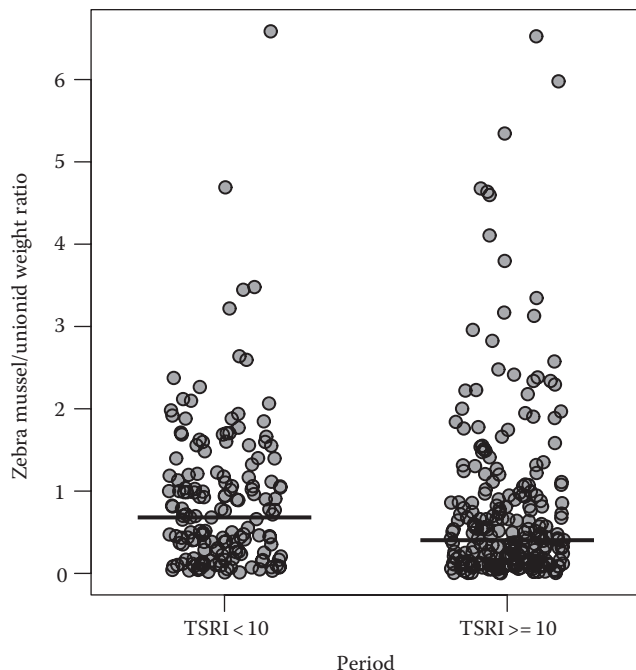
Figure 40.19 The weight ratio of attached zebra mussels to corresponding unionid in seven lakes with *TSRI* < 10 years and in eight lakes with *TSRI* ≥ 10 years (data pooled for all unionid species examined). Horizontal lines are the medians.

was 0.680 for the former time period compared to 0.404 for the latter. In combination, our results suggest that the adverse impact of zebra mussels on unionids decreases about 10 years after zebra mussels invade.

DISCUSSION

General Trends

The population size of an invasive species is one key factor that determines its effects on ecosystems and ecosystem components such as unionids. According to our analysis, impacts of zebra mussels on unionids are high early in an invasion when zebra mussel densities are increasing. Both European and North American data indicated that a high percentage of unionids were infested even when zebra mussel density was low during the early period of expansion. The percentage of unionids infested increased rapidly and reached 100% infestation at mussel densities ca. 200 m^{-2}. In many water bodies, by the time the zebra mussel population reached peak density, the majority of unionids were infested and dead. The dramatic decline of unionids after zebra mussel colonization is well documented both in Europe (Sebestyén 1937, Dussart 1966, Karatayev and Burlakova 1995b, Karatayev et al. 1997, Burlakova et al. 2000) and North America (Haag et al. 1993, Gillis and Mackie 1994, Nalepa 1994, Schloesser and Nalepa 1994, Nalepa et al. 1996, Riccardi et al. 1996, Ricciardi 2003, Strayer and Malcom 2007).

In contrast to the early stages of invasion, effects on unionids seem to decrease as the population of zebra mussels stabilizes or decreases. However, a decline in zebra mussel abundances may not be a general trend. The population may be quite stable for a relatively long period of time after reaching maximum density (Burlakova et al. 2006). Alternatively, the population may cycle (Strayer and Malcom 2006, Strayer et al. 2011) or fluctuate widely (Ramcharan et al. 1992, Stańczykowska and Lewandowski 1993).

The apparent extirpation of unionids from infested water bodies does not happen often (reviewed in Karatayev et al. 1997, Gurevitch and Padilla 2004a,b). Multiple European studies from water bodies colonized with zebra mussels for long periods of time showed that unionids were not extirpated from any of them (Lewandowski 1976b, Karatayev 1983, Miroshnichenko et al. 1984, Miroshnichenko 1987, Ponyi 1992, Burlakova et al. 2000). Although infestation can cause some unionid mortality, unionids not only persevered but also maintained high densities (Karatayev 1983, Miroshnichenko et al. 1984, Miroshnichenko 1987, Karatayev et al. 1997). We found live unionids in water bodies colonized by zebra mussels for >10 years and abundant unionid populations in Lake Lepelskoe where zebra mussels have been present for about 200 years. In the Tsimlyanskoe Reservoir, Russia, unionids (mainly *U. pictorum* and *A. cygnea*) were found to coexist with zebra mussels (Miroshnichenko et al. 1984, Miroshnichenko 1987). The average annual biomass over the entire Tsimlyanskoe Reservoir was 571 g m^{-2} for zebra mussels, 88 g m^{-2} for *U. pictorum*, and 46 g m^{-2} for *A. cygnea* (Miroshnichenko et al. 1984). In Lake Balaton, Ponyi (1992) determined the average density of unionids in 1932 just before the zebra mussel invasion was 3 m^{-2} and was 2 m^2 in 1966–1968. In the Azov Sea, which is within the native range of zebra mussel, one of 13 typical benthic communities included both zebra mussel and Unionidae as subdominant taxa (Vorobiev 1949). Near the mouth of the Don River, Russia, unionids, zebra mussels, and another bivalve *Monodacna* all had high abundances (Vorobiev 1949).

Some unionid communities in North America seem to be recovering after initial declines. Recent studies in the Hudson River found that populations of all native bivalves (unionids and sphaeriids) have stabilized or even recovered (Strayer and Malcom 2007), whereas annual survivorship of adult zebra mussels and aggregate filtration rate of the population declined (Strayer et al. 2011). According to Crail et al. (2011), unionids are extant at several sites outside known refugia in the western basin of Lake Erie, and conditions for unionids in the lake may be improving. Sixteen unionid species were found living in or near Lake Erie, including six sites in the nearshore zone of the lake. Each community consisted of live individuals from two to eight species, with the overall mean density at 0.09 m^{-2} (Crail et al. 2011).

Zebra mussel impacts on unionids may be taxon-specific as based on shell morphology (i.e., thin-shelled Lampsilinae and Anodontinae vs. thick-shelled Ambleminae)

(Lewandowski 1976b, Arter 1989, Haag et al. 1993, Strayer and Smith 1996, Schloesser et al. 1998). It has been shown that unionids "returning" to open-water areas of western Lake Erie were more often thin-shelled, fast-growing species (e.g., *L. fragilis* and *Pyganodon grandis*) (Crail et al. 2011). At least for *L. fragilis*, this is consistent with this species being persistent in a wetland area in western Lake Erie (Nichols and Amberg 1999). Despite the presence of zebra mussels in the wetlands for a number of years, the *L. fragilis* population showed no signs of competition-induced changes in population dynamics, had a limited incidence of recent or past dreissenid infestation (<1%), and displayed successful recruitment on a yearly basis. This seems to contrast with early observations that thin-shelled species were more highly impacted by zebra mussels than thick-shelled species (Schloesser et al. 1996).

Our analysis of multiple water bodies in Europe and North America in different stages of zebra mussel colonization has provided broad insights into unionid–dreissenid interactions. We found a positive relationship between the weight of attached zebra mussels and shell length of the corresponding unionid for water bodies that have been colonized by zebra mussels for less than 10 years. This trend, however, was not observed for water bodies colonized for over 10 years. We also discovered that the ratio of zebra mussel weight to unionid weight was significantly lower in water bodies colonized for over 10 years. These results suggest that adverse impacts of zebra mussels on unionids likely diminish with time.

What are the important features that may allow coexistence of unionids and zebra mussels in a particular habitat? These include factors that inhibit establishment of stable zebra mussel populations and/or allow unionids to escape dreissenid infestation. One of the most frequently reported habitat variables that allow unionid survival is the presence of substrates soft enough for unionids to burrow into and thereby remove attached zebra mussels and/or prevent zebra mussel settlement (Nichols and Wilcox 1997, Nichols and Amberg 1999, Burlakova et al. 2000, Zanatta et al. 2002, Bowers and de Szalay 2004). Factors that are hypothesized to inhibit establishment of stable zebra mussel populations are wave action in shallow water, water level fluctuations, ice scour (Nichols and Wilcox 1997, Burlakova et al. 1998, Bowers and de Szalay 2004, 2005), dense reed beds (Nelson et al. 2009, Sullivan et al. 2010), and remoteness from the source of zebra mussel veligers (Zanatta et al. 2002, McGoldrick et al. 2009). A synergy of various habitat conditions were described from known refuges including large areas of shallow waters (protected bayous) with low flow and warmer temperatures that encourage unionid burrowing (Nichols and Wilcox 1997), hydrological connection of shallow waters to the lake (Bowers and de Szalay 2004, 2005), and fish predation of zebra mussels attached to unionids (Bowers and de Szalay 2007).

Although we found that the percentage of infested unionids increased very quickly with increased zebra mussel density in a water body (Figure 40.14), overall density of zebra mussels is known to depend on substrate availability, morphometry,

and trophic status (Stańczykowska and Lewandowski 1993, Lucy et al. 2005, Burlakova et al. 2006). Each of these factors may contribute to low zebra mussel density in some water bodies and thus allow unionids to coexist. The mechanism of coexistence may also vary with water body type: river, lake, reservoir, or interconnecting river and lake systems. Finally, there may be other, yet unidentified, mechanisms that promote long-term coexistence of zebra mussels and unionids.

RECOMMENDATIONS

Our analysis of multiple water bodies in Europe and North America in different stages of zebra mussel colonization suggests that adverse impacts of zebra mussels on unionids are most detrimental during the first stages of invasion but that impacts diminish over time. We found that the negative impact of zebra mussels on unionids may decrease about 10 years after initial zebra mussel colonization. We have some knowledge about habitat parameters that define a potential refuge (see preceding text), and ongoing studies will help to better understand conditions that define a refuge. If refuges can be defined, then they can be located and protected in water bodies that are at the very first stages of invasion or under imminent risk of invasion to promote unionid survival. Some rare unionid species that are intolerant to the conditions in the refuge may be relocated to uninfested waters.

In comparing studies from different countries, we found that different methods of recording the effects of zebra mussels hamper our ability to make generalizations. Therefore, we recommend that a standard set of methods will be a very productive step for future studies on the impact of invasive bivalves (not dreissenids alone) on unionids. For example, we found that most North American observations lay above the fitted regression line presented in Figure 40.15, suggesting that the number of zebra mussels per unionid in North American water bodies is more strongly related to the field density of zebra mussels than in European water bodies. One possible explanation for this may be that North American scientists report all attached mussels regardless of size, while European scientists generally do not include mussels smaller than 1–2 mm (and sometimes <8 mm) in density estimates (reviewed in Karatayev et al. 1997, Burlakova et al. 2000). From the perspective of the unionid, the weight of attached zebra mussels or the weight ratio of attached zebra mussels to unionid host is probably more important than the number found attached (Hebert et al. 1991, Karatayev et al. 1997, Lucy 2005). Therefore, recording the unionid weight, length, and the *Dreissena* weight is very important for further comparisons, especially considering the strong significant relationship between the ratio of zebra mussel weight to unionid weight and zebra mussel density in a water body (Burlakova et al. 2000, Ricciardi 2003). In addition, methods to estimate densities of zebra mussels and unionids need to be standardized or better documented so that rates and frequencies of infestation

can be better related to time after initial colonization across different water bodies. Use of comparable methods will allow direct comparisons of studies conducted in different countries and continents and make it possible to improve important generalizations on the impacts of zebra mussels on unionids.

We recommend a number of different studies to better understand zebra mussel–unionid competition and coexistence. Determining where the impacts of zebra mussels would be most detrimental and identifying which species of unionids (especially those that are rare and threatened) would be most vulnerable will assist in the development of global management priorities prior to future invasions of not only dreissenids but also other exotic epifaunal byssate bivalves, such as *Limnoperna fortunei*. Studies to identify the stage of dreissenid colonization when impacts on unionids are diminished (if it occurs) are critical. Additional studies on water bodies that were recently colonized versus water bodies known to host zebra mussels for many years will test our generalizations and aid in the development of management options. To be comparable, these studies have to be designed in parallel and carried out using a unified methodology.

Additional studies are needed to understand differences between impacts of quagga mussels versus zebra mussel on unionids and to understand if the presence of both dreissenid species in a water body will have a stronger impact on unionids than the presence of either species alone. While impacts of zebra mussels on unionids are very well described, we often do not have enough comparable data on the impacts of quagga mussels (Karatayev et al., in review). The zebra mussel has greater rates of byssal thread production and higher attachment strength relative to the quagga mussel (Peyer et al. 2009), which may explain why the zebra mussel is more dominant on unionids when both species are equally prevalent on other substrates (reviewed in Zhulidov et al. 2010, D. Zanatta, personal observation).

Finally, more studies are needed to identify conditions that allow dreissenids and unionids to coexist (e.g., habitat, substrates, hydrodynamics). A number of refuges have been already discovered in Europe and North America, and they provide a unique opportunity to study key habitat attributes and subsequently develop predictive models. Such information provides an opportunity to locate and protect additional unionid refuges and to manage sites to promote unionid colonization, survival, and endangered species recovery. This information is also imperative when creating possible refuges during the initial stage of invasion by dreissenids and other byssate exotic bivalves.

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