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The impact of dreissenid mussels on growth of the fragile papershell (*Leptodea fragilis*), the most abundant unionid species in Lake Erie

Robert A. Krebs, Elizabeth M. Barkett, and Matthew T. Begley

**Abstract:** The arrival of zebra mussels (*Dreissena polymorpha* (Pallas, 1771)) and subsequently quagga mussels (*Dreissena bugensis* Andrusov, 1897) (Dreissenidae) in the Great Lakes in the 1980s induced many changes, most notably the devastation of native freshwater mussel species. Recently, empty shells of the fragile papershell (*Leptodea fragilis* Rafinesque, 1820) (Dreissenidae) in Lake Erie (Graf 2002) declined precipitously after the initial peak rise in dreissenid numbers in Lake Erie, thus limiting the devastation of native mussels. Shells of native species once littered beaches (Goodrich and Schalie 1932) but largely disappeared by the 1990s (Schloesser et al. 1998). During the initial peak rise in dreissenid numbers in Lake Erie, thousands of attached dreissenids could be found on a single unionid mussel (Schloesser and Kovalak 1991; Schloesser and Masteller 1999), an effect correlated with unionid mortality (Schloesser and Kovalak 1991; Schloesser and Nalepa 1994; Ricciardi et al. 1996; Schloesser et al. 1998). By attaching to unionid valves, dreissenids hamper movement and burrowing, filter feeding, respiration, and reproduction (reviewed in Karatayev et al. 1997, 2002; Strayer 1999; Burlakova et al. 2000), they induce shell deformities (Lewandowski 1976; Hunter and Bailey 1992; Schloesser et al. 1996), and even reduce glycogen reserves in host unionids (Haag et al. 1993; Baker and Hornbach 1997; Sousa et al. 2011; Bôdis et al. 2013).

In sum, the dreissenid presence may limit food availability whether dreissenids are attached or not (Baker and Leviton 2003), although the impact of variable dreissenid attachment has not been tested due to a lack of populations demonstrating vari-
issenids, declines in diversity in rivers have also been common (Krebs et al. 1997; Zanatta et al. 2002; McGoldrick et al. 2009), but as dreissenid populations have begun to decline in the Great Lakes (Karataev et al. 2002), shell numbers of a few unionid, and particularly the fragile papershell (Leptodea fragilis (Rafinesque, 1820)) have progressively increased along Lake Erie, at least within the western basin (Crail et al. 2011). Bryan et al. (2013) also reported hundreds of live young L. fragilis exposed on the lake bottom by seiches at the shallow far-western tip of Lake Erie, and by November 2012, empty shells were found on beaches as far east as Vermilion, Ohio (41.427°N, 82.356°W). Understanding what now regulates the distribution of unionid mussels following such an environmental perturbation, like the introduction of a dreissenid species, is critical to predict the likelihood of persistence or extirpation of remaining species (Rogam 1993; Strayer et al. 2004). While most Lake Erie tributaries support mussels, and they show minimal populations of dreissenids, declines in diversity in rivers have also been common (Krebs et al. 2010).

The life-history variable of interest to mussel persistence is growth rate, although longevity is also predicted to change where dreissenids are present vs. absent, or where the abundance of dreissenids varies, which can be roughly estimated by the number of byssal thread bundles on fresh shells as an indicator of past attachment. That levels of dreissenid infestation correlate with field densities of dreissenids is established (Ricciardi et al. 1995), although byssal counts may underestimate the number of dreissenids attaching to L. fragilis because dreissenid mussels may also attach to earlier colonizers (clumping). This particularly holds for cases with high biofouling. Moreover, there may be spatiotemporal effects by variability in predation on dreissenids (Bowers and de Szalay 2007). Furthermore, whether fouling is by quagga mussels or by zebra mussels, the latter of which adhere more rapidly and tightly (Peyer et al. 2009), could influence physiological consequences to individual unionids (Burlakova et al. 2014).

Both shell age and growth rate may be estimated from growth lines, the latter as the regression coefficient ($\beta$) of age on shell length (Ghent et al. 1978; Haag and Commens-Carson 2008; Haag 2012). Only shells of L. fragilis were sufficiently abundant to assess impacts of dreissenids, and this is the species for which Nichols and Amberg (1999) identified no changes in growth after the dreissenid invasion in Metzer Marsh, a protected wetland adjacent to Lake Erie where less than 1% of mussels possessed signs of zebra mussel encrustation. To contrast effects of dreissenid attachment, quantitative measurement of growth rates were made from several collections of fresh shells at two beaches in the western basin of Lake Erie and for two collections with low or no dreissenid presence: first pooled shell samples from protected habitats like marshes, river mouths, and other shallow zones in western Lake Erie, and second, shells from collections of L. fragilis from one of the same Lake Erie beaches made long before dreissenid mussels were introduced in North America. Dreissenids are predicted to slow unionid growth as an effect of presence versus absence, or by abundance both between populations and within populations. Basically, regression coefficients of age on shell length should be greater for collections of shells possessing fewer byssal threads.

Materials and methods

Large numbers of fresh empty shells of L. fragilis were collected near the Cedar Point section of the Ottawa National Wildlife Refuge (Ottawa NWR) at a locality called Potters Pond (41.677°N, 83.306°W) in 2008 and 2011 totaling 166 fresh dead L. fragilis and the public beach at Port Clinton (41.515°N, 82.928°W) in 2011 and 2013 with 121 fresh dead. In all cases, individuals used for the study were collected as paired valves, the periostracum was yellow and not worn, and the nacre was shiny. For 26 shells pulled from icy waters in February of 2013 at Port Clinton, shells even contained remnants of tissue. Both of these sites are composed of vast flats of sand and mud, extending out from the beach with depth increasing only very gradually. The benthos at both locations was visibly unstable with ridges in the sand, and timed surveys by wading identified no live mussels in the shallow zones at Potters Pond and just one L. fragilis at Port Clinton (Zanatta et al. 2015). Thus, collected shells likely derived from populations that persist in deeper water or from young individuals living infaunally. Both lake sites lie near the outflows of small rivers, the Portage River at Port Clinton where many live mussels but no L. fragilis were collected, and Cedar Creek near Potters Pond, which is a dredged marina, from which just two mussels were found, one of which was L. fragilis. Across Lake Erie tributaries, L. fragilis is a minor component of the stream fauna (Prescott 2014; Zanatta et al. 2015).

Shell collections therefore provided the best indication of the lake fauna. The preserve permits very limited public access thus preserving available shells, and the Port Clinton site was surveyed in winter when Lake Erie reaches its lowest water level (http://glakesonline.nos.noaa.gov/monitor.html), and collection of shells accumulating from early winter storms appeared to us to be unbiased by public beach access. During annual trips, we were alone on the beach collecting many shells half covered in snow, partially imbedded in ice, or exposed on sandbars offshore. The Cleveland Museum of Natural History possessed 246 L. fragilis shells collected in the western basin between the years 1943–1967. This period was long before dreissenid mussels arrived, but pollution levels may have been greater than currently observed (Regier and Hartman 1973; Allinger and Reavie 2013). Another 32 recently collected empty shells (2010–2011) were available from the flooded river mouths of Crane Creek (41.626°N, 83.209°W), Turtle Creek (41.604°N, 83.153°W), and Old Woman Creek (41.380°N, 82.512°W), as a second contrast to growth in the absence of the invasive dreissenids, although water temperatures were warmer.

For each shell, the left valve was measured (cm) and the age estimated from growth ring counts (Rypel et al. 2008), a procedure that has been well validated (Haag and Commens-Carson 2008), particularly in L. fragilis (Nichols and Amberg 1999). Byssal thread abundance was categorized at three levels (i.e., 0–5 byssal thread bundles, 6–10 byssal thread bundles, and 11+ byssal thread bundles), as Nichols and Amberg (1999) used these same categories of the number of live dreissenids in their study at Metzer Marsh. Therefore, one-way ANCOVA in PAST version 3.0 (Hammer et al. 2001) and linear regression of age on shell length was applied to estimate the slope of the line, which is a surrogate for growth rate. Analyses were run twice for the marsh-collected shells and the historic specimens, first on all data with age log-transformed to linearize results in analyses that included older individuals (Sansom et al. 2013), and second, to restrict results to shells aged six and under, as growth slows with age making data nonlinear (Nichols and Amberg 1999; Haag 2012). No modern shells from beaches exceeded 6 years in age, so restricting age classes also placed all data sets within the same age groups. Another set of analyses assessed effect of infestation rate contrasting the three byssal thread abundance groups (0–5, 6–10, and 11+), assessing age and slope of age on shell length in ANCOVA.

Results

The relationship between age, which was log-transformed, and length in L. fragilis varied significantly across space and time (test of homogeneity of slopes, $F_{1,3,561} = 14.6, p < 0.0001$): Ottawa NWR: $y = 6.3x + 4.7, r^2 = 0.49$; Port Clinton: $y = 5.9x + 4.6, r^2 = 0.54$; river mouths and marshes: $y = 10.3x + 5.3, r^2 = 0.73$; historical collections at Port Clinton: $y = 9.6x + 2.2, r^2 = 0.65$. Difference in slopes for the relationship of age on shell length was not significant between
the dreissenid-exposed areas, the two recent-day collections from Lake Erie beaches ($F_{1,284} = 0.34$, $p = 0.55$), or between the two low or no dreissenid areas (Figs. 1A, 1B: $F_{1,276} = 0.31$, $p = 0.58$).

Mean age also varied among the four *L. fragilis* collections (assessing age in ANCOVA, $F_{3,561} = 140$, $P < 0.0001$). For age, the difference between the two dreissenid-exposed areas, the Ottawa NWR and Port Clinton sets of shells (Figs. 2A–2F), approached significance ($F_{1,284} = 6.33$, $p = 0.051$; 2.9 years at Port Clinton, 2.2 years at Ottawa NWR), and the mean age of shells in the recent marsh collections (at 4.9 years) was significantly greater than the mean age of shells from the historical Port Clinton collection (4.1 years, $F_{1,276} = 177$, $p < 0.0001$). However, the majority of the variation was between areas exposed to more dreissenid mussels and areas protected from or pre-dating the dreissenid presence. Just 1% of the *L. fragilis* shells were scored as 6 years old (Figs. 2A–2F), in the marshes and river mouths, 36% were over 5 years of age, with a maximum age of 12, and 22% of the shells from the historical data set from Port Clinton were over 5 years of age, with a maximum age of 10 (Figs. 1A, 1B).

Within populations exposed to dreissenids, a reduction in the regression coefficient of age on length occurred for individuals burdened with a larger number of dreissenids, based on byssal thread bundles found on shells (Figs. 2A–2F, results presented on untransformed data). Those individuals at the Ottawa NWR with few (Fig. 2A) or only a small number of byssal threads (Fig. 2B) compared with those with more byssal threads (Fig. 2C) possessed a significantly larger slope of age on shell length ($F_{2,162} = 3.54$, $p = 0.031$). While variation among the three groups was not significant for the Port Clinton collections ($F_{2,117} = 0.85$, $p = 0.43$), trends were in the same direction as for collections at the Ottawa NWR, because the highest byssal thread category had the lowest slope (contrasting regressions in Figs. 2D–2E), and 67% of all shells from Port Clinton possessed >10 byssal thread bundles but only 34% of
shells from the Ottawa NWR had this number of byssal thread bundles.

**Discussion**

Living in the presence of dreissenid mussels in Lake Erie comes with costs to individuals of *L. fragilis*, and as Nichols and Amberg (1999) observed, this cost may be avoided or reduced for mussels living in marshes or other protected areas like stream mouths. These shallow areas appear to provide a refuge from dreissenids even today (Zanatta et al. 2015), especially as the growing dominance of quagga mussels over zebra mussels may be relaxing the competitive interactions that have been so damaging to communities of native unionid mussels (Ricciardi et al. 1995; Schloesser et al. 1998; Burlakova et al. 2014). In addition, the relationship among shell size, growth rings, and byssal thread counts suggest multiple effects on life history even on the one species that may...
sustain reasonable levels of abundance in the open waters of Lake Erie (Bryan et al. 2013, 2014). Age structure inferred from recently collected empty shells shifted to younger individuals in the populations exposed to large numbers of dreissenid mussels and growth has slowed. Haag (2012) reports this species already to be an anomaly within the Unionidae for a short average life of just 5 years and an ability to reproduce in its first year. Our evidence suggests that in the presence of dreissenids, few individuals live to an age of 5 (mean age of shells was less than 3 years), while the mean age of shells collected in the marsh and those of historical collections from Lake Erie averaged over 4 years. Perhaps the younger age of the *L. fragilis* shells in historical Port Clinton collections relates to the poor water quality of Lake Erie in the mid-1980s and 1990s (Crail et al. 2014) to dammed benthic communities, especially of mayflies (Britt 1955). As noted, growth rate in *L. fragilis* remained similar to the later marsh collections.

Although not every contrast made among the four sets of shells or among different groups based on byssal thread number was individually significant, most were, and each contrast produced the same predicted pattern of decline with either dreissenid presence or an increase in dreissenid numbers; shell size of *L. fragilis* increased more slowly with age for populations living with abundant dreissenids than in marshes or when present in the lake before the dreissenid invasion. Shell growth was particularly slow for shells on which byssal thread counts were in the highest group, although that pattern was highlighted only at the Ottawa NWR where dreissenid encrustation was relatively less than at Port Clinton. Basically, the much higher infestation rate at Port Clinton was associated with fewer young or small individuals that were free of byssal threads. A high abundance of dreissenids may limit growth of all individuals whether they were directly infested or not infested at all (Haag et al. 1993; Strayer and Smith 1996).

None of these results are surprising, but they do provide evidence of the mechanism by which dreissenids limit the return of communities of native mussels. Baker and Levinton (2003) reported that dreissenids compete with unionids for food even where direct infestation of individuals does not occur. Young unionids may escape this competition for a while, as they feed infaunally within the substrate (Yeager et al. 1994). Only as mussels become larger must they expose themselves at the surface and feed in the water column, and active water exchange is required for reproduction (Vaughn and Hakenkamp 2001). Thus, selection may start favoring a shift in life history to a more opportunistic mode, sensu Haag (2012): a short lifespan, low age at maturity, moderate to very high fecundity, long-term brooding, and a fast growth rate. But no change in extant populations will occur rapidly. Instead, *L. fragilis* and the giant floaters (*Pyganydodon grandis* (Say, 1829)), the two fastest growing unionid species (Haag, 1829), the putative and only pro-

Other changes to the lake environment potentially have improved opportunities for *L. fragilis* to increase. Freshwater drum (*Aplodinotus grunniens* Rafinesque, 1819), the putative and only proposed host species of *L. fragilis* (Watters et al. 2009), has become very abundant based on fishing reports that suggest increases in abundance lake-wide starting around 2006 despite declines in many other fish species (ODW 2013). This fish once preferentially fed on midges (Chironomidae) (Bur 1982) and now regularly consumes zebra mussels in Lake Erie (Morrisson et al. 1997).

Other unionids also persist, including pink shell splitter (*Potamius alatus* (Say, 1817)), deertoe (*Truncilla truncata* Rafinesque, 1820), and fawnfoot (*Truncilla donaciformis* (L. Lea, 1828)), which also use freshwater drum as a host fish, but they are present in much lower numbers (Crail et al. 2011; Zanatta et al. 2015), and whether they reproduce in the lake or are found as migrants from coastal refuges is not known. Sustaining high abundance requires growth beyond reproductive maturity to enable sufficient reproduction in the presence of dreissenids.

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