

Co-existence of zebra mussels and freshwater unionids: population dynamics of *Leptodea fragilis* in a coastal wetland infested with zebra mussels

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Abstract: In 1996, thousands of live *Leptodea fragilis* were collected from a marsh located in the western basin of Lake Erie that was infested with zebra mussels (*Dreissena polymorpha*). Despite the presence of zebra mussels at this site for a number of years, this *L. fragilis* population showed no signs of competition-induced changes in population dynamics. Biofouling was limited: fewer than 1% of the *L. fragilis* showed evidence of recent or past zebra mussel colonization. Successful recruitment occurred yearly, with multiple year classes collected that ranged in age from 1 to 12 years. However, age and shell length were not well correlated. Seventy-one percent of the individuals collected were 51–80 mm long, but ranged in age from 2 to 4.5 years. Three different patterns of growth or shell deposition were found. Some individuals grew rapidly, reaching 105 mm in 3.5 years, while others grew only 4.5 mm over the same time period. A few grew poorly during some years but very rapidly in others. Individuals with a shell length of 41 mm or more were sexually mature and females were more common than males. The strong recruitment and steady growth of this population showed no change between the years before and after the zebra mussel invasion, indicating that this marsh is functioning as a natural refugium from potential problems caused by zebra mussels.

Résumé : En 1996, des milliers de *Leptodea fragilis* ont été récoltés vivants dans un marécage infesté de Moules zébrées (*Dreissena polymorpha*) dans le bassin ouest du lac Érié. En dépit de la présence des moules depuis bon nombre d'années, cette population de *L. fragilis* ne semble pas avoir modifié sa dynamique à cause de la compétition. L'envahissement semble être un phénomène limité, puisque moins de 1% des *L. fragilis* montrent des signes d'avoir été colonisés, récemment ou depuis longtemps, par des moules. Le recrutement a lieu chaque année et les multiples classes d'âge rencontrées s'échelonnent de 1 à 12 ans. Cependant, il n'y a pas de corrélation nette entre l'âge et la longueur de la coquille. Soixante et onze pour-cent des individus récoltés avaient 51–80 mm de longueur, mais étaient âgés de 2 à 4,5 ans. Trois patterns différents de croissance ou de formation de la coquille ont été observés. Certains individus ont une croissance rapide, atteignant 105 mm à l'âge de 3,5 ans, alors que d'autres ne croissent que de 4,5 mm durant le même temps. Certains croissent peu certaines années et très rapidement d'autres années. Les individus dont la coquille mesure 41 mm ou plus ont atteint leur maturité sexuelle et les femelles sont plus abondantes que les mâles. Le recrutement important et la croissance continue de cette population sont restés ce qu'ils étaient avant l'invasion des Moules zébrées. Ce marécage représente donc un refuge naturel contre les problèmes potentiels reliés à la présence des Moules zébrées.

[Traduit par la Rédaction]

Introduction

One of the most devastating ecological impacts of the zebra mussel (*Dreissena polymorpha*) invasion is the virtual elimination of native clams or unionids from Lake Erie (Haag et al. 1993; Schloesser and Nalepa 1994; Schloesser et al. 1996). While there are still some remnant unionid individuals throughout the open waters of western Lake Erie,

their body condition is declining (Haag et al. 1993). This has led to concerns that even if zebra mussel populations decreased in the next few years, unionid populations would be at such nonviable levels throughout Lake Erie and its connecting waterways that recovery would be limited at best. Efforts are under way to remove and maintain brood stocks of unionids removed from inland waterways that are presently subject to zebra mussel infestation (Dunn and Layzer 1997; Dunn and Sietman 1997; Neves 1997). In Lake Erie, unionid populations crashed so quickly that no brood-stock removal was achieved.

The recent discovery of a large population of live unionids uninfested with zebra mussels in a western Lake Erie wetland (Nichols and Wilcox 1997) shows that some unique habitats may be providing refugia for unionids. Lake-connected wetlands such as Metzger Marsh and others in western Lake Erie appear to be sites where many unionid

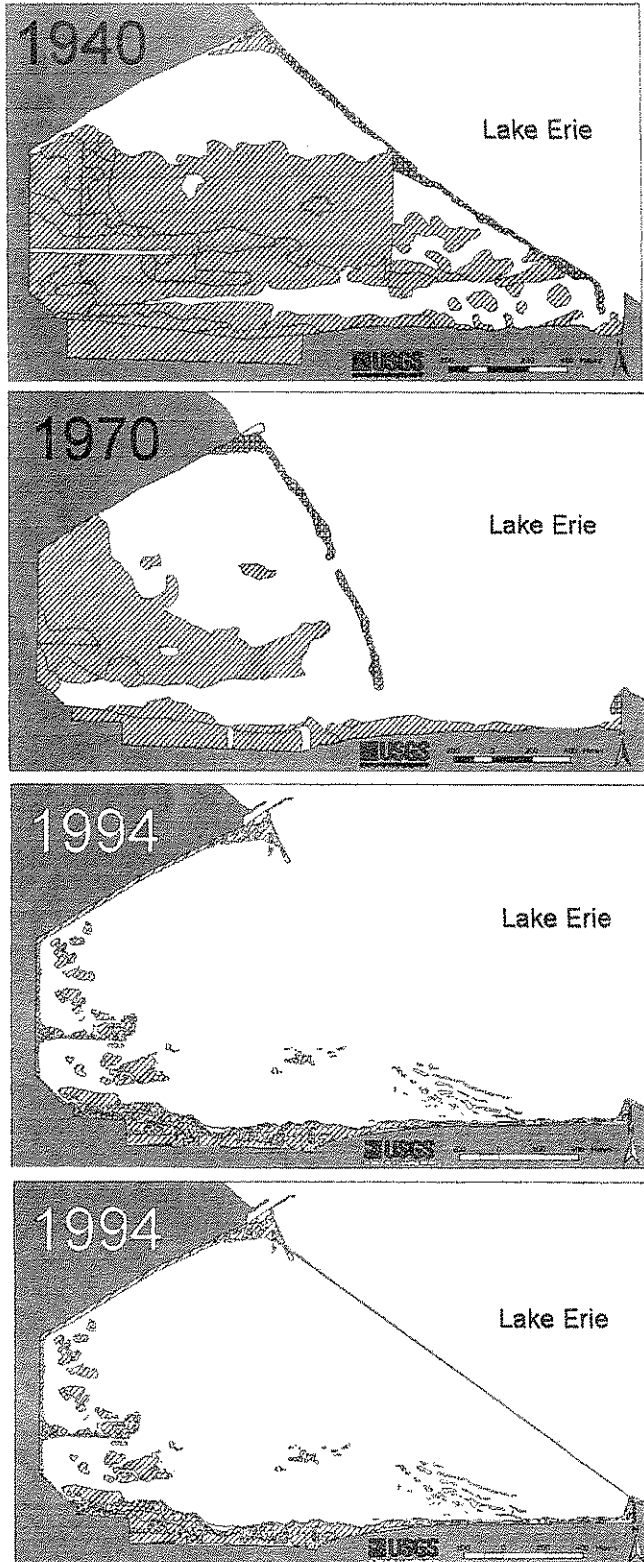
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Fig. 1. Schematic of aerial photographs of Metzger Marsh, western Lake Erie, showing the destruction of the barrier beach and subsequent erosion of the wetland vegetation between 1940 and 1994. Hatched areas represent patches of wetland vegetation. The bottom drawing shows the location of the artificial barrier beach built at the site.



species continue to survive. These populations could serve as "seed banks" to ultimately recolonize the lake if zebra mussel densities decline. Such sites may also prove valuable as holding facilities for unionids relocated from open lake areas for long-term maintenance. However, while we know that Metzger Marsh provides environmental conditions that have limited zebra mussel colonization of unionids, zebra mussels do not have to attach to a unionid to cause its death. Strayer and Smith (1996) documented the die-off of non-biofouled unionids in the Hudson River due to elimination of the food supply by upstream populations of zebra mussels.

To determine whether such sites as Metzger Marsh are functioning as long-term refugia for unionids, we selected 1 species, *Leptodea fragilis*, from the 20 live species found at the marsh for further analysis of population dynamics. This species was selected because it dominated the community in numbers and biomass. Our objectives were to determine if the growth rates and recruitment patterns of this species changed after zebra mussels invaded the area.

Study site

Metzger Marsh is a lake-connected wetland located 48 km east of Toledo, Ohio (Fig. 1). Prior to 1940, portions of this 360-ha site were diked, actively farmed, and then abandoned and allowed to revert to wetland. The wetland embayment was protected from storm activity by a barrier beach, which gradually eroded as the sediment supply decreased because of progressive armoring of the shoreline of the lake. By 1990, much of the original wetland had eroded. In 1994, a consortium of federal, state, and private organizations joined forces to restore the wetland and provide improved habitat for fish and wildlife. A dike was constructed across the opening of the embayment to mimic the protective function of the lost barrier beach, and there were plans to dewater the wetland to promote seed germination and growth of emergent plants. During water-level drawdown in the summer of 1996, thousands of live native unionids representing 20 species (Table 1) were discovered. These unionids, including the *L. fragilis* population, were removed from the marsh as water levels declined during July and August, identified to species, measured (shell length), numbered, and relocated to temporary holding facilities.

Zebra mussels are believed to have invaded this area in 1989. They were well established in many areas of Lake Erie by 1989 (e.g., Fraleigh et al. 1993; Kovalak et al. 1993) and large numbers were found in the marsh when it was examined in 1991 (D.W. Wilcox, U.S. Geological Survey, 1451 Green Road, Ann Arbor MI 48105, U.S.A., personal communication). Zebra mussel distribution was limited to the deeper, lakeward part of this marsh (Fig. 2). Two types of zebra mussel colonization occurred in this front half of the marsh: extensive layers, several centimetres thick, totally covering the coarse sand substrate in the troughs between the wave-induced sand ridges, and individual clusters of mussels limited to colonizing every available hard structure such as logs, rocks, or emergent vegetation that were scattered over a soft, mud substrate (except unionids). The area colonized by extensive mats of zebra mussels extended about

150 × 300 m. Overwintering of some zebra mussels had occurred, as shell lengths ranged from 1 to 40 mm in all areas where zebra mussels were found.

Zebra mussel colonization of unionids was limited. Less than 1% showed any signs of zebra mussel encrustation. A subsample of 1000 unionids chosen at random contained only 8 that were or had been colonized. Of these eight, six were colonized by fewer than 5 zebra mussels (maximum zebra mussel size was 10 mm), while two unionids were colonized by 7–10 adult mussels. Four of these eight unionids also had attached byssal thread remnants.

Methods

Sex determination

As the water levels declined in Metzger Marsh during the drawdown phase of the restoration processes, *L. fragilis* (and other species) were removed from the marsh and placed in coolers filled with damp paper. They were brought to holding facilities at the Great Lakes Science Center until other suitable temporary quarters could be found. Upon arrival at the laboratory, owing to stress incurred during drawdown and transport, many of these unionids shed or aborted gametes and embryos. One hundred of these animals were randomly selected and placed in individual containers. Shell morphometrics (length, width, and posterior and anterior height) were determined, shells were photographed, and the presence of egg, spermatozoa, or glochidia was determined. Further size-based selection of small animals ($N = 75$, shell length under 50 mm) was done to determine, through direct observation of gamete/embryo shedding and examination of the marsupium, at what size these animals become reproductively viable.

Age determination

Absolute age was determined by using both internal annuli and the dark external annuli of the shells as described in Kennish (1980), McCuaig and Green (1983), Tevesz and Carter (1980), and Neves and Moyer (1988). Shells were sectioned using a fine-grade hacksaw blade or a low-speed circular saw with a copper blade (Bueller Isomet) and then polished using silicon carbide wet grinding papers. Sections were coated with a thin layer of glycerin and examined under a dissecting microscope. The distance from the umbo to the internal growth band and external growth band was measured using an ocular micrometer. Strong, well-developed external growth bands, comprised of one light band followed by one dense dark band, were assumed to represent a period of growth followed by growth interruption. Potential differences in growth rates in the entire population, as shown by the incremental increase in shell length each year, by age in years, were initially compared using regression analysis, specifically the modified Walford plot (e.g., McCuaig and Green 1983), followed by analysis of covariance to determine statistical significance. Results were considered significantly different at $P \leq 0.05$.

Growth rates of this unionid before and after zebra mussels entered the marsh were compared by examining shell-deposition rates of the 1985 and 1990 year classes for the first 5 years of life. Twenty-five randomly selected members of the 1985 year class were used to represent growth under conditions prevailing before the zebra mussel invasion. Twenty-five randomly selected members of the 1990 year class were used to represent growth during and after zebra mussel colonization. In both cases, animals representing "normal" growth patterns were selected. The first 5 years were selected for study, as they are most representative of the most rapid period of shell growth. Results were compared using regressions and analysis of variance and were considered significantly different at $P \leq 0.05$.

Table 1. Species of live native clams collected at Metzger Marsh, Lake Erie, in 1996.

<i>Amblema plicata</i>
<i>Elliptio dilatata</i>
<i>Fusconia flava</i>
<i>Lampsilis cardium</i>
<i>Lampsilis radiata luteola</i>
<i>Lasmigona complanata</i>
<i>Leptodea fragilis</i>
<i>Obliquaria reflexa</i>
<i>Obovaria olivaria</i>
<i>Pleurobema sintoxia</i>
<i>Potamilus alatus</i>
<i>Pyganadon grandis</i>
<i>Quadrula pustulosa</i>
<i>Quadrula quadrula</i>
<i>Strophitus undulatus</i>
<i>Toxolasma parvus</i>
<i>Truncilla donaciformis</i>
<i>Truncilla truncata</i>
<i>Uniomeres tetralasmus</i>
<i>Utterbackia imbecilis</i>

Results

Leptodea fragilis dominated the unionid community in Metzger Marsh, comprising 46% of the total number of unionids collected (Table 1). We collected 2700 live *L. fragilis* and an additional 300 fresh shells (with unionid body tissue inside) ranging in shell length from 17 to 169 mm. The dominant size class was in the 51- to 71-mm range (Fig. 3). The unionids were not randomly distributed in the wetland. The distribution of thin-shelled species such as *L. fragilis* and *Pyganadon grandis* could not be determined, since these animals followed the water during drawdown. Most of the thick-shelled, less motile species such as *Amblema plicata* and *Quadrula* spp. were found mainly in five locations (Fig. 2). The five sites where the thick-shelled unionids occurred were similar in water depth (1 m) and substrate (soft silt-clay). This sediment had a soft, pudding-like consistency with an average organic content of 10% (range 9.63–11.65%); 55% of the sediment had a grain size less than 500 μm . Two of the sites contained sparse submersed vegetation. Site A (Fig. 2), which was relatively isolated from the rest of the marsh during drawdown because of a rock berm, contained the greatest diversity of unionid species and the oldest individuals found in the marsh (45+ years of age for *A. plicata* and 12+ years for *L. fragilis*).

A number of parameters, such as growth, vary between male and female *L. fragilis*. Sex determination was easy in this species, since the shells show distinct external sexual dimorphism, with the posterior inflation typical of the female shell (Fig. 4). This shell characteristic showed 100% correlation with the presence of eggs or embryos in the marsupium of the 100 animals examined. Posterior shell inflation first appears at a shell length of 41–50 mm, and no animals smaller than 41 mm were seen releasing gametes or embryos, or contained gametes/embryos in their marsupium.

Fig. 2. Distribution of zebra mussels and thick-shelled unionids collected from Metzger Marsh, western Lake Erie, during the water level drawdown in the summer of 1996. "Dense zebra mussels" refers to areas where extensive colony mats covered the substrate and "scattered zebra mussels" to areas where minimal substrate colonization occurred but all other objects (vegetation, rocks, logs, etc.) were thoroughly colonized with the exception of the unionids. "A" marks the site where the oldest and largest individuals of all species were collected.

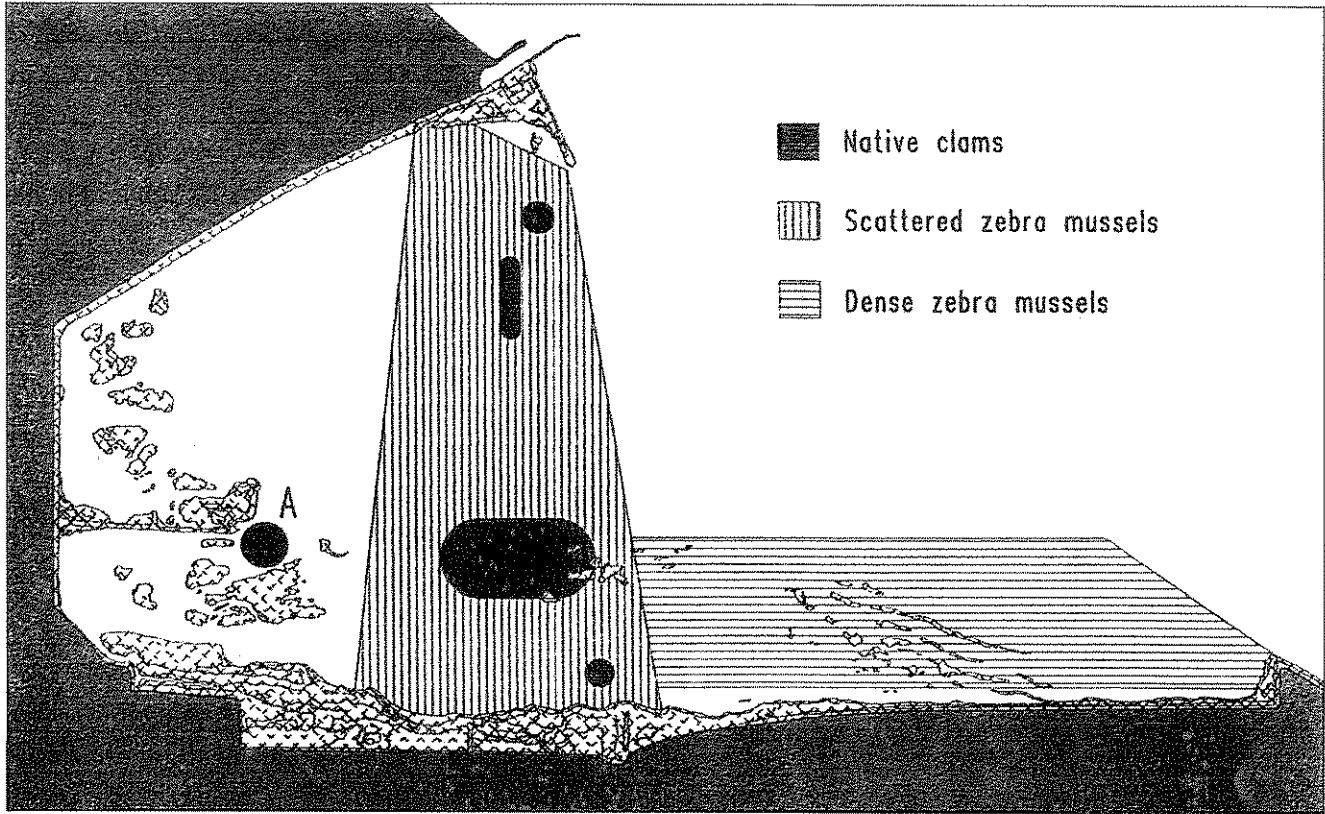
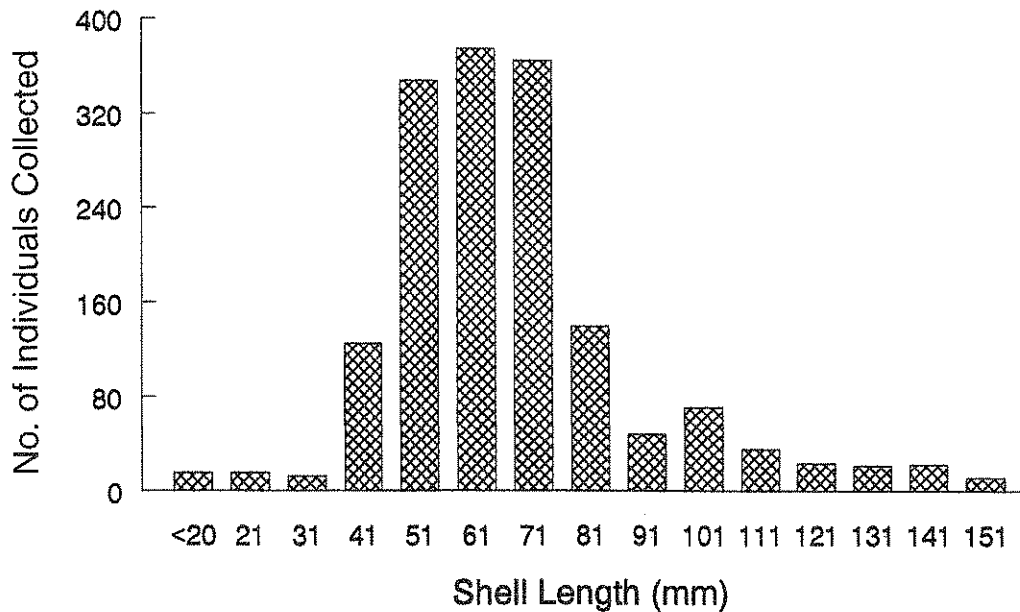


Fig. 3. Shell-length frequencies of all the *Leptodea fragilis* collected from the entire Metzger Marsh during the summer of 1996.

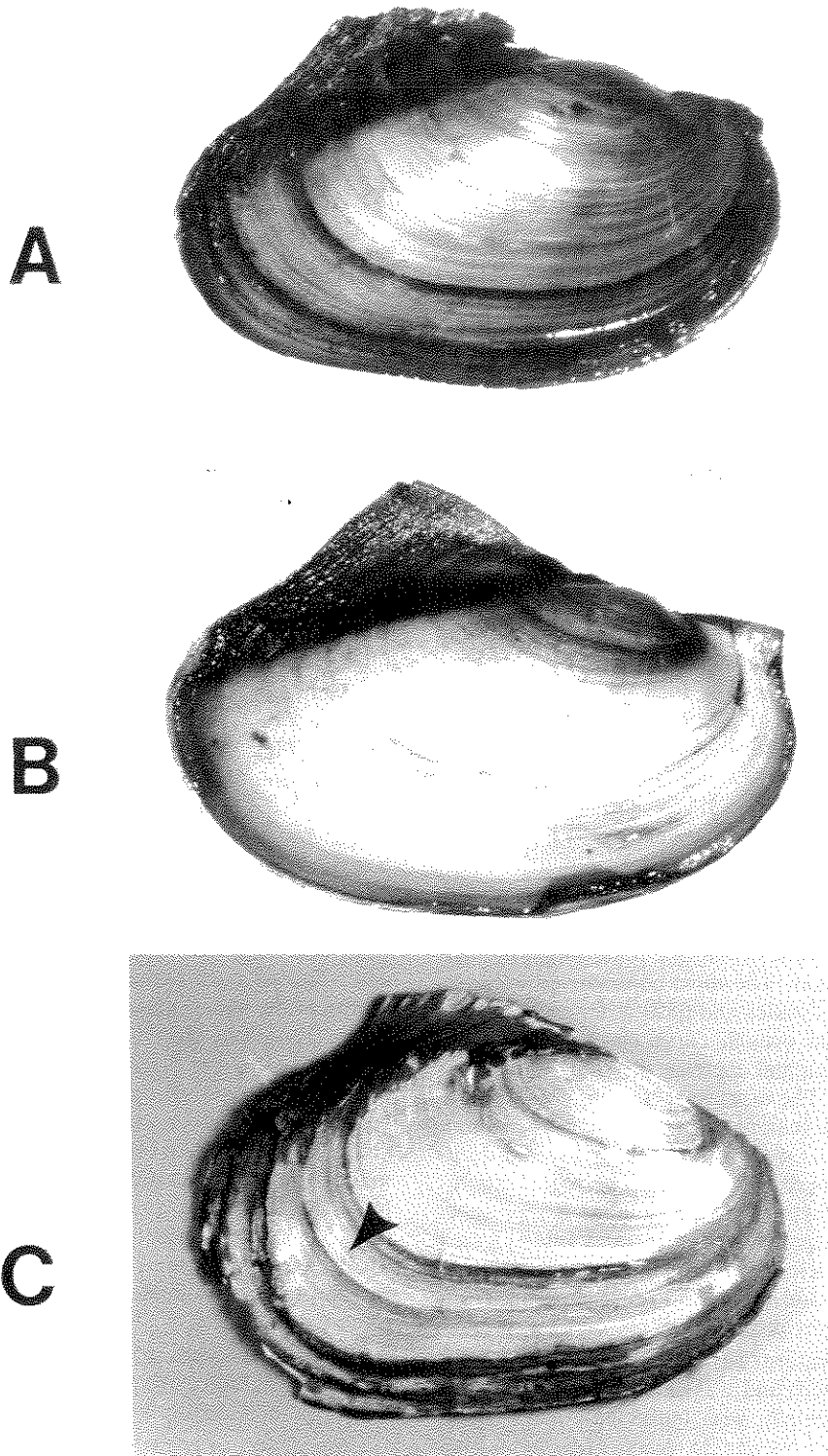


Based on gamete/embryo release, there was a 2:1 ratio of females to males in the marsh, and 90% of all animals longer than 41 mm were reproductively viable in August 1996.

Age and shell length

Age estimates obtained using either internal or external annuli were not significantly different ($P \leq 0.05$). In 5% of

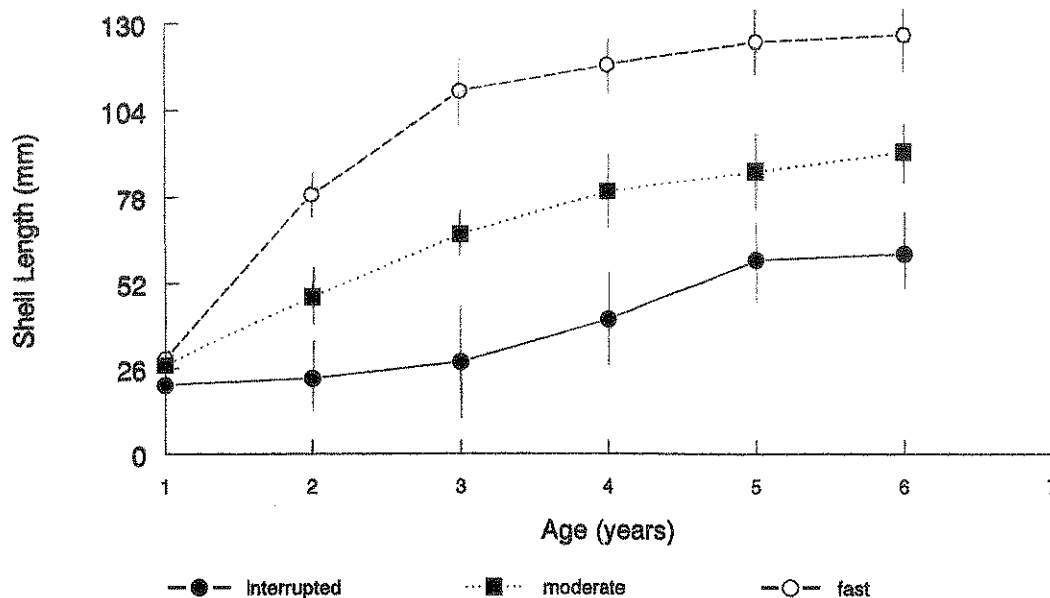
Fig. 4. Examples of sexual dimorphism and different growth patterns seen in *Leptodea fragilis* collected from Metzger Marsh during the summer of 1996. (A) Normal males. (B) Fast-growing males. (C) A female with an interrupted growth pattern. The arrowhead indicates a year of limited growth. All three animals are 110–115 mm in shell length and all were reproductively viable when caught.



the shells sectioned ($N = 75$), aging through external marks only resulted in underestimation, by an average of 1 year, of the unionid's age. In one specimen, internal and external

annuli disagreed by 2 years, the external annuli providing the lowest age estimate. The oldest animals collected, either live or fresh shell, were 10–11 years old and came from the

Fig. 5. Average incremental shell increase per year in *Leptodea fragilis* collected from Metzger Marsh, western Lake Erie, in 1996 that exhibited normal, fast, and interrupted growth rates. Twenty-five individuals were randomly selected from a pool of 100 for each growth type. The shells were then sectioned to determine true age.



upper part of the marsh (site A; Fig. 2). Representatives of every year class from 1985 to 1996 were collected, with 3- to 5-year-olds comprising 71% of the 3000 *L. fragilis* present. Shell length did not necessarily indicate age. For example, the average shell length of a *L. fragilis* 2+ years of age (1994 year class) was 51 mm, but sizes of this year class ranged from 39 to 80 mm (based on both internal and external shell annuli). Similarly, the 1993 year class averaged 63 mm, with a range of 53–108 mm, and the 1991 year class averaged 109 mm, with a range between 72 and 145 mm.

There are three significantly different growth rates or patterns in individuals in this population (Figs. 4–6). These growth rates vary by sex and result in a wide range of shell lengths for each year class. The most common growth pattern, occurring in 45% of males and 65% of females, is periodic, a typical sigmoidal growth curve characterized by a steady decline in incremental increase in shell length per year as the animal ages. The average incremental increase in shell length is 27 mm in year 1+, 21 mm in year 2+, 19 mm in year 3+, 17 mm in year 4+, 13 mm in year 5+, and dropping to 5–10 mm/year thereafter (Fig. 5). The regression referred to as normal growth presented in Fig. 6 represents incremental shell-length increases for 25 randomly selected animals of various age-classes. The regression parameters are $L_{t+1} = 1.06L + 2.6$, and are significantly different from the other two growth rates presented.

The second growth pattern was found only in males (in 45% of all males collected) and was characterized by a very rapid increase in shell length, with individuals reaching an average length of 110 mm by age 3+ years (Figs. 4–6). This was also a periodic, sigmoidal type of growth, with a decline in the amount of shell deposited each year; it was the amount of growth per year that was significantly different. The regression presented in Fig. 6, referred to as fast growth, represents incremental shell increases for 25 ran-

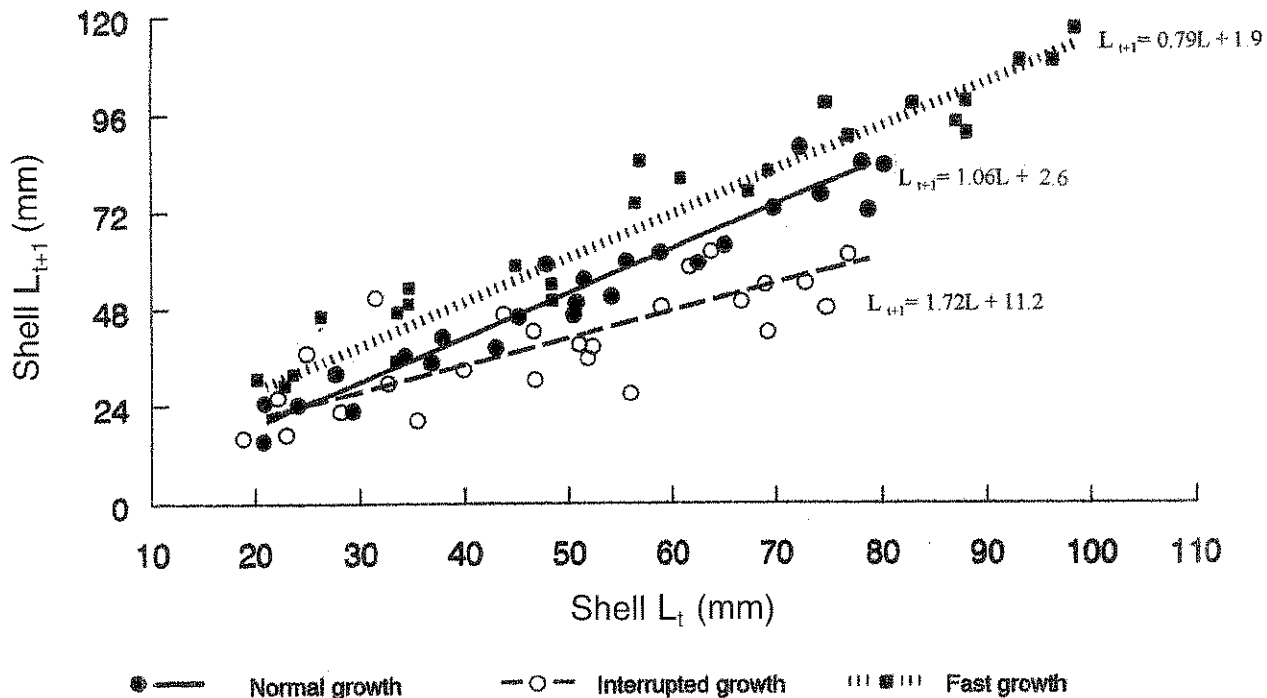
domly selected animals of various age-classes. The regression parameters are $L_{t+1} = 0.79L + 1.9$, and are significantly different from the other two growth rates presented.

The third growth pattern was found in both males (10% of all males collected) and females (35% of all females collected) (Figs. 4–6). It was aperiodic, or random, growth, with the amount of shell deposition per year alternately increasing or decreasing. For example, *L. fragilis* grew in length by 25 mm at age 2+ years, but only increased by 5 mm at age 3+ years, and this was followed by a growth spurt of 20 mm during year 4. Both internal and external annuli reflected the limited shell growth during the same year, and all annuli appeared to be identical regardless of year. The years of reduced growth in these animals did not represent the same calendar year, nor the age at sexual maturity, although the first incidence of slow growth was usually seen between years 3 and 5. In some individuals, this limited growth occurred at age 3+ years, in others at age 5+ years, etc. In no cases did this slow growth occur two years in a row and usually only occurred once in an animal. The regression presented in Fig. 6, referred to as interrupted growth, represents incremental shell increases for 25 randomly selected animals of various age-classes. The regression parameters are $L_{t+1} = 1.72L + 11.2$, and was significantly different from the other two growth rates presented.

These three types of growth rates appeared to be randomly distributed throughout the marsh, with individuals of each type collected at site A (Fig. 2).

Comparison of growth rates before and after zebra mussel colonization of the marsh revealed no significant difference in growth between the 1985 and 1990 cohorts (Fig. 7). For the 1985 year class, the regression correlation was 0.96, $L_{t+1} = 0.62L + 18.0$. For the 1990 year class, the regression correlation was 0.97, $L_{t+1} = 0.61L + 18.5$.

Fig. 6. Regression comparison of incremental increase in shell length per year for each type of growth rate seen in *Leptodea fragilis* from Metzger Marsh. All three regressions are significantly different. Parameters are discussed in the text.



Discussion

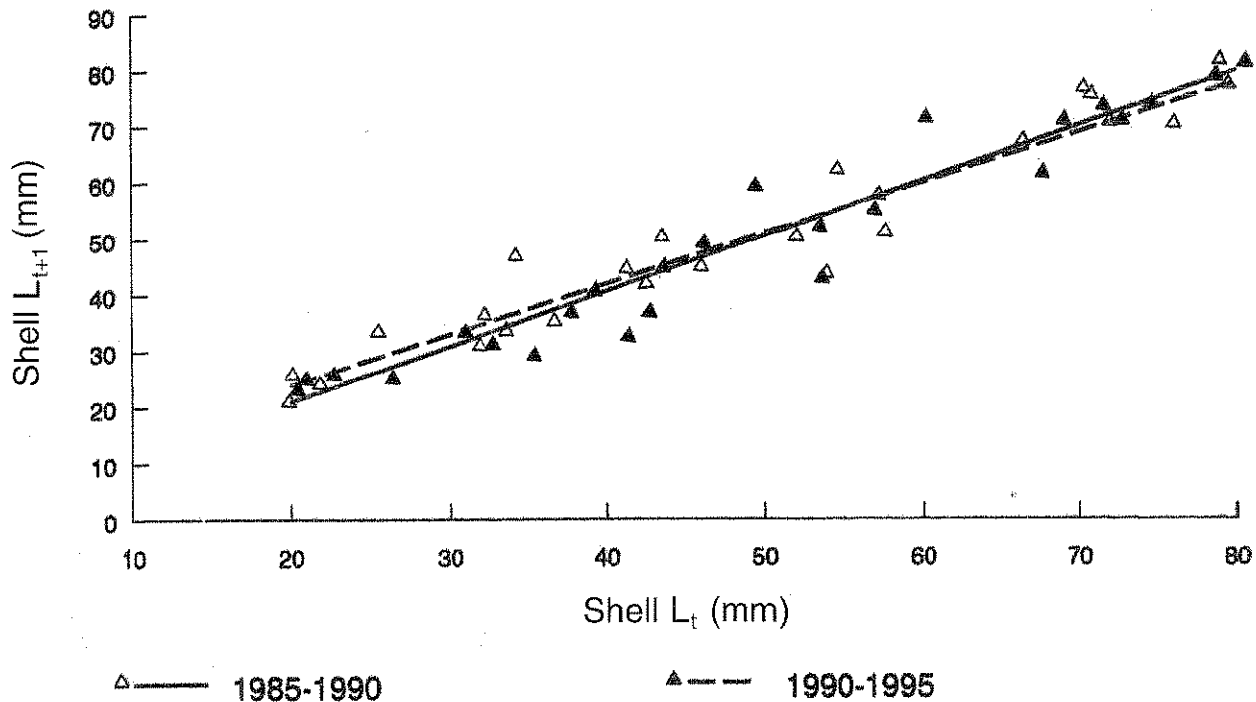
Relative growth rates and recruitment patterns indicate that areas of Metzger Marsh were a natural refugium for this *L. fragilis* population. A comparison of relative growth rates over the last 10 years (Fig. 7) provides the strongest proof that the invasion of this area by zebra mussels has not resulted in food limitation as has been reported for other sites. Growth rates, or the amount of shell deposited during each year of life (i.e., a 3- or 4-year-old individual, etc.), showed no statistical difference from 1985 to 1995 (excluding animals exhibiting fast or interrupted growth patterns, based on the calculation). Of course, bivalve growth rates are related to a number of environmental parameters other than food supply, including population density, substrate type, amount of suspended inorganic matter, water-flow rate, and water temperature (e.g., Hallam 1965; Cerrato 1980; Lutz and Rhoads 1980). Any environmental perturbation at this site should have caused a change in the growth rate of the *L. fragilis* population from 1985 to 1995. No such change was seen. This indicates that Metzger Marsh was providing a very consistent environment from year to year after 1985 in spite of the invasion of the surrounding waters by zebra mussels.

One problem that occurs in looking at potential changes in the relative growth rates of *L. fragilis* across time is factoring in the different patterns of growth seen in this population. However, the percentage of the population showing the various patterns of growth remained stable between 1985 and 1995. Specifically, the number of animals exhibiting interrupted growth patterns did not increase and the number of males showing very rapid growth did not decline. These different growth patterns are commonly seen in both marine

and freshwater bivalve populations and are generally attributed to differences in microhabitat or to inherent genetic variability (e.g., Craig and Hallam 1963; Hallam 1965; Newkirk et al. 1977; Cerrato 1980; Strömgren and Nielsen 1989; Hadley et al. 1991). Because of the extreme disruption in distribution patterns resulting from the dewatering of Metzger Marsh, we cannot determine the exact microhabitat originally occupied by *L. fragilis*. However, as mentioned earlier, all animals exhibiting all three types of growth were collected from site A in the marsh (Fig. 2). This site is somewhat isolated from the rest of the marsh because of an old road bed that forms a berm along one side and contained the oldest individuals of all species collected in the marsh.

Of greatest concern is the portion of the population showing periods of growth interruption (Figs. 5 and 6) and the limited number of young of the year collected (Fig. 3), and whether these patterns reflect a recent environmental shift, such as limitation of the food supply. We do not believe that the growth interruption seen in some animals is related to a shift in environmental conditions because (i) it was seen in the animals before zebra mussels arrived in 1989, (ii) the number of affected individuals did not increase or decrease in frequency after zebra mussels entered the marsh, (iii) the period of slow growth was random, following neither calendar year nor physiological age, and (iv) it was found in individuals collected in all areas of marsh. We believe this growth depression is related to some form of spawning stress. This growth pattern was more common in females than males, never occurred in consecutive years, and did not occur until after reproductive maturity was reached. However, examination of the *L. fragilis* shell did not show a difference in the appearance between any of the growth interruption marks: all the annuli looked like true year-end

Fig. 7. Regression comparison of growth rates of *Leptodea fragilis* (normal growth pattern) for the 1985 year class (before the zebra mussel invasion) and 1990 year class (after the zebra mussel invasion). Only the first 5 years of growth are plotted (exponential growth period) ($N = 25$ for each year class). There was no significant difference in growth rates between year classes. Parameters are discussed in the text.



annuli and not the thinner, less dense spawning checks (see Kennish 1980). So, although our hypothesis is that this growth depression is in some way related to reproductive stress, we cannot at this time determine the exact cause. The possibility exists that not all individuals spawn yearly, with minimal growth occurring during spawning years and "normal" growth during non-reproductive years. The high percentage of reproductive animals removed from Metzger Marsh may be due to the stimulus of the water drawdown. Further studies of an undisturbed population are needed.

Although every year class is present in this population, the percentage of very young animals collected was low. We know that sampling problems did affect the collection of very young unionids, of all species, throughout the 364-ha marsh. It was very difficult to visually locate animals less than 20 mm long under such conditions. This skewed the age structure of the population toward 3- to 5-year-olds. This small number of year 1-2+ bivalves collected does not necessarily indicate recruitment failure. Young unionids are very difficult to sample accurately, which leads to demographic estimates favoring older individuals (e.g., Negus 1966; Tudorancea 1972; Green 1980; Strayer et al. 1981).

In general, age- and length-frequency data show continual, successful recruitment of *L. fragilis* in the marsh from 1985 to 1995. This is another indication that food resources had not become limiting in the area after zebra mussel arrived, although no direct measures of food resources could be made, since the marsh was in the process of being dewatered when the unionids were discovered. Recruitment is hindered when food supplies are limited, either through limitation of reproductive output or mortality of young ani-

mals. The presence of multiple year classes (as well as the consistent growth rates for each age cohort) in this population suggests that energy resources were not limiting in this habitat.

There is no indication of food limitation in Metzger Marsh, and in all likelihood, these lake-connected wetlands are not sites where food limitations will develop in the future. Though we cannot reconstruct the food supply that existed before the marsh-restoration project began, other studies involving marsh bivalves (e.g., Peterson and Fry 1987; Dame 1996) indicate that decomposition of emergent and submergent vegetation along the shoreline provides much of the energy resources assimilated by the local bivalve community. Although Metzger Marsh has suffered a serious decline in vegetation cover since the 1940s, much of its shoreline contained both emergent and submergent macrophytes in the 1980s and 1990s. Thus, there was spatial separation between zebra mussels and the food source. The unionids in this marsh were located between the potential food source (littoral vegetation) and the main zebra mussel population.

As a point of reference, we are fairly confident that annual formation follows a typical temperate-climate yearly cycle in Metzger Marsh. In most temperate-zone bivalve populations, external and internal annuli are usually formed in late fall or early winter, when water temperatures drop and growth ceases (e.g., Negus 1966; Coon et al. 1977; McCuaig and Green 1983). However, in some temperate-zone populations, external annuli are produced more than once a year (Coker et al. 1922; Tevesz and Carter 1980) or only once every 2 years (Downing et al. 1992). Growth-interruption marks deposited more than once a year usually

are caused by physiological stress due, for example, to physical handling, spawning, storm activity, or rapid temperature change (Lutz and Rhoads 1980), and generally have a slightly different appearance than yearly marks upon examination of shell cross sections (Kennish 1980). These types of external marks frequently have no paired internal mark at all. As mentioned earlier, all the external annuli in our *L. fragilis* shell are paired with internal annuli. These internal annuli are identical in appearance throughout the shell, alleviating any concern about the periodicity of annular formation. Work by Neves and Moyer (1988) has indicated that using internal annuli is most reliable technique for aging unionids.

Conclusions

The *L. fragilis* population in Metzger Marsh has survived in spite of the near total extirpation of this species and other unionids from the open waters of Lake Erie.

Wetland sites such as Metzger Marsh appear to be natural refugia for unionid populations, affording protection against both zebra mussel biofouling and food competition. Wetland habitats are limited in number, but they can provide an additional tool for the intensive management of unionid populations, helping to ensure the survival of these animals in the Great Lakes and other regions invaded by zebra mussels.

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