PRIMARY RESEARCH PAPER

The effect of invasive macrophytes and water level fluctuations on unionids in Texas impoundments

Lyubov E. Burlakova · Alexander Y. Karatayev

Abstract The effects of invasive macrophytes, water level fluctuations and predation on freshwater unionids *Pyganodon grandis* and *Utterbackia imbecillis* were studied in three small impoundments in Northeastern Texas in 2003–2005. Mussel density was sampled with quadrats. Mortality, associated with the water level fluctuations and predation, was estimated by collecting dead shells on the shore at about two month intervals. In two ponds, horizontal distribution of unionids was limited by dense beds of invasive and noxious macrophytes (mainly Eurasian watermilfoil *Myriophyllum spicatum* and American lotus *Nelumbo lutea*): mussel densities were significantly lower in these macrophyte beds ($P < 0.001$). In the third pond with the lowest density of macrophytes (stonewort *Chara* sp.), unionids were distributed more evenly, and the average unionid biomass was the highest among all ponds studied. Vertical distribution of unionids in all ponds was likely limited by low oxygen at

depth >2 m. The total amount of shells found on the shore per year varied from 0.1% to 28% of the total population in the pond and was negatively correlated with water level ($r = –0.72$ to $–0.81$, $P < 0.005$). Mammalian predators consumed up to 19% of the total unionid population and predation was facilitated by water level fluctuations.

Introduction

Freshwater unionids are very important components of aquatic ecosystems. They often dominate benthic biomass and production (Negus, 1966; Hanson et al., 1989); impact clarity and quality of water and plankton primary production by removing phytoplankton as well as suspended matter by filtration; affect nutrient dynamics through excretion and biodeposition of faeces and pseudofaeces; release nutrients from the sediment to the water column, and increase water and oxygen content in sediments through bioturbation (reviewed in McMahon & Bogan, 2001; Vaughn & Hakenkamp, 2001; Strayer et al., 2004).

Unionids are one of the most imperiled groups of animals in North America, and among the major causes for their decline is habitat

L. E. Burlakova (✉) · A. Y. Karatayev
Department of Biology, Stephen F. Austin State University, SFA Station, P.O. Box 13003, Nacogdoches, TX 75962-3003, USA
e-mail: lburlakova@sfasu.edu

A. Y. Karatayev
e-mail: akaratayev@sfasu.edu

destruction (Bogan, 1993; Williams et al., 1993; Richter et al., 1997). The creation of dams and impoundments that change hydrologic regime of rivers is one of the forms of habitat destruction, resulting in reduced water flows, increased water level fluctuations, accumulation of silt, interrupted mussel life cycle and dispersal, and a subsequent reduction in mussel fauna (Vaughn & Taylor, 1999; reviewed in Watters, 2000; Richardson et al., 2002). The introduction of invasive species is another major threat to their biodiversity, and reservoirs often facilitate invasions (Havel et al., 2005). The negative effect of zebra mussel introduction on unionids is well documented both in Europe and in North America (Sebestyen, 1937; Ricciardi et al., 1996; Schloesser et al., 1996; Burlakova et al., 2000). In contrast, the effect of invasive macrophyte introductions on unionids is less known (Strayer, 1999).

We suggest that the majority of factors affecting unionid populations (water level fluctuation, siltation, introduction of invasive species, predation, etc.) are similar in large and small reservoirs. Therefore small impoundments can become convenient models to study unionid population dynamics, which would be much more difficult to conduct in larger reservoirs.

We investigated the effect of invasive macrophytes, water level fluctuations and predation on two common unionid species *Pyganodon grandis* (Say) and *Utterbackia imbecillis* (Say) in three small impoundments in Texas.

Materials and methods

Study area

Studies were conducted at Camp Maxey, the Texas Army National Guard facility, in 2003–2005. Camp Maxey (2,600 ha) is located in northeastern Texas in Lamar County, in the Northern Oak Savannah and its watersheds belong to the Red River Basin. Lamar County has a subtropical, humid climate with hot summers and cool winters.

We examined the population density of unionid bivalves in three impoundments: Lamar Lake, Neff Lake, and Lee Moore Lake. All these ponds

were created before the camp was established (1941). Recently Lamar Lake and Neff Lake became colonized by noxious macrophytes Eurasian watermilfoil (*Myriophyllum spicatum* L.) and American lotus (*Nelumbo lutea* Willd.), while Lee Moore Lake is overgrown mainly with stonewort *Chara* sp. *Myriophyllum spicatum* is a submersed perennial plant that branches profusely near the water surface and produces very high stem density. *Myriophyllum spicatum* is one of the most widely distributed of all nonindigenous aquatic plants in North America; its presence is confirmed in 45 U.S. states, and in the Canadian provinces of British Columbia, Ontario and Quebec (http://nas.er.usgs.gov). *Nelumbo lutea* is a perennial aquatic herb with spongy, long rhizomes. It reproduces by seeds which may remain viable for decades (Steyermark, 1963). It is native to North America, and widespread in the eastern and central United States. Once established, colonies of *N. lutea* expand by rhizome growth that is reported to be as much as 15–20 m a year (Hall & Penfound, 1944; Rogers, 1981), and these large colonies may restrict small boat navigation and fishing. The species is considered as threatened in Michigan, endangered in New Jersey and Pennsylvania, yet banned as potentially invasive in Connecticut (http://plants.usda.gov).

Lake Lamar (33°46′31″ N, 95°32′51″ W) is the largest pond in Camp Maxey (Table 1). This reservoir is a typical macrophyte dominated pond, with >50% of surface area covered with vegetation. The three bays of the reservoir are shallow, muddy and completely overgrown with *M. spicatum* and the rapidly spreading *N. lutea*. The prevalent bottom substrates are silts and sometimes clay. In all ponds studied, sediments in depths greater than 2.5–3 m were represented by fine silt.

In Neff Lake (33°47′09″ N, 95°33′59″ W) silts and plant remains are the prevailing substrates in areas covered with macrophytes. Sands, clays, and gravels are present only in the area of the dam. More than 60% of the pond surface was covered with macrophytes including *N. lutea*, *M. spicatum*, and cattails (*Typha* spp.). Only the middle part of the pond and the dam area were free of vegetation. Neff Lake was partially drained in October 2004, to repair its dam, and as a result, a portion

Table 1 Environmental characteristics of studied impoundments in Camp Maxey, Texas

Lake	Area (ha)	Maximum depth (m)	Average depth (m)	Transparency (m)	Conductivity (µS cm⁻¹)	Total dissolved solids (mg l⁻¹)	pH	Turbidity (NTU)	Oxygen (mg l⁻¹)
Lamar	13–16	4.8	1.6	2.5 ± 0.5 (15)	140 ± 27 (23)	91.0 ± 17.6 (23)	7.94 ± 0.93 (23)	7.7 ± 11.1 (8)	8.4 ± 2.2 (18)
Neff	3.5–4.2	3.4	1.4	2.0 ± 0.1 (12)	135 ± 24 (20)	87.9 ± 15.6 (23)	7.56 ± 0.87 (20)	2.0 ± 2.5 (6)	8.6 ± 2.1 (15)
Lee Moore	0.6–1.0	3.7	1.1	1.1 ± 0.5 (14)	67 ± 14 (23)	43.6 ± 9.2 (23)	7.15 ± 0.73 (23)	4.5 ± 2.3 (4)	8.0 ± 2.1 (31)

The data are averages (±standard deviation, sample size in parentheses) of surface samples collected in 2003–2005

of littoral zone from 5 to 15 m wide was exposed to the air for several weeks.

Lee Moore Lake (33°47′24″ N, 95°32′42″ W) is the smallest among all impoundments studied (Table 1). Bottom sediments in shallow areas (up to 0.5 m depth) are silty sand, detritus, and clay; deeper areas are covered with fine silt. Only ca. 10% of the pond surface was covered with submerged macrophytes, mainly a stonewort *Chara* sp. For convenience, and to be consistent with their official names we will refer later in the paper to these impoundments as "lakes."

Abiotic factors

The calculations of lake surface areas were based on 1995 aerial photography and GPS points taken with a sub-meter Trimble Pro-XRS GPS Unit. Surface areas were determined by ArcGIS 8.3 software using SQL statements with a Visual Basic Script. Abiotic parameters including water temperature, dissolved oxygen, pH, specific conductivity, total dissolved solids, and turbidity were measured using a Hydrolab Quanta (Hydrolab Corporation®). Transparency was measured at maximum lake depth with a Secchi disc. At each sampling site, depth, prevalent substrate type, and percentage of macrophyte coverage were recorded.

Density

To determine the distribution and abundance of unionids, samples were collected in October 2003, August 2004, and October 2005. Only two species of unionids were found in the studied lakes: *P. grandis* (giant floater) in Lamar and Lee Moore lakes, and *U. imbecillis* (pond papershell) in Lamar and Neff lakes (Table 2).

In Lamar Lake, we collected quadrat samples from 5 permanent transects in 2003, and from 7 transects in 2004 and 2005. In Neff Lake three parallel transects were established at the dam area (the only part of the lake where unionids were found in quadrats), and three transects in the rest of the lake. In addition, we used time searches in Neff Lake to find unionids in areas where the population was very sparse. In Lee Moore Lake we sampled mussels from five

Table 2 Average density (mussel m^{-2}), biomass (live weigh, g m^{-2}), total population size (mussels) (±95% confidence interval), mortality as total number of shells per year collected at permanent sites, and mammalian predation on unionid bivalves (*P. grandis* and *U. imbecillis*) in studied impoundments in Camp Maxey

Lake, year		Density (m^{-2})	Biomass (g m^{-2})	Population size	Mortality	% of shells with predation marks	% mortality from total population	% predation of total population
Lamar	2003	0.52 ± 0.30	47.7 ± 34.7	6,681 ± 3,372	105	18.1	n.c.	n.c.
	2004	0.24 ± 0.11	33.7 ± 18.4	4,551 ± 2,275	30	0	n.c.	n.c.
	2005	0.42 ± 0.21	101.2 ± 56.2	9,078 ± 5,702	624	11.9	n.c.	n.c.
Neff	2003	4.26 ± 2.01	60.5 ± 27.6	7,217 ± 2,234	9	0	0.1	0.0
	2004	1.30 ± 0.62	18.5 ± 8.3	1,788 ± 827	491	68.2	27.5	18.7
	2005	2.11 ± 0.74	23.8 ± 11.1	1,910 ± 696	24	91.7	1.3	1.2
Lee Moore	2003	1.62 ± 0.54	218.8 ± 77.9	8,974 ± 2,955	55	9.1	0.6	0.1
	2004	1.18 ± 0.77	147.9 ± 82.6	5,090 ± 2,551	23	0.0	0.5	0.0
	2005	0.94 ± 0.84	116.7 ± 119.2	3,529 ± 3,187	826	55.4	23.4	13.0

n.c.—not calculated

permanent transects. All transects were initiated on the shore and ran perpendicular to the shore towards the center of the lake. Transects were distributed within each lake based on bottom sediments and distribution of macrophytes, to include all major habitat types within each lake. At each transect, three 1 m^2 or ten to twelve 0.25 m^2 replicate quadrat samples were collected at 0.5 m depth intervals down to the maximum depth where unionids were found. Samples were collected with the aid of a surface supplied air diving system (Pioneer 275, Brownie's Third Lung). Within each quadrat, sediments down to at least 5 cm were checked for the presence of mussels. All collected mussels were counted, weighed to the nearest 0.1 g (blotted live weight) and released back to the lakes. To determine the size-frequency distribution of live and dead mussels, we measured their shell length with calipers to the nearest millimeter.

Mortality

To estimate the mortality associated with the water level fluctuations and predation, we collected unionid shells on lake shores approximately every 2 months between October 2003 and October 2005. Water level in each lake at the beginning of our study was marked as "zero" with a metal pole, and later at each sampling time we recorded changes (in cm) in the water level relatively to this "zero." All shells were collected from the shores of Lee Moore and Neff lakes, but due to the relatively large size of Lake Lamar's shoreline, two permanent sites were established there for shell collection. At each sampling date we counted all collected shells, measured them with calipers (when possible), and recorded visible marks of predation (scratches on shells, damaged beaks or posterior ends, etc.). Estimation of predation by collecting shells is a common technique (Hanson et al., 1989; Neves & Odom, 1989).

Statistical analysis

We used stratified sampling formulae to estimate the total population size and confidence intervals (Manly, 1992). To find the relationship between unionid density and macrophyte overgrowth, we calculated Pearson correlation coefficient between log-transformed density in quadrats at depths <2 m and arcsine-transformed percentage of macrophyte overgrowth in the quadrats. To compare density and biomass of unionids on different substrates within and among lakes we used ANOVA on log-transformed primary data (Zar, 1996). To determine the dispersion pattern of unionids in each lake, we calculated the Green's coefficient of dispersion (GC) from quadrat samples for each lake and year across sampled depths. This index has been shown to be

relatively unaffected by population density and sample size (Myers, 1978) and ranges from –1.0 (uniform) to +1.0 (clumped); random patterns yield zero values (Krebs, 1999). We applied χ^2-test to variance/mean ratio to test for agreement with Poisson distribution (Elliott, 1977); the distribution was considered aggregated if the test was significant ($P \leq 0.05$). To find the correlation between mortality rate and water level, we calculated Pearson correlation and linear regression between the log-transformed number of shells found in each lake ($\ln (N + 1)$) and water level (m) in the lake. To compare the size-frequency distributions of shells with marks of predation *vs.* shells without marks, we calculated the percentage of each size group from total for all lakes and years and then tested for differences with a Fisher–Freeman–Halton test (a generalization of the Fisher's exact test for r by c contingency table) with asymptotic *P*-value (Freeman & Halton, 1951).

For all statistical tests we used Statistica software (STATISTICA version 6, StatSoft, Inc. 2001). Effects were considered statistically significant at $P < 0.05$. When multiple tests were conducted on the same data, we used a sequential Bonferroni correction to adjust the critical alpha considered for statistical significance (Rice, 1989). Where appropriate, we present the critical alpha (α) with the results of each statistical test.

Results

Abiotic factors

Chemical parameters of water measured in lakes Lamar and Neff were quite similar (Table 1). In contrast, Lee Moore Lake had a lower pH and almost twice lower conductivity and the amount of total dissolved solids. While surface water was saturated with oxygen, the percentage of dissolved oxygen significantly decreased with depth (Fig. 1). The difference between the surface and bottom concentrations of dissolved oxygen varied significantly among sampling months and was the highest in August, when the surface water temperature exceeded 32°C ($P = 0.039$, 1-way ANOVA). There was also a significant decrease in
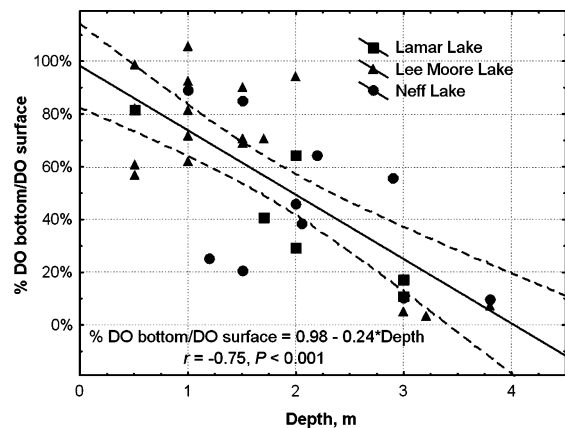

Fig. 1 Relationship between the amount of dissolved oxygen at the bottom (in percent of oxygen concentration at the surface) and depth in Camp Maxey impoundments

temperature with depth ($r = –0.51$, $P = 0.002$, $N = 33$). The average difference in temperature between surface and 2 m depth was 2.9 ± 0.4°C ($\pm$SD), maximum 9.3°C.

Spatial distribution

In Lamar and Neff lakes both heavily overgrown with *M. spicatum* and *N. lutea*, unionid density was negatively correlated with the percentage of macrophyte coverage ($r = –0.49$, $P < 0.001$, $0.010 < \alpha < 0.0125$, $N = 332$). In contrast, in Lee Moore Lake there was no significant correlation between unionid density and *Chara* overgrowth ($r = –0.07$, $P = 0.43$, $N = 147$). In heavily overgrown lakes Lamar and Neff, both densities and biomass of unionids varied significantly among transects (Lamar Lake: $P < 0.025$, $0.025 < \alpha < 0.05$; Neff Lake: $P < 0.002$, $0.013 < \alpha < 0.017$, 2-way ANOVA on log-transformed density and biomass). Transects with dense macrophyte beds had significantly lower unionid density and biomass (Lamar Lake: $P < 0.001$, $0.010 < \alpha < 0.017$; Neff Lake: density: $0.0005 < P < 0.033$, $\alpha = 0.025$; biomass: $0.0003 < P < 0.012$, $\alpha = 0.05$, Fisher LSD test) than transects without macrophytes. In contrast, in Lee Moore Lake, unionids were distributed more evenly and their density did not vary among transects ($P > 0.22$, 2-way ANOVA).

Density and biomass of unionids changed significantly with depth ($0.017 < P < 0.025$,
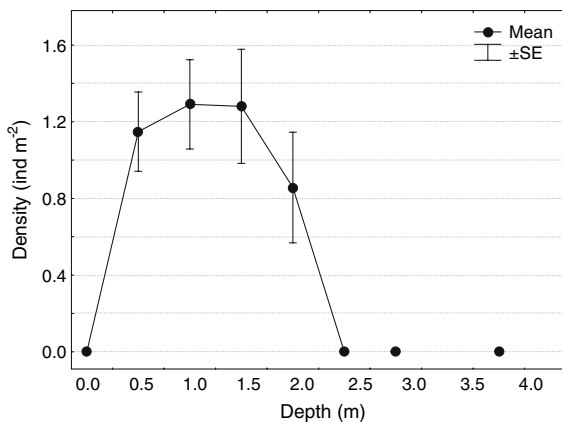
Fig. 2 Density distribution of unionids with depths in Camp Maxey impoundments (pooled data for 2003–2005)

$0.017 < \alpha < 0.05$, Kruskal–Wallis test on all pooled data), with the highest densities and biomass found in shallow areas (0.5 and 1 m), and the lowest at 2 m depths ($P < 0.001$, multiple comparisons test) (Fig. 2). Unionids were not found below 2 m in all sampled lakes. Mussel densities on pure silt substrates were among the lowest. Mixtures of silt and clay, silt on rocks, or silty sand had higher densities compared to pure silt ($0.007 < P < 0.044$, $\alpha = 0.05$, Dunnett test).

The Green coefficient of mussel dispersion ranged from –0.10 to 1.00 for different depths (mean ± SD for Lamar Lake: 0.12 ± 0.14; Neff Lake: 0.16 ± 0.11, Lee Moore Lake: 0.34 ± 0.43). Significant spatial aggregation ($P < 0.05$) was found for 69% of cases ($N = 32$), while no significant departure from the Poisson distribution was found only in 31% of the cases.

Mortality

The number of dead shells found on the shore negatively correlated with water level (Fig. 3). The relationship between mortality and water level can be described by linear regression: ln $(N + 1) = 3.05(\pm0.27) – 3.45(\pm0.57)$ x, $R = –0.67$, $P < 0.001$, where N—amount of dead unionid shells on the shore, and x—water level in the pond (m) (all coefficients were significant at $P < 0.001$, t-test). The total amount of shells found per year on the shore varied from 0.1% of total population size in years with small water level fluctuations, to 28% in years when the lake
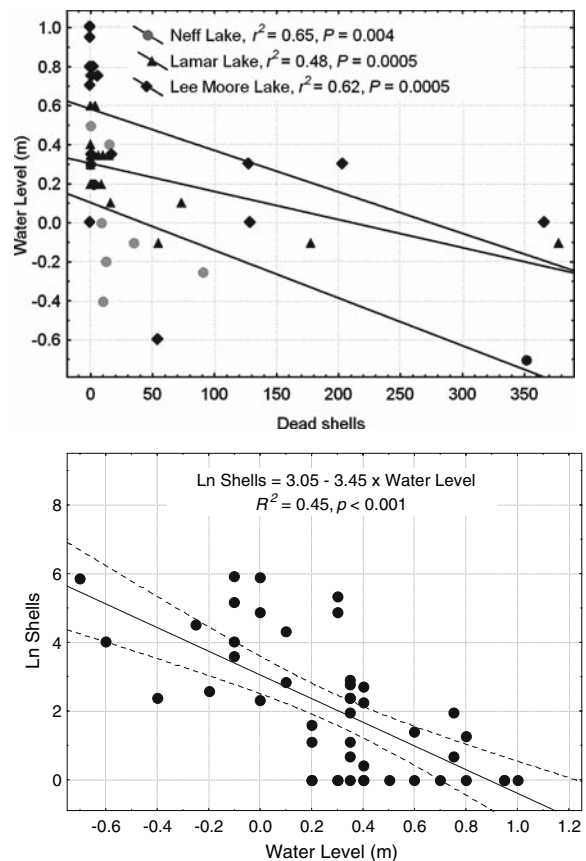

Fig. 3 Relationship between the number of collected shells and water level for each of Camp Maxey impoundments (upper figure) and pooled data (lower figure). Data were collected in 2003–2005. Water level at each sampling date was measured relatively to the water level in each lake at the beginning of our study in October 2003 (marked as "zero"). Correlation coefficients and their significance are given for each impoundment

experienced large drawdowns or droughts (Table 2). In Lamar Lake in an unusually dry 2005 we found >600 dead stranded mussels (app. 7% of the population).

On average, 43% (maximum 100%) of all unionids found on lake shores during 3 years of study had visual marks of predation. At the time of dramatic decrease in water level, predation was particularly high: thus 95% of 352 shells collected at the shore of Neff Lake during its drawdown (October 2004) had marks of predation. In average, 21% of live mussels (from 1.6% to 51.7%) found from 0.5 to 2 m depths during sampling in 2003–2004 also had predation marks. The size-frequency distribution of *P. grandis*
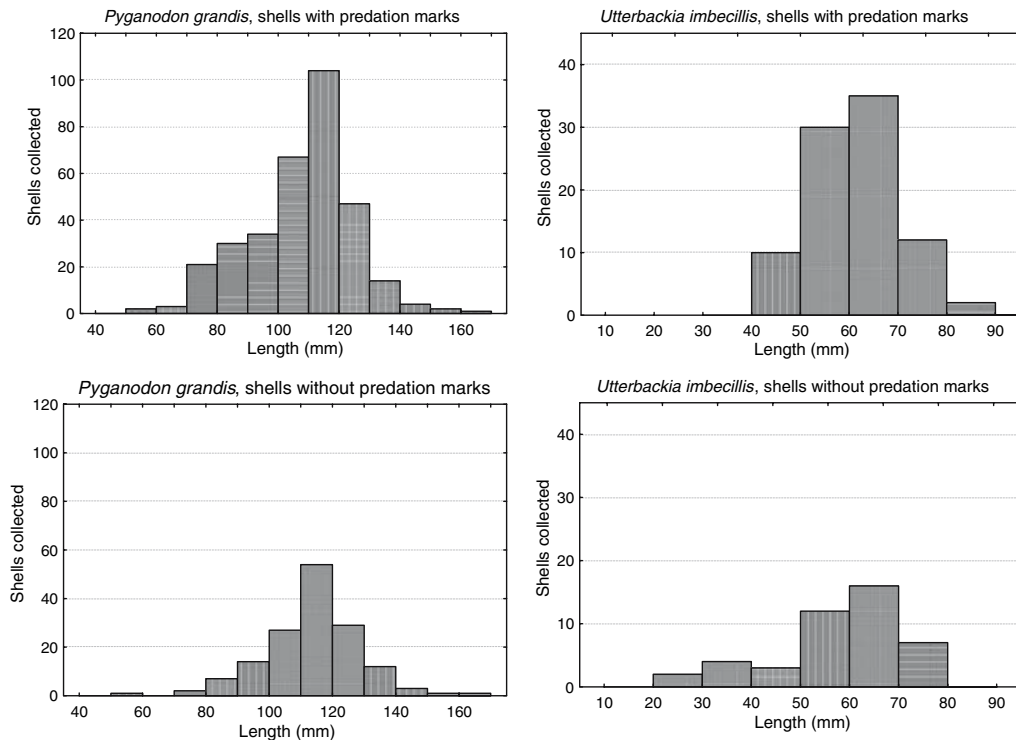
Fig. 4 Size-frequency distributions of shells with (upper) and without (lower) marks of predation found on the shores of Camp Maxey impoundments in 2003–2005. Left columns—*P. grandis*, right—*U. imbecillis*

shells with marks of predation collected in Lamar and Lee Moore lakes during our study, was not significantly different from distribution of undamaged shells (*P* = 0.37, Fisher–Freeman–Halton test, Fig. 4). However, there was a significant difference between *U. imbecillis* shells with and without predation marks (*P* = 0.001; Fig. 4) indicating that a disproportionately large number of larger shells had predation marks.

Discussion

Spatial distribution

Lamar Lake and Neff Lake are typical macrophyte-dominated lakes, with >50% of surface area covered with invasive and noxious vegetation. Sampling of transects established in heavy overgrown areas failed to reveal any live mussels. As a result, unionid densities were significantly lower in areas with higher macrophyte abundance. In contrast, in Lee Moore Lake where macrophytes

were represented by *Chara* sp., unionids were distributed quite evenly across the lake, forming a "belt" along shores. Therefore, excessive macrophyte overgrowth seems to be the major factor limiting spatial unionid distribution. Cvancara (1972) also found a lower unionid density in the part of Long Lake with extensive cover of macrophytes. Both *M. spicatum* and *N. lutea* produced dense large mats of vegetation, intercepting sunlight and restricting water movement either by profuse branching presents in the former or by large floating leaves in the latter plant. In contrast, short sparse beds of *Chara* in Lee Moore Lake did not produce such an effect. As a result, the highest average biomass and one of the highest total population sizes of unionids were found in the smallest lake.

Dense macrophyte stands can change the habitat and negatively affect mussel populations due to decreased water movement and increased shading effect. As a result, macrophyte beds have elevated water temperature and frequent diel oxygen depletion (Mohseni et al., 2001; Caraco &

Cole, 2002), especially in shallow areas and at the sediment-water interface (Unmuth et al., 2000), and can also cause high diel pH (>9.0; Halstead & Tash, 1982). The oxygen depletion at the bottom may significantly increase in the fall, when dense mats of macrophytes decay. In addition, aquatic plants change the substrate due to accumulation of fine sediments (Mohseni et al., 2001). Dense macrophyte beds can interfere with food delivery, and, possibly, with establishment of unionid larvae (glochidia) in the sediment. The substrates with abundant root masses could be more difficult to penetrate for burrowing mussels. The exact mechanism of the negative effect of invasive and noxious macrophytes on unionid abundance however remains unknown, and probably is a combination of all the factors listed above. Perhaps the same mechanism that causes strong decline in unionid density in macrophyte beds is responsible for a dramatic decline in *Corbicula fluminea* (O. F. Müller) in *Hydrilla* beds in Lake Nacogdoches, Texas (Karatayev et al., 2003). Therefore, the introduction of invasive and noxious macrophytes can cause a dramatic decline in unionid abundance, and may have strong negative impact on their diversity. In contrast to the very well known negative effect of *Dreissena polymorpha* (Pallas) on native clams (Sebestyen, 1937; Ricciardi et al., 1996; Schloesser et al., 1996; Burlakova et al., 2000), the effect of invasive macrophytes on unionids has been given much less attention (Strayer, 1999), and definitely calls for future investigations.

We also hypothesize that phytoplankton-dominated lakes could be a better habitat for unionids than macrophyte-dominated lakes with dense beds of aquatic plants. Therefore, transformation of phytoplankton-dominated lakes into macrophyte-dominated lakes may be associated with a strong reduction in unionids.

In most cases unionids had aggregated spatial distribution. In all lakes, the highest mussel densities and biomass were found at dam areas, while the lowest densities and biomass were found on pure deep silts. We hypothesize that dam areas may be the last refuge for unionids when the amount of favorable habitats in a reservoir decreases (e.g. as a result of severe macrophyte overgrowth). For example, in Neff

Lake the area close to the dam was the only place where unionids were found during samplings. Although unionids may also inhabit other areas of the lake at lower densities, we did not detect them by time searches or quadrat sampling. The dam area could be a favorable habitat for mussels due to (1) lack of dense macrophyte beds; (2) favorable substrates, and (3) steep decline in depth that may facilitate quick escape during water fluctuations. Although very steep slopes may prevent mussels from affixing to the substrate (Ghent et al., 1978; Green, 1980), *P. grandis* is known to migrate vertically to avoid emersion caused by seasonal changes in water level (White, 1979). By our observations, the mussels get easily trapped and stranded in flat areas with a very low slope. We recommend that the dam areas should be checked first for quick detection of unionids in shallow reservoirs, especially those with excessive macrophytes development.

The highest densities and biomass of unionids were found in shallow areas (between 0.5 and 1 m), whereas mussel abundance decreased deeper into the lake, and no live mussels were found deeper than 2 m in all lakes studied. Shallow areas have previously been reported to have higher unionid densities and biomass (Stone et al., 1982; Hanson et al., 1988). Most unionids prefer shallow habitats, possibly due to their poor hypoxia tolerance especially at the juvenile stage, and even hypoxia-tolerant species can be retarded in growth and reproduction during summer hypoxia (reviewed in McMahon & Bogan, 2001). Our data also indicate that insufficient dissolved oxygen may be one of the possible reasons why deeper areas in the studied ponds were devoid of mussels. Accumulation of stagnant water in the deepest part next to the dam is typical for many reservoirs. This bottom layer can become near-anoxic, and excessively cold; in addition, deleterious substances such as sulfide, ferrous, and manganous ions may accumulate in this layer along with nutrients leaching from the sediments (reviewed in Baxter, 1977; Watters, 2000). Hanson et al. (1988) explained lower densities of *Anodonta grandis simpsoniana* Lea at deeper depths by their active response to avoid lower temperatures and/or some characteristics of

substrate. The lack of mussels in depths greater than 2 m in our study may be also partly due to substrate – only a very thick layer of pure silt was found at these depths in all studied lakes. Ellis (1936) has shown that a silt accumulation of 0.6–2.5 cm depth resulted in app. 90% mortality in 20,000 mussels from 18 species. Although these thin-shelled species that we studied (*P. grandis* and *U. imbecillis*) are known to inhabit reservoirs, preferentially selecting mud sediments (Huehner, 1987; Downing et al., 2000; McMahon & Bogan, 2001), a combination of certain factors (e.g. lower oxygen, temperatures, very thick silt, other chemicals, etc.) may limit their depth distribution.

Mortality

The littoral zones in natural lakes are regularly subjected to a short period of flooding during the spring or rainy season, followed by a long period of exposure. In contrast to natural lakes, long periods of flooding in reservoirs alternate with short periods of exposure, drastically reducing the abundance and diversity of aquatic macrophytes and benthic animals in the drawdown zone (reviewed in Baxter, 1977; Watters, 2000; Richardson et al., 2002). It has been shown that a substrate subjected to 2–12 h exposure to air required more than 4 months to regain biomass similar to unexposed habitat (Blinn et al., 1995). The major flow-rate oscillations due to droughts and controlled water releases from reservoirs cause lethal exposure of unionids to air during low water (Miller et al., 1984; Samad & Stanley, 1986; Vaughn & Taylor, 1999; Howells et al., 2000).

Restriction of many unionid species to shallow waters makes them susceptible to emersion. Declining water levels can expose relatively immobile bivalves for weeks or months to air. *Pyganodon grandis* has thin shell margins that do not completely seal when closed, resulting in rapid water loss and poor tolerance to emergence (Byrne & McMahon, 1994). We found that service drawdowns and droughts were the major cause of unionid mortality in studied ponds, and can kill up to 28% of the total population. Large mortality of unionids due to dewatering of reservoirs has been frequently reported in literature (Samad & Stanley, 1986; Howells et al., 2000; Richardson et al., 2002; reviewed in Watters, 2000), however there is almost no data published that quantify the effect of water level fluctuation on unionid mortality.

Annual mortality calculations based on shoreline shell collections is really an estimation of "unnatural," accidental mortality caused by external reasons such as droughts, dewatering, and predation. Most of the shells of unionids that die "naturally" in the lake remain underwater and, therefore, were not possible to count. This natural mortality of *P. grandis* may be low (Anthony et al., 2001). In Lamar Lake, the mortality rate in cages where we kept *P. grandis* for a year was 8% (author's unpublished data), however this rate might be higher than in natural conditions. Low mortality rate in adult stages, of between 5% and 12% per year, was found for other species of unionids (Bauer, 2000). Therefore, unionid mortality caused by drawdowns can be three times higher that natural mortality.

About half of the shells collected on shores during the 3 years of our study had some marks of predation. Sometimes, nearly all of the shells found were bitten or damaged by predators; thus, 95% of *U. imbecillis* shells collected at the shores of Neff Lake during its October 2004 drawdown had marks. Estimated mortality from predation based on the number of damaged shells comprised from 0.1 to 19% of the total population. Therefore, mammalian predators could be another factor limiting unionid populations in these ponds. However, this predation is more likely to be compensatory than additive, and takes place mainly when water level drops. Therefore, decrease in water level facilitates mammalian predation.

Muskrats (*Ondatra zibethicus* (L.)) are the best known predators of unionids and can consume from 3% to 16% of a population (Hanson et al., 1989; Neves & Odom, 1989). Other predators known to consume unionids, are raccoons (*Procyon lotor* (L.)), river otters (*Lutra canadensis* Schreber) (Toweill, 1974), striped skunks (*Mephitis mephitis* (Schreber)), minks (*Mustela vison* Schreber), and turtles (*Graptemys* sp.) (reviewed in Tyrrell & Hornbach, 1998). Raccoons and striped skunks are common in Camp Maxey,

while muskrats, river otters, and minks are much more rare (Dr. W. Godwin, Stephen F. Austin State University, personal communication). On average about 20% of live mussels (up to 52%) found in 2003–2004 at all depths (from 0.5 to 2 m) also had predation marks. Most likely, raccoons and striped skunks are the shallow-water predators (Tyrrell & Hornbach, 1998), and river otters are the deeper-water predators in Camp Maxey lakes.

It was found that unionid shells in the midden piles of muskrats and other small mammals were on average longer than mussels in the adjoining body of water, indicating that the mammals are size-specific predators (Convey et al., 1989; Tyrell & Hornbach, 1998, Hanson et al., 1989). We found no evidence of size selective predation on the most abundant large-bodied species *P. grandis* (Fig. 4). However, for smaller species *U. imbecillis* there was a significant difference between size frequency distribution of shells with and without predation marks. This effect may be partly due to the lesser sample size in small (20–30 mm, $N = 6$) and large (>70 mm, $N = 14$) size groups. On the other hand, predators might find and consume larger specimens of *U. imbecillis* (>40 mm in length) more easily than smaller individuals.

Conclusion

The introduction of invasive and noxious macrophytes can cause a dramatic decline in unionid abundance. Dense stands of *M. spicatum* and *N. lutea* limited densities and spatial distribution of unionids, and large areas in Lamar and Neff lakes overgrown with these macrophytes were devoid of unionids. The exact mechanism of the negative effect of invasive macrophytes on unionid abundance however remains unknown, and may be a combination of many factors (i.e. oxygen depletion, elevated temperatures, shading effect, accumulation of fine sediments, etc.) and definitely calls for future investigations. Vertical distribution of unionids was likely limited by low oxygen at deep areas and by water level fluctuation and predation in shallow areas. We found that service drawdowns and droughts

were the major source of unionid mortality in studied ponds. The total amount of shells found on the shore per year varied from 0.1% to 28% of the total population and was negatively correlated with water level. Mammalian predators consumed up to 19% of total unionid population and predation was facilitated by water level fluctuations.

Important factors affecting unionid populations in these small Texas ponds included water level fluctuation, macrophyte overgrowth, and predation. These same factors will also affect unionid populations in large reservoirs. Since it is more economical to conduct research in small reservoirs, then small impoundments can be convenient models to study the effect of various environmental factors on unionid populations.

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