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Effects of exotic common reed (*Phragmites australis*) on wood frog (*Lithobates sylvaticus*) tadpole development and food availability

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Exotic species contribute to aquatic habitat degradation. In the context of declining amphibian populations, the introduction of alien species has been the subject of numerous studies but few have been dedicated to exotic plants. We hypothesized that the establishment of the exotic common reed (*Phragmites australis*) in North America would lengthen larval anuran development and decrease the survival rate by modifying habitat structure, changing water characteristics, and decreasing food availability. We tested these hypotheses by studying the larval development of the wood frog (*Lithobates sylvaticus*) during an experiment in field enclosures. Within each enclosure, we created habitats with three different reed densities (zero, medium, and high). Tadpoles were placed in the enclosures and were followed for six weeks up to metamorphosis, during which we monitored water quality and phytoplankton composition. At the end of the experiment, tadpoles at medium and high reed densities developed more slowly than under the control. However, tadpole survival was similar across treatments. For a given developmental stage, total body length did not differ among treatments. Phytoplankton abundance varied with reed density, and groups known to be consumed by tadpoles were negatively influenced by reed density. We found no impact of reed density on pH, total phenolic concentration, or conductivity. Our results suggest that common reed establishment can influence amphibians with rapid development such as wood frogs. Though larval survival rates were similar across treatments, slower development under high reed densities implies a longer exposure to the risk of the pond drying out and to predators.

Keywords: allelopathy; amphibians; invasive species; larval development; phytoplankton; wood frog

Introduction

Exotic and invasive plants are increasingly recognized as responsible for worldwide habitat degradation (Gurevitch and Padilla 2004; Didham et al. 2007). Aquatic environments (fresh, brackish, and marine) are particularly affected by the invasion of exotic plants, as 78.2% of the exotic plants in North America are found in these habitats (Lichvar and Kartesz 2009). Invasion by nonnative plants is considered to be one of the greatest threats to plant and animal species (Wilcove et al. 1998) and to the integrity of ecosystems and their functions in North America (Drake et al. 1989; Randall 1996). Some studies have noted an alteration of nutrient cycles, geomorphologic processes, fire regimes, and hydrology in invaded wetlands (Blossey 1999; Weidenhamer and Callaway 2010). Studies on the impact of plant invasion on animal communities are increasing and most of these have focused on fish (Witte et al. 2000), invertebrates (Gerber et al. 2008), birds

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(Holland-Clift et al. 2010), and mammals (Cox 1999). While the impact of plant invasion is mostly negative, in some cases, positive effects are also reported, such as when the invading species provides refugia or food (Dutra et al. 2011).

Amphibians are not exempt from the threat of exotic plant invasion, especially when the productivity and stability of their aquatic breeding habitat is altered. Given their complex life cycles, pond-breeding amphibians should be most at risk from the effects of plant invasion during their larval stage, when amphibians are most sensitive to environmental changes (Alford and Richards 1999). For instance, a change in habitat structure can influence duration of the larval development and survival rate for some larval anuran species (Purrenhage and Boone 2009). Watling et al. (2011) found a negative behavioral response (increased frequency of surfacing for respiration) of two tadpole species raised in water with extracts of the widespread invasive shrub amur honeysuckle (*Lonicera maackii*). In a recent study, Cotten et al. (2012) attributed differential effects of leaf litter from Chinese tallow (*Triadica sebifera*) on tadpole size and survival, to the timing of breeding of the species tested (early vs. late breeders). Maerz, Brown, et al. (2005) found a reduced larval performance of American toads (*Anaxyrus americanus*) raised with purple loosestrife (*Lythrum salicaria*) extracts. Their study associated tadpole mortality with phenolic secondary compounds (tannins) in the leaves. These phytotoxic substances can decrease plant competition or grazing activity and are also known to inhibit bacteria, fungi, and microalgae development (Callaway et al. 2008). Invasive plants not only influence the amphibian larval stage, but can also affect metamorphosed individuals. For example, Japanese knotweed (*Fallopia japonica*) indirectly reduces foraging success of adult green frogs *Lithobates clamitans melanota* by potentially reducing arthropod abundance (Maerz, Blossey, et al. 2005).

Common reed (*Phragmites australis*) is native to North America, but an invasive exotic Eurasian haplotype of common reed (*P. australis*, haplotype M) is experiencing a large-range expansion in North American brackish and freshwater wetlands (Mal and Narine 2004; Lelong et al. 2007). Rapidly expanding populations of the exotic common reed pose a major management problem in natural areas because once established, they are nearly impossible to eradicate. Compared with its native counterparts, haplotype M produces more shoots, grows taller, and has a higher growth rate (Vasquez et al. 2005; League et al. 2006). It produces dense, nearly monospecific stands that may alter the ecological functions of wetlands by modifying physical and biogeochemical processes, reducing water level, and producing biomass that decomposes slowly (Windham and Lathrop 1999). However, impacts of reed invasion on fauna are not as clear. Studies report both positive and negative effects on certain invertebrate taxa (Angradi et al. 2001; Talley and Levin 2001). The few studies conducted on birds and mammals revealed a negative impact through a decrease in suitable habitat (Hauber et al. 1991) and changes in species patterns (Benoit and Askins 1999), whereas evidence of the effect on fish is equivocal (Able and Hagan 2000; Aday 2007). Research on amphibians in the context of reed establishment remains anecdotal (Meyer 2003), and has chiefly focused on the effect of leaf detritus degradation among a suite of plant species (Maerz et al. 2010). Amphibians are potentially strongly influenced by reed invasion because of their early developmental stages linked to aquatic environments and habitat structure.

Here, we report the results of a manipulative experiment on the effects of common reed shoots on anuran tadpole development. We hypothesized that the establishment of the exotic common reed negatively influences larval anuran development through the emission of secondary phenolic compounds that reduce habitat quality, namely, water characteristics and food availability (phytoplankton). Based on the extensive review of

Martin and Murray (2011), we predicted that the influence of reed establishment increases with reed density. We evaluated the performance (survival rate and development) of wood frog (*Lithobates sylvaticus*) tadpoles in enclosures containing three densities of *P. australis* (zero, medium, and high density). Wood frogs breed in ponds, reach metamorphosis rapidly, and are common in our study area. We used this species as a model for species with similar characteristics such as Spring peepers (*Pseudacris crucifer*) and American toads (*Anaxyrus americanus*) to test our hypotheses. We chose a control without plants to reflect conditions in newly invaded wetlands such as abandoned borrow pits and newly created or restored wetlands with little or no aquatic vegetation that are frequented by the species. To ascertain the immediate effects of reed establishment on amphibian development, we conducted the experiment without the influence of the dead reed material normally found in high quantity in well-established natural reed stands.

Methods

Enclosure design

We collected common reed shoots around an invaded wetland in the Iles-de-Boucherville National Park, Quebec, Canada (45.61°N, 73.46°W) in April 2010. Portions of rhizomes with associated soil were transferred each to a pot (15 cm height × 20 cm diameter). Each portion of rhizome included between two and five young shoots (average of 3.5) nearly 8 cm in height. We also collected soil from a noninvaded portion next to the wetland for the zero reed density treatment. This soil was autoclaved (30 min at 121°C maximum) to avoid contamination from common reed seeds.

We constructed nine enclosures from 130 L plastic containers (40 × 40 × 80 cm) with holes drilled in the sides near the top to facilitate potential water overflow following rain. These holes were above the water level of the wetland to prevent water input into the enclosures. We placed six pots on the bottom of each enclosure. We filled the spaces between pots with rocks, gravel, and silica sand up to the top of the pots. In each enclosure, we created one of three types of reed beds according to the treatments: control without reed (six unplanted pots), medium density (three planted pots, three unplanted pots), and high reed density (six planted pots). We covered the top of the enclosures with a plastic grid (mesh of 1 cm^2) to allow the plant to grow out of the enclosure while hindering vertebrate predators. In addition, we overlaid the grid with mosquito netting to prevent frog escape from the enclosure, allowing a 0.1 m^2 in the center of the plastic grids to permit reed shoot growth.

On 15 April 2010, two weeks before tadpole introduction, we installed the enclosures in a wetland of the Parc Nature de la Pointe-aux-Prairies (Montreal, Quebec, Canada; 45.68°N, 73.52°W). The park managers keep the water level of the wetland constant. The enclosures were placed in shallow portions of the wetland so that the water of the marsh could not get inside the enclosures. There was no water exchange between our enclosures and the wetland, but the placement of the mesocosms in the wetland maintained the water temperature at natural levels. After the installation, we filled the plastic containers with the water of the wetland to a depth of approximately 20 cm. Enclosures were placed following a randomized complete block design with a total of three blocks in different sections of the wetland. The mean number of reed shoots in medium and high density enclosures was 17 and 33.3, equivalent to 53.1 and 104.1 plants m^{-2}, respectively. Larochelle (2011) reports mean reed densities in stands ranging between 79 and 111 shoots per meter square in freshwater wetlands from the same geographical area. In our experiment, the high-density enclosures (104.1 shoot per meter square) fall within the high range of the observed field density. Rain was usually sufficient to compensate evaporation, but 43 days after the installation of enclosures (27 May 2010), we supplemented mesocosms with 1 L of filtered wetland water to prevent desiccation.

Wood frog larval development

We collected three wood frog egg masses in the Mont St-Bruno National Park, Quebec, Canada (45.55°N, 73.31°W) on 20 April 2010. We kept the eggs in a bucket with their original pond water and plants. Egg masses were kept at 19°C in a room with halogen lamps with a controlled photoperiod matching the natural photoperiod. Tadpoles hatched three days later and were reared until they resorbed the vitellus, around Gosner stage 23 (Gosner 1960). On 30 April 2010, we randomly selected tadpoles from the three masses and placed 15 tadpoles in each enclosure, initiating the experiment with a density of 0.4 individuals/L (e.g., Purrenhage and Boone 2009). At the time of initiation, reed shoots had reached nearly 12 cm in their new environment and phytoplankton had enough time to colonize the enclosures. We visited the enclosures at least once a week to assess tadpole development. As soon as we detected the first tadpole at Gosner stage 42 (i.e., appearance of forelimbs), we added floating foam platforms in the enclosures for metamorphs and started to monitor enclosures daily.

The experiment ended on 10 June 2010 (41 days after tadpole introduction) with the metamorphosis of the first larvae in the enclosures. We collected all tadpoles from the mesocosms by dip-netting. We anesthetized tadpoles with an aqueous solution of 0.01% MS 222 (Tricaïne methanesulfonate; Sigma, Ontario, CA) buffered with sodium carbonate. We assessed the Gosner stage with a binocular microscope and photographed each tadpole for later morphological measurements. Tadpole morphology was measured by coupling photos from the ventral part and from the ImageJ analysis software (Abràmoff et al. 2004) in order to determine total length (i.e., body and tail length).

We analyzed the probability of larval survival across reed density with a logistic regression with random intercepts (Gelman and Hill 2007). Specifically, the model included a random effect for each block and treatments within blocks to account for the design of the experiment. We analyzed larval stage, a discrete variable, using ordinal logistic regression with the same random effects as described above (Gelman and Hill 2007). Ordinal logistic regression is the extension of logistic regression for a response variable with more than two ordered categories (e.g., tadpole stage). In our case, we created three groups of Gosner stages (early, intermediate, and late stages) to ensure a similar number of individuals in each group. The first group consisted of individuals of Gosner stages ≤ 37, the second group included individuals of Gosner stages 37 to 39 ($37 <$ stage ≤ 40), and the third group featured individuals of Gosner stages > 40. The first and second group consisted of 42 individuals each, whereas the third group contained 40 individuals. We analyzed total body length with a linear mixed model featuring block and treatment nested within block as random effects (Gelman and Hill 2007). To account for potential variation in tadpole size across developmental stages, we included the stage groups defined above (early, intermediate, and late stages) as a factor in addition to the reed treatment and the stage × reed treatment interaction. We set the alpha level at 0.05 in all analyses.

Water and phytoplankton analysis

We took 0.75 L water samples from the middle of the water column in situ in each enclosure 15, 30, and 41 days following tadpole introduction. Samples were maintained at

4°C, during transfer and storage, before analysis. We fixed 0.5 L of each sample with Lugol's iodine solution directly after transport and preserved it in dark conditions at 4°C for phytoplankton analyses (see below). We used the 0.25 L remaining to measure pH (Oakton ion6; Oakton Instruments, Vernon Hills, IL), conductivity (YSI EC300; YSI Incorporated, Yellow Springs, OH), and total phenolic content. We assessed the reduced total phenolic concentration of the first two samples (i.e., 15 and 30 days following tadpole introduction) 48 h after collection with Folin–Ciocalteu reagent (Sigma, Ontario, CA). We measured the absorbance at 750 nm after the colorimetric reaction using a spectrophotometer. We expressed the results as Gallic acid equivalents (GAE).

We used linear mixed models to analyze water characteristics across the two factors (reed treatment and date) and their interaction. Again, we included block and reed density within block as random effects in our models.

We identified and counted phytoplankton with inverted microscopes after concentrating the phytoplankton on a round microscope slide topped with a sedimentation chamber. We used transects and determined all individuals encountered to the lowest taxonomic level possible. We used linear mixed models for the most common species in the analyses to compare phytoplankton abundance (cells/mL) for each highest taxonomic group (e.g., order) across reed density, sampling date, and their interaction. We treated block and reed density nested in block as random effects.

All analyses were conducted in R 2.15.1 (Ihaka and Gentleman 1996), with packages lme4 (Bates et al. 2012) and ordinal (Christensen 2012). Model diagnostics, i.e., residuals against fitted values, normality of random effects, normality of residuals and homoskedasticity for linear mixed models, did not suggest departures from model assumptions. For some of the response variables, the variance of the treatments within blocks random effect was close to 0, and in such cases, we only included the block random effect to ensure model convergence.

Results

Wood frog larval development

The first individual reached metamorphosis 41 days after tadpole introduction, at which time the experiment was terminated. A total of 124 larvae (out of 135 individuals) survived in the enclosures. Tadpole survival probability was high and did not differ across treatments (control: prob. of survival = 0.90, 95% CI: 0.69–0.97; medium reed density: prob. of survival = 0.95, 95% CI: 0.79–0.99; high reed density: prob. of survival = 0.97, 95% CI: 0.83–0.99). At the end of the experiment, the Gosner stage of tadpoles ranged between 27 and 46. Tadpoles with Gosner stages < 37 (early stages) and Gosner stages 37 to 40 (intermediate stages) occurred more often under medium ($\beta_{\text{medium vs. control}}$: –0.95, 95% CI: –1.78 to –0.12) and high reed densities ($\beta_{\text{medium vs. high}}$: –0.95, 95% CI: –1.77 to –0.13), relative to the control (Figure 1). Conversely, late developmental stages (Gosner stages > 40) occurred more often under control than under medium and high reed densities. No differences occurred between medium and high reed densities (Figure 1).

The effect of reed density on tadpole body length did not differ with developmental stage (i.e., tadpole stage × reed density interaction, $F_{4,\ 109} = 0.43$, $p = 0.79$). Tadpole length varied with the developmental stage group (i.e., early, intermediate, late stages; $F_{2,\ 109} = 13.57$, $p < 0.001$). Nonetheless, after accounting for tadpole developmental stage, there were no differences in length among treatments within each stage (reed density, $F_{2,\ 4} = 0.61, p = 0.59$).

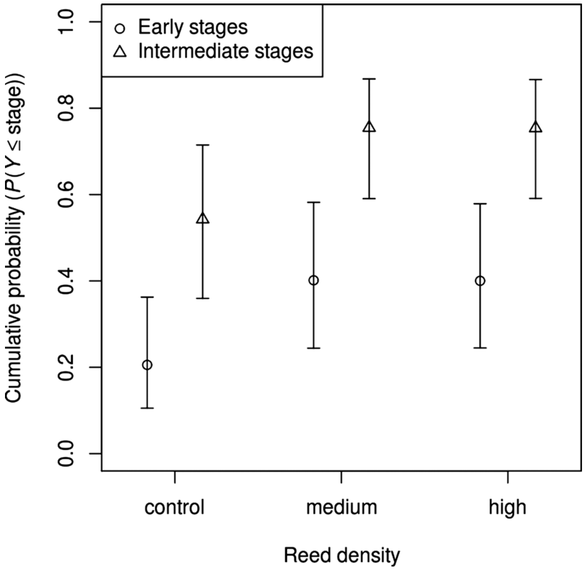

Figure 1. Probabilities of having tadpoles in early, intermediate and later stages in enclosures at different reed densities and in control. Notes: The probability of having tadpoles in early (Gosner stage ≤ 37) and intermediate (37 < Gosner stage ≤ 40) developmental stages was greatest in enclosures at medium and high reed densities. Conversely, the probability of having tadpoles in the later stages (group 3, Gosner stage > 40) is greatest in the control (not shown). Estimates were obtained from ordinal logistic regression with random intercepts and error bars denote 95% CI.

Water quality

There were no interactive effects between reed density and date in any of our water quality analyses. Reed density in our enclosures did not influence the water quality variables measured, whereas phenolic concentration and water conductivity varied with sampling date (Table 1). Water conductivity at the end of the experiment was lower than during the first two sampling periods (Table 1). The total phenolic concentration was lower early in the experiment than at the end (Table 1). Water pH was neither influenced by reed density nor sampling date (Table 1).

Table 1. Sequential ANOVA table (Type I) of the linear mixed model on water characteristics under different reed densities (control, medium, and high) and dates in mesocosms.

Response variable	Source	*F*	df1, df2	*p*
Phenols (mg/L GAE)	Treatment	1.93	2, 10	0.20
	Date	11.27	1, 10	0.007
	Treatment × Date	1.39	2, 10	0.29
Conductivity (S/m)	Treatment	0.07	2, 4	0.93
	Date	77.09	2, 12	<0.001
	Treatment × Date	0.53	4, 12	0.72
pH	Treatment	0.25	2, 4	0.79
	Date	2.02	2, 12	0.18
	Treatment × Date	0.07	4, 12	0.99

Phytoplankton community

We recorded 33 phytoplankton species or genera in our samples (Table 2), with representatives of eight algal divisions: Chlorophyta (green algae), Cyanophyta (blue-green algae), Bacillariophyta (diatoms), Chrysophyta (golden brown algae), Cryptophyta, Xanthophyta (brown algae), Euglenophyta (euglenoids), and codonellids (ciliates). The most abundant species were *Pseudanabaena limnetica* and *Cryptomonas erosa*. We counted 29, 23, and 24 different species for the control, medium, and high reed density treatments, respectively. Seven species were exclusive to the control and four were found only in the reed treatments. An average of 15.6 species (standard error = 0.31) were found in a given sample, and cell concentration ranged between 480 cells/mL and 3017 cells/mL.

We conducted analyses on each of the phytoplankton groups, except for Xanthophyta, which were too rare. The effect of reed density varied with date for Cyanophyta (reed density × date interaction, $F_{2,10} = 4.16$, $p = 0.048$, Table 3). Specifically, the abundance of Cyanophyta differed most between the two sampling dates at moderate reed densities (Figure 2a). Cyanophyta were generally more abundant in the control than either the medium or high reed density treatments, whereas Chlorophyta were most abundant in the control (Figure 2b). Euglenophyta were less abundant in both control and medium reed density than in high reed density treatments (Figure 2c). The other phytoplankton groups did not vary with reed density. Most groups varied in abundance with date. For instance, Chlorophyta and Euglenophyta appeared in greater abundance later in the season, whereas Bacillariophyta and Cryptophyta were most abundant early in the season (Table 3). Codonellids did not vary with either reed density or sampling date.

Table 2. Algal taxa found in samples in mesocosms with different reed densities taken 30 days and 41 days after the start of the experiment.

Taxa	Genera-species	Taxa	Genera-species
Chlorophyta	*Chlamydomonas* sp.[‡]	Bacillariophyta	*Achnanthes microcephala*[†]
	Carteria sp.		*Astrerionella Formosa*
	Cosmarium sp.		*Cocconeis placentula*
	Eudorina elegans		*Epithemia zebra*
	Scenedesmus abundans var. *brevicauda*[†]		*Fragilaria capucina* var. *rumpens*[†]
	Scenedesmus dimorphus[†]		*Fragilaria nanana*[†]
	Spirogyra sp.[†‡]		*Gomphonema constrictum* var. *capitatum*[†]
Cryptophyta	*Cryptomonas erosa*[‡]		*Gomphonema parvulum*[†]
Xanthophyta	*Mallomonas* sp.		*Gomphonema* sp.[†]
Cyanophyta	*Anabaena* sp.[§]		*Navicula radiosa*[†]
	Chroococcus turgidus		*Navicula* sp.[†]
	Dactylococcopsis raphidioides		*Nitzschia clausii*[†]
	Pseudanabaena limnetica[†]		*Nitzschia palea*[†]
	Woronichinia neageliana		
Chrysophyta	*Mallomonas* sp.		
Euglenophyta	*Euglena* sp.		
	Phacus sp.		
	Trachelomonas charkawiensis		
Codonellidae	*Tintinnopsis* sp.		

Notes: Symbols denote genera found in tadpole guts in three different studies: [†]Brown et al. (2006), [‡]Waringer-Löschenkohl and Schagerl (2001), [§]Pryor (2003).

Table 3. Sequential ANOVA table (Type I) of the linear mixed model on log-transformed phytoplankton abundance under different reed densities (control, medium, and high) and dates in experimental mesocosms.

Phytoplankton group	Source	*F*	df1, df2	*p*
Cyanophyta	Treatment	15.07	2, 10	0.001
	Date	26.92	1, 10	<0.001
	Treatment × Date	4.16	2, 10	0.048
Chlorophyta	Treatment	6.61	2, 4	0.054
	Date	10.78	1, 6	0.017
	Treatment × Date	1.42	2, 6	0.313
Bacillariophyta	Treatment	0.83	2, 10	0.464
	Date	4.33	1, 10	0.064
	Treatment × Date	0.63	2, 10	0.552
Cryptophyta	Treatment	1.73	2, 10	0.223
	Date	10.81	1, 10	0.008
	Treatment × Date	1.46	2, 10	0.278
Euglenophyta	Treatment	7.39	2, 10	0.010
	Date	16.69	1, 10	0.002
	Treatment × Date	2.94	2, 10	0.100
Codonellids	Treatment	0.77	2, 10	0.489
	Date	1.37	1, 10	0.269
	Treatment × Date	1.86	2, 10	0.206

Discussion

The results of our field experiment showed that the presence of the common reed can increase the duration of wood frog larval development. Indeed, we observed that tadpoles in the medium and high reed densities were in earlier developmental stages than those in the control. In contrast, a study on the invasive reed canary grass, *Phalaris arundinacea*, reported the opposite trend for wood frogs, with tadpoles under high grass densities reaching metamorphosis more quickly than under low grass densities (Rittenhouse 2011). For pond-breeding amphibians such as wood frogs, the larval stage is the most vulnerable phase because mortality in preterrestrial stages is high (Wilbur 1980).

Phragmites australis disrupts wetland hydrology by reducing the water level (Windham and Lathrop 1999). Thus, lengthening tadpole development in natural environments can decrease the probability of survival due to a prolonged exposure to threats such as predation, decreasing water level or pond drying, especially during dry years. On the other hand, a prolonged period of larval development can lead to larger size at metamorphosis and increased survival of individuals in the terrestrial life stages (Altwegg and Reyer 2003). Larval amphibians have plastic responses to perceived threats such as predators and shortened hydroperiod (Morey and Reznick 2004, but chemical cues released from reed shoots are apparently not perceived as a threat by wood frog tadpoles. We observed high survival rates for tadpoles in all treatments in this short-term experiment on reed establishment; however, differences may occur in the longer term, particularly for species with larval development spanning two seasons.

Water characteristics influence frog larval development (Pierce 1985) and we hypothesized that the water quality would vary with the reed density. However, our results showed that the water chemistry changed little across treatments. Like many plants, *P. australis* exudes secondary compounds to reduce competition with other plants. These allelopathic substances are phytotoxic to ‘non-coevolved neighbors’ (Callaway and

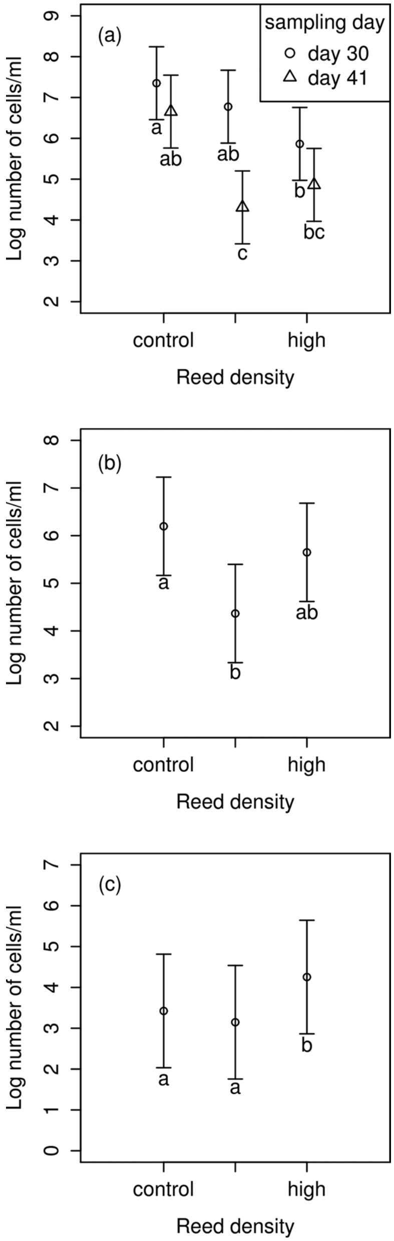

Figure 2. Effect of reed density on the abundance (±95% CI) of Cyanophyta (a), Chlorophyta (b), and Euglenophyta (c) within experimental mesocosms. Notes: Means across treatments are computed for day 41, and the differences between groups were assessed with Tukey's multiple comparisons (grouping indicated with lowercase letters).

Aschehoug 2000). We did not detect a difference in phenolic concentrations among the treatments, such as those reported by Maerz, Brown, et al. (2005) or Brown et al. (2006) in their studies of *Lythrum salicaria* on American toads (*Anaxyrus americanus*) and gray treefrogs (*Hyla versicolor*). We used living material, as opposed to the decaying or dried material (senescent leaves) that was used in the studies cited above. The concentration of phenolic compounds in leachates from litter of some plant species is higher than from green leaves (Kuiters 1990). Interestingly, the phenolic concentrations in our control (no reed) treatment on the two dates of measurement averaged 2.7 mg/L and 3.98 mg/L, respectively. These concentrations exceed those reported for the native plant *Typha latifolia* used as a control by Maerz, Brown, et al. (2005) in their study of *A. americanus* development. The latter study found no difference in tadpole performance between the native plant control and water. Maerz, Brown, et al. (2005) reported that secondary phenolic compounds of *Lythrum salicaria*, at average concentrations of 15.73 mg/L, decreased tadpole survival. In a concurrent study, we measured phenol concentration in common reed stands ($n = 4$ wetlands) and *T. latifolia* stands ($n = 4$ wetlands), with mean concentrations (±SD) of 4.17 ± 1.78 mg/L and 4.01 ± 1.13 mg/L, respectively (Perez, unpublished data).

Maerz et al. (2010) and Cohen et al. (2012) indicated that plant traits such as concentrations of phenolic compounds in dead leaves or litter decomposition rate are more indicative of effects on larval amphibians than plant origin per se. The exotic common reed modifies wetland hydrology and vegetation structure (Windham and Lathrop 1999). Among the species investigated, Maerz et al. (2010) reported slower decomposition rates for dead leaves of the exotic species (haplotype M) than the native reed species. Furthermore, Maerz et al. (2010) reported longer mean larval periods, lower mass at metamorphosis, and fewer metamorphosed individuals of larval wood frogs in the presence of exotic reed detritus than in the presence of common reed detritus. These results are consistent with our findings on living reed biomass.

Our prediction that phytoplankton abundance would decrease with invasive plant density was only partially confirmed. At medium and high densities, invasive reed tended to reduce the abundance of some algal groups, such as Cyanophyta, with species such as *Pseudanabaena limnetica* and *Anabaena* sp. Both are components of tadpole diets (Pryor 2003; Brown et al. 2006). Algae are the main diet for wood frog tadpoles during development, so a shift in algal community composition and abundance can influence tadpole development, survival, growth rate, and their community interactions (Kupferberg et al. 1994). Despite the elevated abundance of certain phytoplankton groups under high reed densities, tadpole development was slower than under low reed densities. These results might be due to a combination of reduced prey items (e.g., Cyanophyta) and behavior. Indeed, tadpoles modify their activity in the presence of certain chemical cues from predators or conspecifics (Eklöv 2000; Pearl et al. 2003). Common reed potentially emit nonlethal compounds other than phenols that influence behavior without decreasing survival per se and this could explain the slower development in the presence of reed.

In a recent experiment, Rogalski and Skelly (2012) reported positive effects of reed litter on bullfrog (*Lithobates catesbeianus*) development, namely higher survival, larger final mass, and later developmental stage in the reed treatment relative to the control. These results suggest that the effect of reed establishment on amphibians is complex and potentially varies across the stage of invasion and species. However, this hypothesis remains speculative and should be addressed formally.

The introduction of invasive plants can have direct or indirect effects on animal populations (Maerz, Blossey, et al. 2005; Brown et al. 2006; but also see Rittenhouse 2011). Common reed litter decomposes slowly and only 85% of the dead stems will decay within one year (Belova 1993). Litter accumulation increases with stand age: litter biomass in a 20-year-old common reed stand can be twice that of a stand aged five years (Rooth et al. 2003). This suggests that a mature reed population will have a greater influence on tadpole larval development and on its habitat (e.g. water quality, food availability) than a recent invasion. In support of this hypothesis, Hunter et al. (2006) reported lower fish abundance in sites recently invaded by common reed than in sites at later stages of invasion. Wood frogs have a rapid larval development, but the impact of common reed establishment is potentially greater for species that breed later in the season and for species with development spanning over two seasons. However, bullfrogs do not seem to follow this pattern, as the performance of their tadpoles in the presence of reed litter is greater than with the litter of native species (Rogalski and Skelly 2012).

In this field experiment, we showed that the live biomass of reed recently established in freshwater wetlands negatively impacts tadpole development, namely by extending the developmental period. Although we did not observe effects on tadpole survival or size, phytoplankton groups known to be consumed by tadpoles were less abundant under high reed densities. Given that the common reed disrupts wetland hydrology, we predict that reed establishment will have the greatest effect on larval development during dry years.

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