2017

Response of Amphibian and Invertebrate Communities to Wetland Mitigation in the Greater Yellowstone Ecosystem

Leah K. Swartz
University of Montana

RESPONSE OF AMPHIBIAN AND INVERTEBRATE COMMUNITIES TO WETLAND
MITIGATION IN THE GREATER YELLOWSTONE ECOSYSTEM

By

LEAH KLAER SWARTZ

B.S. University of Montana, Missoula, Montana, 2012

Thesis

Presented in partial fulfillment of the requirements for the degree of

Master of Science in Wildlife Biology

The University of Montana
Missoula, MT
2017

Approved by:

Scott Whittenburg, Dean of the Graduate School
Graduate School

Dr. Winsor H. Lowe
Division of Biological Sciences

Dr. Blake R. Hossack
U.S. Geological Survey

Dr. Lisa A. Eby
Wildlife Biology Program, Department of Ecosystem and Conservation Sciences

Swartz, Leah K., M.S., 2017
Wildlife Biology

Response of amphibian and invertebrate communities to wetland mitigation in the Greater Yellowstone Ecosystem

Chairperson: Dr. Winsor H. Lowe

ABSTRACT

Wetlands play a critical role in supporting freshwater biodiversity and ecosystem services, but human activities have resulted in large-scale loss and degradation of these habitats across the globe. To offset the decline of wetland area, mitigation wetlands are now frequently constructed, but their ability to replace the functions of natural habitats, including providing habitat for native fauna, remains uncertain. A recent highway reconstruction project in northwestern Wyoming caused impacts to and the destruction of multiple natural wetlands. To mitigate this loss, new wetlands were constructed along the highway corridor. To evaluate the performance of these created wetlands relative to reference (not affected by road construction activities) and impacted wetlands (impacted but not destroyed by road construction), I measured habitat variables, sampled aquatic invertebrates, and conducted repeated counts of amphibian larvae and Columbia spotted frog egg masses. My findings indicate that taxonomic richness of macroinvertebrates was lower in created wetlands than impacted or reference wetlands, with similar richness in impacted and reference wetlands. Age of constructed wetlands was positively correlated with taxonomic richness of invertebrates, but no relationship existed between richness and wetland isolation. The most important environmental variable related to macroinvertebrate richness was percent cover of aquatic vegetation, with the number of taxa positively correlated with vegetation cover. Community composition of invertebrates in created wetlands differed from that in reference and impacted sites, with created wetlands lacking some passive dispersers. Amphibians exhibited species-specific responses to wetland creation, with tiger salamander, boreal toad, and boreal chorus frog larvae occurring at higher densities in created wetlands than reference and impacted wetlands. Columbia spotted frogs exhibited the opposite response, occurring at higher densities in reference and impacted wetlands than created wetlands. Early drying of created wetlands resulted in catastrophic reproductive failure on several occasions, potentially resulting in an ecological trap or population sink for amphibians. Impacted wetlands were similar to reference wetlands in habitat characteristics, invertebrate, and amphibian communities, highlighting the resiliency of natural wetlands to minor disturbance. Managers with the goal of benefitting native wildlife species should take into account the life history requirements (e.g. minimum hydroperiod) of all target species when creating and restoring wetlands.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

CHAPTER 1: RESPONSE OF AQUATIC MACROINVERTEBRATE COMMUNITIES TO WETLAND MITIGATION IN THE GREATER YELLOWSTONE ECOSYSTEM

ABSTRACT

Wetlands play a critical role in supporting freshwater biodiversity and ecosystem services, but human activities have resulted in large-scale loss and degradation of these habitats across the globe. To offset the decline of wetland area, mitigation wetlands are now frequently constructed, but their ability to replace the functions of natural habitats remains uncertain. For instance, wetlands provide important habitat for aquatic organisms, including macroinvertebrates. However, post-construction monitoring of mitigation wetlands often focuses exclusively on aquatic vegetation and physical characteristics, assuming that aquatic species will be present if suitable habitat restoration is achieved. To mitigate impacts to natural wetlands caused by recent road reconstruction project in the southern Greater Yellowstone Ecosystem, the Wyoming Department of Transportation created new wetlands along the highway corridor. From 2013 to 2015, I sampled aquatic invertebrates in 10 created wetlands and 7 wetlands that were impacted but not destroyed by road construction activities. I compared these to 13 reference wetlands. I used the program SPECRICH to estimate invertebrate taxonomic richness and non-metric multidimensional scaling to examine differences in community composition. I also used linear mixed effects and generalized linear models to test for the effect of wetland design features (wetland age, isolation, depth, vegetation, size, and pH) on invertebrate richness. My findings indicate that taxonomic richness of macroinvertebrates was lower in created wetlands than impacted or reference wetlands, with similar richness in impacted and reference wetlands. Age of constructed wetlands (range $= 0 - 10$ years) was positively correlated with taxonomic richness, but no relationship existed between richness and wetland isolation. The most important environmental variable related to taxonomic richness was percent cover of aquatic vegetation, with the number of taxa positively correlated with vegetation cover. Community composition of invertebrates in created wetlands differed from that in reference and impacted sites, with created wetlands lacking some passive dispersers. Overall, constructed wetlands harbored a diminished and altered subset of the invertebrates found in both reference and impacted wetlands, casting doubt on their ability to replace the structure and function of natural wetlands within the short time period required by mitigation permits.

INTRODUCTION

Freshwater wetlands perform numerous essential abiotic and biotic functions, including water purification, flood protection, carbon storage, and providing habitat for diverse flora and fauna (Contanza et al. 1997). Human activities such as urban development, agriculture, and road construction have caused a large-scale reduction in wetland area worldwide (Zedler and Kercher 2005). Of the estimated 89 million acres of wetlands present in the contiguous United States in the 1780s, over half have been drained, dredged, or filled (Johnston 1994). Conservation education and legislation have slowed this trend in recent years (Dahl 2011), and mitigation of wetland loss due to large scale projects such as road construction and industrial development is now required under Section 404 of the Clean Water Act (Hough and Robertson 2008). Today, the Section 404 permitting process is largely guided by the 1989 executive policy of "no net loss": loss of wetlands area and function must be mitigated by an equal or greater number of acres of gain, achieved either through wetland restoration or construction (Turner et al. 2001). In North America alone, over 3,000,000 ha of wetlands have been created or restored in the past 20 years (Copeland 2010). Nevertheless, the capacity of mitigation wetlands to replace natural wetland functions remains uncertain.

Both wetland restoration and creation are used to fulfill Section 404 permitting requirements (Grenfell et al. 2007). Wetland restoration refers to restoring natural wetland structure and function to an area with previous wetland history that has been degraded. Wetland creation refers to the construction of an entirely new wetland in a formerly upland area. Because created wetlands do not have a history of inundation, successional processes are essentially starting from a blank slate. Wetland restoration is generally more successful at replicating the biotic communities and ecosystem services of nearby reference wetlands (Sebastián-González

and Green 2016, Spadafora et al. 2016), but permit conditions often require onsite mitigation through wetland construction.

Evaluating the success of wetland construction projects is challenging. It is logistically and fiscally impossible to monitor all of the factors that contribute to wetland function, and most mitigation wetlands are not monitored at all (GAO 2005). When monitoring does occur, it is typically short term (2 – 5 years), and focuses on the establishment of vegetation and hydric soils, which may be poor surrogates for wetland function (Cole and Shafer 2002). Because invertebrates represent the most diverse taxonomic group within most wetlands and play a critical role in nutrient cycling, they may be good surrogates for comparing function of created and reference wetlands (Balcombe et al. 2005, Ruhí and Batzer 2014).

Many factors may influence colonization of new habitats by wetland invertebrates. First, invertebrate species vary in their ability to disperse to newly created wetlands (Bilton et al. 2001). Active dispersers, such as species with flying adult stages, will likely arrive first, followed by passive dispersers that rely on external vectors like wind or other animals to disperse (Coccia et al. 2016). Distance from a source population and wetland size should influence the likelihood of colonization and persistence of both active and passive dispersers at new wetlands (MacArthur and Wilson 1967). Second, physical habitat characteristics such as depth, vegetation, and water chemistry influence which species can persist. Third, biotic interactions, including predation and competition, might further structure invertebrate communities in newly created wetlands, with predators like fish, amphibians, and invertebrates exerting strong top-down influences (Hanson and Riggs 1993). Invertebrates can quickly colonize newly constructed wetlands and even reach similar levels of richness as nearby reference wetlands in a relatively short period of time (3 – 20 years) (Balcombe et al. 2005, Coccia et al. 2016), but community

composition often remains distinct, even many years after wetlands are constructed (Moreno-Mateos et al. 2012). This is particularly true in cold climates where invertebrate activity is limited to a short ice-free period each year (Moreno-Mateos et al. 2012, Ruhí et al. 2012).

To mitigate wetland impacts associated with the recent reconstruction of Highway 287 over Togwotee Pass between Moran and Dubois Wyoming, the Wyoming Department of Transportation (WYDOT) constructed new wetlands along the highway corridor. This area falls within the Greater Yellowstone Ecosystem, one of the largest nearly intact temperate ecosystems in the world. Wetlands in the GYE comprise only 3% of the total land area, but provide habitat for a disproportionate number of plant, bird, mammal, amphibian, reptile, and invertebrate species (Nicholoff 2003). Despite their importance, wetlands have been understudied in the GYE and throughout the Intermountain West (Copeland et al. 2010).

My objective was to evaluate function of created (n = 10) and impacted (n = 7) wetlands relative to reference (n = 13) wetlands, using macroinvertebrate taxonomic richness and community composition as a proxy. Created wetlands were excavated with heavy equipment down to the water table and planted with a wetland seed mix and willow cuttings. Impacted wetlands are those that sustained impacts from the road construction activities (i.e., modified banks, some filling, erosion control, etc.) but were not completely destroyed. Reference wetlands are those that did not sustain impacts from road construction and thus should provide a good baseline against which to compare constructed and impacted sites.

Because of the short growing season and cold climate of the GYE, I hypothesized that succession in created wetlands would be slower than in more moderate climates (Moreno-Mateos et al. 2012, Ruhí et al. 2012), so I predicted that taxonomic richness would be lower in created wetlands than in reference or impacted wetlands and that community composition would differ.

In addition, I wanted to determine which environmental and design features were correlated with taxonomic richness. I predicted that distance to nearest natural wetland and time since construction would be positively correlated with taxonomic richness in created wetlands. Across all wetland types, I predicted that percent cover of aquatic vegetation, wetland size, and depth would be positively associated with richness, while elevation would be negatively associated with taxonomic richness.

METHODS

Study Area

To assess differences in invertebrate taxonomic richness and community composition among wetland types, I sampled aquatic macroinvertebrates in created, impacted, and reference wetlands (n= 10, 7, 13, respectively) once per year from 2013 to 2015. Wetlands were located in the Bridger-Teton National Forest along highway 287/26 between Moran, Wyoming and Togwotee Pass, 12 km east of Grand Teton National Park, USA (Fig. 1). In 2013 and 2014, I sampled a reduced subset of the wetlands that were sampled in 2015, but I sampled each type of wetland each year (Table 1). In 2015, I sampled all created wetlands that held water, as well as the closest reference and impacted wetlands. Sampled wetlands ranged in elevation from 2,100 to 3,050 m.

Vegetation surrounding wetlands is dominated by conifer forest at higher elevations (lodgepole pine [*Pinus contorta*], whitebark pine [*Pinus albicaulis*], Engelmann spruce [*Picea engelmannii*], and Douglas fir [*Pseudotsuga menziesii*]) and mixed sagebrush (*Artemisia tridentata*) – grassland vegetation at lower elevations. This area is characterized by long, cold winters with heavy snowfall and short, cool summers. Precipitation in Moran averages 59.66 cm

(23.49 in) annually, falling primarily as snow between November and April. Temperatures vary considerably throughout the year, with an average January high temperature of -3.61 C° (25.5 F°) and average July high temperature of 25.3 C° (77.6 F°). Average annual snowfall is 369.57 cm (145.5 in). Snow generally persists until late April or early May at low elevations, and as late as July at the top of Togwotee Pass. Wetlands typically thaw and fill with snowmelt between early May (lower elevations) and early June (higher elevations).

Sampling

To collect a representative sample of invertebrates from created, impacted, and reference wetlands, I conducted nine 1.5 m sweeps using a D-framed net (500 um mesh) in each site (Radar et al. 2001). I conducted two sweeps along each axis of the wetland (north-south and east-west) at a shallow point and a mid-depth point, as well as one in the deepest part of the wetland. I sampled all wetlands in late July when invertebrate diversity should be highest and immature invertebrates should be developed enough for identification (Duffy 1999). Invertebrates from the nine sweeps were pooled into a single container and preserved in 70% ethanol for later identification to the lowest taxonomic level practical by Montana Ecoservices (2536 S Dennis St, Kennewick, WA 99337) (Merritt and Cummins 1996, Wiggins 1996, Larsen et al. 2000).

Because wetland invertebrates in the western United States have received relatively little research attention, keys for the larval stages of many species do not exist. Amphipoda, Mollusca, Ephemeroptera, and Coleoptera were identified to genus level, while Diptera, Hemiptera, Odonata, and Hirundinea were identified to family level. Collembola, Oligochaeta, and Hydracarina were not identified to lower taxonomic levels. When some members of a group were identified to a lower taxonomic level than others, I aggregated to the higher taxonomic

level so resolution was consistent across all sites. For example, snails of the genus *Lymnaea* were sometimes identified to species (*Lymnaea elodes* and *Lymnaea stagnalis*) but could sometimes only be assigned to the genus due to immature or damaged specimens. For consistency among sites, I lumped them all to genus.

Based on a literature review, I developed an *a priori* suite of environmental and design characteristics that I hypothesized would influence richness and composition of wetland invertebrate communities. I measured total wetland area and wetted wetland area using the area estimation tool in a Garmin e-trex Global Position System (GPS). I defined total wetland area as the high-water line or boundary of wetland creation disturbance (i.e., willow plantings in created wetlands). Wetted wetland area was the portion of the wetland that held water in early June when wetlands achieved their maximum size. Elevation was also recorded from a GPS unit. Distance to nearest reference wetland was calculated using the line measurement tool in Google Earth (version 7.1.7.2606). I measured maximum depth of each wetland at the same time as wetted wetland area. I measured pH biweekly using a YSI Multimeter (Model 63). I sampled vegetation within the same week that I collected invertebrate samples in late July, using a 1-m squared quadrat every 80 meters along the wetland shore, both at 1 m and 5 m out from the shore. In each quadrat, I estimated percent cover of aquatic vegetation. I also recorded presence of fish when they were detected.

Data Analysis

Taxonomic richness

I estimated taxonomic richness for each wetland using the program SPECRICH (Hines 1996). SPECRICH uses observed relative abundance of each taxonomic group to calculate estimated

richness and standard error, while accounting for heterogeneous detection probabilities among taxa (Burnham and Overton 1979). One advantage to this method is that because SPECRICH only requires counts ranging from one to five, considerable time and resources can be saved over traditional species richness estimators, which use raw counts and assume homogeneous detection probabilities.

Difference in richness among wetland types

I tested for differences in log-transformed taxonomic richness among wetland types using a linear mixed effects model implemented in the R package *nlme* (Pinheiro et al. 2016) with wetland type and standardized elevation as explanatory variables. I included site as a random effect to account for repeated sampling of some wetlands over multiple years. I included elevation in all models as a nuisance covariate since it is not strictly a design feature, but should have strong effects on richness due to differences in growing season length and temperature across elevation gradients (Rahbek 1995).

Effects of environmental and design features on richness

To assess the influence of habitat features on invertebrate taxonomic richness, I used only the data from 2015 because we did not measure the full complement of environmental variables in previous years. I fit multiple generalized linear models (GLMs), using backwards selection, to determine which variables best explained variation in richness. Because wetted wetland area was often considerably less than total wetland area, particularly for created wetlands, I used wetted wetland area in these models. All pairwise correlations between explanatory variables were below the $|r| = 0.7$ threshold that is typically used to identify redundant variables in regression analyses (Dormann et al. 2013). The only two variables that approached this threshold were

elevation and wetland area (Pearson's r = -0.62). Because elevation was considered a nuisance variable, I left it in all models. Maximum depth appeared to have a quadratic relationship with taxa richness, so I added a squared term to the model. Starting with a global model that included elevation, wetted wetland area, maximum depth, maximum depth squared, pH, and percent cover of aquatic vegetation, I performed backwards selection, removing variables with the least partial significance until only significant variables remained ($p < 0.1$).

Wetland age and distance to nearest natural wetland

For created wetlands only, I used linear mixed effects models to test for effects on species richness of wetland age and distance to nearest natural (reference or impacted) wetland using data from all years. Again, site was included as a random effect to account for repeated sampling of some sites over multiple years and standardized elevation was included a nuisance covariate. I also included a quadratic term on wetland age to test for a leveling off of richness over time.

Multivariate analysis of community composition

To compare species assemblages among wetland types, I constructed Bray-Curtis community dissimilarly matrices based on rank orders of species abundance data from each wetland. I used non-metric multi-dimensional scaling (NMDS) implemented in the R package *vegan* (Oksanen et al. 2017) to visualize differences. Because there is no way to account for repeated sampling of some wetlands over multiple years in NMDS, I used only the data from 2015 when the full suite of wetlands was sampled. Next, I conducted an indicator species analysis to investigate which taxonomic groups were driving observed differences in community composition among wetland types (Dufrêne and Legendre 1997). This method calculates indicator values as a product of the relative frequency and relative average abundance (in this

case, rank order) for each taxonomic group in each wetland type. Indicator values range from 0 to 1, with values of 1 indicating perfect association with a particular wetland type. Indicator values were tested for statistical significance using a Monte-Carlo permutation test with 1000 iterations. All statistical analyses were completed in Program R version 3.3.2 (R Core Team 2016).

RESULTS

Taxonomic richness

Seventy-five invertebrate taxa from 13 orders were identified in our wetland samples (Appendix 1). Observed richness ranged from 5 to 25 invertebrate taxa per wetland and estimated richness ranged from 6 to 51.63 invertebrate taxa per wetland. The mixed effects model showed that after accounting for elevation, reference (mean = 21.40, 95% CI = 17.98, 25.47) and impacted (mean = 18.46, 95% CI = 14.32, 23.80) wetlands had significantly higher taxonomic richness than created wetlands (mean = 15.76, 95% CI = 12.99, 19.13) (Table 2, Figure 2). I found strong evidence that invertebrate richness declined with elevation, with an estimated 11 more taxonomic groups of invertebrates at the lowest elevation wetlands (2100 m) than the highest elevation wetlands (3050 m).

Effects of environmental and design features on invertebrate richness

On average, created wetlands were shallower than reference or impacted wetlands and three out of ten were dry or nearly dry by the end of July 2015 (Table 3). No reference or impacted wetlands dried over the same time period. Created wetlands also had smaller surface areas, lower mean percent cover of aquatic vegetation, and slightly higher pH than reference wetlands. There were no major differences in habitat variables between reference and impacted

wetlands (Table 3). Fish were detected in two impacted and one reference wetland, all of which were permanent and had a stream or river connection. Other than fish, adult amphibians, particularly barred tiger salamanders (*Ambystoma mavortium*), and predatory invertebrates were the dominate predators in these wetlands.

After accounting for elevation, the top model describing the influence of habitat features on taxonomic richness across all wetland types in 2015 only included percent cover of aquatic vegetation (Table 4). Invertebrate richness was positively correlated with percent cover of aquatic vegetation.

Wetland age and distance to nearest natural wetland

Within created wetlands, after accounting for elevation, I found no evidence that taxonomic richness increased with wetland age (Table 5). However, examination of the residual plot showed that one wetland was an outlier, with much lower species richness than others at similar elevations. I removed this outlier from the dataset and ran the model again. Based on the remainder of sites, taxonomic richness increased with wetland age (Figure 3, Table 6). A quadratic effect of wetland age was not supported. Created wetlands were constructed on average 274.4 meters away from the nearest natural wetland (SD = 156.77 meters). I did not find evidence of a relationship between distance to nearest natural wetland and taxonomic richness (Table 7).

Multivariate analysis of community composition

Consistent with lower richness, communities in created wetlands clustered separately from communities in reference and impacted wetlands in the NMDS plot (Figure 4). This

indicates that invertebrate communities in created wetlands were compositionally different from those in reference wetlands, while those in impacted wetlands were similar to reference wetlands. The stress value (0.21) on two axes of ordination was at the upper end of the acceptable range (Clarke and Warwick 2001), indicating some lack of fit. Increasing the number of dimensions to three reduced stress to 0.14, but since the interpretation was the same between the two plots I decided to present the two-dimensional solution for easier visual interpretation. Reference wetlands were the most similar to one another in community composition, with much larger 95% confidence ellipses around created and impacted wetlands.

Indicator species analysis also highlighted differences in community composition among wetland types (Table 8). Because based on the NMDS ordination, communities in reference and impacted wetlands were so similar, I grouped these wetland types together for this analysis. Three taxa, Notonectidae (backswimmers, order Hemiptera), *Berosus,* and *Helophorus* (order Coleoptera) were identified as indicators of created wetlands. *Berosus* and *Helophorus* were only found in three wetlands each, but were exclusively found in created wetlands, while Notonectidae was found in eight wetlands (five created, one impacted, and two reference). In contrast, five taxa were identified as indicators of reference/impacted wetlands: *Pisidium* (pea clams, order Veneroida), Chaoboridae (phantom midges, order Diptera), Oligochaeta (aquatic worms), *Procloeon* (mayfly, order Ephemeroptera), and Hydracarina (water mites). Of these, *Pisidium* was the strongest indicator –of the 17 wetlands where it was found, only one was a created wetland (Quarry).

DISCUSSION

Understanding the capacity of created mitigation wetlands to support the full range of native species is critical, especially as natural wetlands continue to be modified and destroyed. I sampled the invertebrate community along a highway corridor in northwest Wyoming to compare taxonomic richness and community composition among created, impacted, and reference wetlands. Created wetlands had fewer macroinvertebrate taxa than reference wetlands, while impacted wetlands had intermediate richness values, but were not significantly different from reference wetlands. Community composition also differed between created and reference wetlands, but not between reference and impacted wetlands.

I also measured and tested for the effects of habitat features including wetland size, depth, pH and aquatic vegetation on invertebrate taxonomic richness across all wetland types. Created wetlands were shallower, had less aquatic vegetation, and had slightly higher pH than reference wetlands, while impacted wetlands were similar to reference wetlands in all measured environmental variables. Increasing elevation was associated with reduced taxonomic richness across all wetland types, likely due to shorter growing seasons and harsher conditions at higher elevations (de Mendoza and Catalan 2010). After accounting for elevation, the model that best explained differences in richness across wetland types included just percent cover of aquatic vegetation as an explanatory variable.

With the exception of one outlier, I found strong evidence that invertebrate richness in created wetlands increased with wetland age. This pattern is likely due to vegetation establishment as wetlands develop and a time lag for some taxa to colonize new ponds (Ruhí et al. 2013, Coccia et al. 2016). The importance of aquatic vegetation in structuring invertebrate communities is a common result across studies of invertebrates in constructed wetlands (Stewart

and Downing 2008, Ruhí et al. 2016). Increasing aquatic vegetation may allow more species to persist by providing structural habitat, food resources, and predator refuge (Batzer et al. 1999).

Most studies examining invertebrate response to wetland mitigation have been conducted in areas with warm climates (Balcombe et al. 2005, Ruhí et al. 2009, Batzer et al. 2015). In contrast, the GYE is characterized by long winters and wetlands are only ice-free for a few months out of the year, which might slow dispersal and establishment in newly created wetlands. In cold climates, invertebrate communities in created wetlands may take longer to converge with reference sites (Ruhí et al. 2012). The lack of support for a quadratic effect of wetland age indicates that even 8 to 10 years after wetland construction, taxonomic richness had not equilibrated. This implies that perhaps mitigation wetlands constructed in cold climates should be monitored for longer than wetlands in warmer climates.

Consistent with lower taxonomic richness in created wetlands, NMDS ordination showed that community composition differed between created wetlands and reference wetlands, while impacted wetlands had similar communities to reference wetlands. Notably, the indicator taxa for reference and impacted wetlands included 3 groups without flying adult stages (Pisidium, Oligochaeta, and Hydracarina). While some species of Hydracarina (water mites) are known to parasitize adult winged insects (Smith and Cook 1991), these taxa may be limited in their potential to colonize new wetlands by their weak dispersal ability. Oligochaeta (aquatic worms) and Pisidium (pea clams) require hydrologic connectivity or an external vector to colonize newly constructed wetlands. Supporting this result, the only created wetland where we found Pisidium is the second oldest in the study area (Quarry) and was constructed relatively close to nearby natural wetlands. Quarry is also frequented by waterfowl, which often transport aquatic invertebrates among sites (van Leeuwen et al. 2012).

I included impacted wetlands in this study because development does not always cause complete destruction of a wetland, but often destroys or impairs of just a small portion of the site. One important finding from this research was that impacted wetlands did not differ significantly from natural wetlands in physical habitat characteristics, invertebrate richness, or invertebrate community composition. This result suggests that natural wetlands can be quite resilient to some disturbance and if the impact is minimal (i.e. <25% of the perimeter), wetlands retain their functionality. This result also supports current policies that encourage developers to avoid and minimize impacts to existing wetlands whenever possible, rather than relying on wetland construction to mitigate destruction of natural wetlands.

Beyond climate, wetland hydroperiod is one of the most important drivers of community composition of wetlands (Wellborn et al. 1996, Ray et al. 2016). In my study area, created wetlands were designed to have temporary – intermediate hydroperiods and were much shallower than nearby reference and impacted wetlands (Table 3). In 2015, eight out of ten created wetlands dried partially (i.e. at least one isolated waterbody dried completely) and one created wetland dried completely by late July while no reference or impacted wetlands dried in this same time frame. Therefore, I was surprised to find little support for the effects of depth on invertebrate richness across wetland types. In the Intermountain West, shallow wetlands are expected to be more vulnerable to drying under future climate change, reinforcing the importance of designing mitigation wetlands that are deep enough to be resilient to climatic fluctuations, which can function as refuges for aquatic biota as natural wetlands continue to disappear (Corn et al. 2003, Brooks 2009, Hossack et al. 2013, Sepulveda et al. 2015).

Interestingly, the outlier that I removed (Swan Pond) because it had much lower taxonomic richness than other wetlands is also the oldest created wetland in my study area

(constructed in 2005), is at low elevation, and is located less than 300 meters away from the created wetland (Quarry) with the highest taxonomic richness across all wetlands. Constructed in 2008, Quarry is the second oldest created wetland in my study area. Differences between these two sites are obvious: Quarry has abundant emergent and submersed aquatic vegetation and holds water throughout the summer months. In contrast, Swan Pond has very little aquatic vegetation and is controlled by a ditch coming directly from the creek. Consequently, Swan Pond has extremely variable annual hydroperiods and much colder water than other sites. This dichotomy clearly illustrates the importance of design features in addition to time since construction in controlling the invertebrate communities that reside in created wetlands.

Overall, wetland creation has the potential to offset negative effects of wetland loss on freshwater biodiversity, but it is still unclear whether constructed wetlands can replicate the structure and function of lost reference wetlands. This study provides further evidence that wetland invertebrates are capable of rapidly colonizing newly constructed wetlands, but that diversity and community composition within constructed wetland may take many years to converge with nearby reference wetlands, particularly in areas limited by harsh climatic conditions and short growing seasons. Wetlands impacted by road construction retained similar invertebrate communities to reference wetlands, suggesting that wetlands can be resilient to some human impact.

LITERATURE CITED

Balcombe, C. K., J. T. Anderson, R. H. Fortney, and W. S. Kordek. 2005. Aquatic macroinvertebrate assemblages in mitigated and natural wetlands. Hydrobiologia 541:175–188.

Batzer, D. P., R. B. Rader, and S. A. Wissinger, editors. 1999. Invertebrates in freshwater wetlands of North America: Ecology and Management. John Wiley and Sons.

Batzer, D. P., B. E. Taylor, A. E. DeBiase, S. E. Brantley, and R. Schultheis. 2015. Response of Aquatic Invertebrates to Ecological Rehabilitation of Southeastern USA Depressional Wetlands. Wetlands 35:803–813.

Bilton, D. T., J. R. Freeland, and B. Okamura. 2001. Dispersal in Freshwater Invertebrates. Annual review of Ecology and Systematics 32:159–181.

Brooks, R. T. 2009. Potential impacts of global climate change on the hydrology and ecology of ephemeral freshwater systems of the forests of the northeastern United States. Climatic Change 95:469–483.

Burnham, K., and W. Overton. 1979. Robust estimation of population size when capture probabilities vary among animals. Ecology 60:927–936.

Clarke, K. R., and R. M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition. PRIMER-E, Plymouth UK.

Coccia, C., B. Vanschoenwinkel, L. Brendonck, L. Boyero, and A. J. Green. 2016. Newly created ponds complement natural waterbodies for restoration of macroinvertebrate assemblages. Freshwater Biology 1640–1654.

Cole, C. A., and D. Shafer. 2002. Section 404 wetland mitigation and permit success criteria in Pennsylvania, USA, 1986-1999. Environmental Management 30:508–515.

Contanza, R., R. D'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R. V O'Neill, J. Paruelo, R. G. Raskin, P. Sutton, and M. van den Belt. 1997. The value of the world's ecosystem services and natural captital. Nature 387:253–260.

Copeland, C. 2010. Wetlands: An Overview of Issues.

Copeland, H. E., S. a. Tessman, E. H. Girvetz, L. Roberts, C. Enquist, A. Orabona, S. Patla, and J. Kiesecker. 2010. A geospatial assessment on the distribution, condition, and vulnerability of Wyoming's wetlands. Ecological Indicators 10:869–879. Elsevier Ltd.

Corn, P. S., A. R. Blaustein, T. L. Root, J. M. Kiesecker, L. K. Belden, D. H. Olson, and D. M. Green. 2003. Amphibian breeding and climate change: Importance of snow in the mountains. Conservation Biology 17:622–627.

Dahl, T. 2011. Status and trends of wetlands in the conterminous United States 2004 to 2009. Washington, D.C.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, C. Mcclean, P. E. Osborne, B.

Reineking, B. Schröder, A. K. Skidmore, D. Zurell, and S. Lautenbach. 2013. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:027–046.

Duffy, W. 1999. Wetlands in Grand Teton and Yellowstone National Parks. Pages 733–753 *in* S. A. Batzer, Darold P., Rader, Russell B., Wissinger, editor. Invertebrates in Freshwater Wetlands of North America: Ecology and Management. John Wiley and Sons.

Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecological Monographs 67:345–366.

GAO [US Government Accountability Office]. 2005. Wetlands Protection - Corps of Engineers Does Not Have an Effective Oversight Approach to Ensure That Compensatory Mitigation Is Occurring. Report GAO-O5-898. GAO, Washington DC

Grenfell, M. C., W. N. Ellery, S. E. Garden, J. Dini, and A. G. van der Valk. 2007. The language of intervention: A review of concepts and terminology in wetland ecosystem repair. Water SA 33:43–50.

Hanson, M. A., and M. R. Riggs. 1993. Effects of fish predation on wetland invertebrates: a comparison with and without fathead minnows. Wetlands 15:167–175.

Hines, J. E. 1996. SPECRICH software to compute species abundance from enpirical species abundance distribution data. USGS-PWRC. <http://www.mbr-pwrc.usgs.gov/software/specrich.html>.

Hossack, B. R., M. J. Adams, C. a Pearl, K. W. Wilson, E. L. Bull, K. Lohr, D. Patla, D. S. Pilliod, J. M. Jones, K. K. Wheeler, S. P. McKay, and P. S. Corn. 2013. Roles of patch characteristics, drought frequency, and restoration in long-term trends of a widespread amphibian. Conservation biology 27:1410–20.

Hough, P., and M. Robertson. 2008. Mitigation under Section 404 of the Clean Water Act: where it comes from, what it means. Wetlands Ecology and Management 17:15–33.

Johnston, C. 1994. Cumulative impacts to wetlands. Wetlands 14:49–55.

Larsen, D. J., Y. Alarie, and R. R.E. 2000. Predacious Diving Beetles (Coleoptera: Dytiscidae) of the Neurotic Region. NRC-CNRC, National Research Council of Canada Monograph Publishing Program, NRC Press, Ottawa.

van Leeuwen, C. H. A., G. van der Velde, B. van Lith, and M. Klaassen. 2012. Experimental quantification of long distance dispersal potential of aquatic snails in the gut of migratory birds. PLoS ONE 7.

MacArthur, R. H., and E. O. Wilson. 1967. The Theory of Island Biogeography. Princton University Press, Princton.

de Mendoza, G., and J. Catalan. 2010. Lake macroinvertebrates and the altitudinal environmental gradient in the Pyrenees. Hydrobiologia 648:51–72.

Merritt, R., and K. Cummins. 1996. An introduction to the aquatic insects of North America.

Moreno-Mateos, D., M. E. Power, F. a Comín, and R. Yockteng. 2012. Structural and functional

loss in restored wetland ecosystems. PLoS biology 10:e1001247.

Nicholoff, S. H. 2003. Wyoming bird conservation plan, version 2.0. Lander, WY.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, R. Minchin, Peter, R. . O'Hara, L. Simpson, Gavan, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. 2017. Vegan: Community Ecology Package. R package version 2.4-2.

Radar, R. B., D. P. Batzer, and S. A. Wissinger. 2001. Bioassessment and Management of North America Freshwater Wetlands. John Wiley and Sons, New York.

Rahbek, C. 1995. The elevational gradient of species richness: a uniform pattern? Ecography 18:200–205.

Ray, A. M., W. R. Gould, B. R. Hossack, A. J. Sepulveda, D. P. Thoma, D. A. Patla, R. Daley, and R. Al-Chokhachy. 2016. Influence of climate drivers on colonization and extinction dynamics of wetland-dependent species. Ecosphere 7.

Ruhí, A., and D. P. Batzer. 2014. Assessing Congruence and Surrogacy Among Wetland Macroinvertebrate Taxa Towards Efficiently Measuring Biodiversity. Wetlands 34:1061–1071.

Ruhí, A., D. Boix, S. Gascón, J. Sala, and X. D. Quintana. 2013. Nestedness and successional trajectories of macroinvertebrate assemblages in man-made wetlands. Oecologia 171:545–556.

Ruhí, A., J. Herrmann, S. Gascón, J. Sala, and D. Boix. 2012. How do early successional patterns in man-made wetlands differ between cold temperate and Mediterranean regions? Limnologica 42:328–339.

Ruhí, A., G. Winfield Fairchild, D. J. Spieles, G. Becerra-Jurado, and D. Moreno-Mateos. 2016. Invertebrates in created and restored wetlands. Pages 525–564 *in* D. P. Batzer and D. Boix, editors. Invertebrates in Freshwater Wetlands, An International Perspective on Their Ecology. Springer International Publishing, Switzerland.

Ruhí, a., D. Boix, J. Sala, S. Gascón, and X. D. Quintana. 2009. Spatial and temporal patterns of pioneer macrofauna in recently created ponds: Taxonomic and functional approaches. Hydrobiologia 634:137–151.

Sebastián-González, E., and A. J. Green. 2016. Reduction of avian diversity in created versus natural and restored wetlands. Ecography 39:1176–1184.

Sepulveda, A. J., M. T. Tercek, R. Al-Chokhachy, A. M. Ray, D. P. Thoma, B. R. Hossack, G. T. Pederson, A. W. Rodman, and T. Olliff. 2015. The shifting climate portfolio of the greater Yellowstone area. PLoS ONE 10.

Smith, I. M., and D. R. Cook. 1991. Water mites. Pages 523–592 *in* T. J.H. and A. . Covich, editors. Ecology and classification of North American freshwater invertebrates. Academic Press, San Diego.

Spadafora, E., A. W. Leslie, L. E. Culler, R. F. Smith, K. W. Staver, and W. O. Lamp. 2016. Macroinvertebrate community convergence between natural, rehabilitated, and created

wetlands. Restoration Ecology 24

Stewart, T. W., and J. a. Downing. 2008. Macroinvertebrate communities and environmental conditions in recently constructed wetlands. Wetlands 28:141–150.

Turner, R. E., a M. Redmond, and J. B. Zedler. 2001. Count it by acre or function: Mitigation adds up to net loss of wetlands. National Wetlands Newsletter 23:5–16.

Wellborn, G. a., D. K. Skelly, and E. E. Werner. 1996. Mechanisms Creating Community Structure Across a Freshwater Habitat Gradient. Annual Review of Ecology and Systematics 27:337–363.

Wiggins, G. B. 1996. Larvae of the North American Caddisfly Genera (Trichoptera).

Zedler, J. B., and S. Kercher. 2005. Wetland Resources: Status, Trends, Ecosystem Services, and Restorability. Annual Review of Environment and Resources 30:39–74.

Table 1. Wetlands surveyed for invertebrates each year from 2013 through 2015.

Site	Wetland Type	Year Constructed	Years Surveyed
12DC	Created	2012	2015
13AC	Created	2012	2013, 2014, 2015
16BC	Created	2010	2013, 2014, 2015
19AC	Created	2012	2015
24CC	Created	2012	2015
25AC	Created	2012	2015
26BC	Created	2012	2013, 2014, 2015
ML	Created	2014	2014,2015
QU	Created	2008	2013, 2014, 2015
SP	Created	2005	2013, 2014, 2015
12CI	Impacted	-	2015
15AI	Impacted	-	2013, 2014, 2015
17AI	Impacted	-	2015
17BI	Impacted	-	2013, 2014, 2015
19BI	Impacted	-	2015
25BI	Impacted	-	2013, 2014, 2015
26AI	Impacted	-	2015
16CR	Reference	-	2013, 2014, 2015
17DR	Reference	-	2015
17ER	Reference	-	2013, 2014, 2015
21AR	Reference	-	2015
21BR	Reference	-	2015
21CR	Reference	-	2015
25CR	Reference	-	2013, 2014, 2015
HE	Reference	-	2013, 2014, 2015
MW	Reference	-	2013,2014
ND	Reference	-	2013,2014
OX	Reference	-	2013,2014
RW	Reference	-	2013, 2014, 2015
SD	Reference	-	2015

Table 2. Coefficient estimates from linear mixed model of log invertebrate taxonomic richness by wetland type and elevation. The intercept is the mean taxonomic richness for reference wetlands. Site was included as a random effect to account for sampling some wetlands over multiple years.

	Coefficient	Std. Error	df	t-value	P>t
(Intercept)	1.330	0.039	30	34.042	0.000
Created	-0.133	0.058	26	-2.280	0.031
Impacted	-0.064	0.071	26	-0.912	0.370
Elevation	-0.086	0.027	26	-3.165	0.004

Table 3. Physical habitat characteristics summarized by wetland type, based on data collected in 2015.

Variable	Created (n=10) Mean (sd)	Impacted (n=7) Mean (sd)	Reference (n=10) Mean (sd)
Wetted wetland area (m^2)	2644.7 (3768.83)	5377.71 (3637.66)	3678(3773.19)
Elevation (m)	2515.5 (342.21)	2678.14 (182.54)	2556.8 (329.63
Max depth (cm)	38.35 (25.62)	124.08 (45.59)	111.7 (35.81)
pH	8.46 (0.69)	7.68 (1.08)	7.92 (0.54)
Aquatic vegetation (% cover)	24.07(29.48)	46.43 (33.39)	49.39(33.06)

Table 4. Coefficient estimates and associated standard errors, t-values, and P-values (significant < -.10) from the top model of the effect of habitat variables on log taxonomic richness.

	Coefficient	Std. Error	t-value	P>t
(Intercept)	1.166	0.069	16.882	0.00
Aquatic veg	0.002	0.001	1.848	0.0769
Elevation	-0.038	0.046	0.838	0.410

Table 5. Coefficient estimates from model of log taxonomic richness by wetland age and distance to nearest natural wetlands, after accounting for elevation for created wetlands only, with site as a random effect to account for repeated sampling of some sites over multiple years (Swan Pond included)

	Coefficient	Std. Error	df	t-value	P>t
(Intercept)	1.220	0.110	10	11.129	0.000
Elevation	-0.125	0.065	8	-1.919	0.091
Wetland Age	-0.006	0.025	10	-0.263	0.798

Table 6. Coefficient estimates from model of log taxonomic richness by wetland age and distance to nearest natural wetlands, after accounting for elevation for created wetlands only, with site as a random effect to account for repeated sampling of some sites over multiple years (Swan Pond removed)

	Coefficient	Std. Error	df	t-value	P>t
(Intercept)	1.054	0.085	10	12.303	0.000
Elevation	-0.153	0.044	8	-3.456	0.011
Wetland Age	0.064	0.024	10	2.633	0.030

Table 7. Coefficient estimates from model of log taxonomic richness by distance to nearest natural wetland and elevation after accounting for elevation for created wetlands only, with site as a random effect to account for repeated sampling of some sites over multiple years.

	Coefficient	Std. Error	df	t-value	P>t
(Intercept)	1.292	0.111	11	11.598	0.000
Elevation	-0.118	0.056	7	-2.098	0.074
Distance to nearest wetland	-0.000	0.000	7	-1.001	0.350

Table 8. Indicator species analysis results for created and reference/ impacted wetlands. Only taxa with a p-value ≤ 0.1 are shown. Frequency is the total number of wetlands in which a given taxon was found.

Taxa	Flying Adult Stage	Wetland Type	Indicator Value	Prob.	Frequency
Notonectidae	Yes	Created	0.426	0.032	8
Berosus spp.	Yes	Created	0.300	0.047	3
Helophorus spp.	Yes	Created	0.300	0.035	3
Pisidium spp.	No	Reference/Impacted	0.921	0.001	17
Chaoboridae	Yes	Reference/Impacted	0.459	0.068	11
Oligochaeta	No	Reference/Impacted	0.458	0.071	12
Procloeon spp.	Yes	Reference/Impacted	0.353	0.065	6
Hydracarina	No	Reference/Impacted	0.353	0.064	6
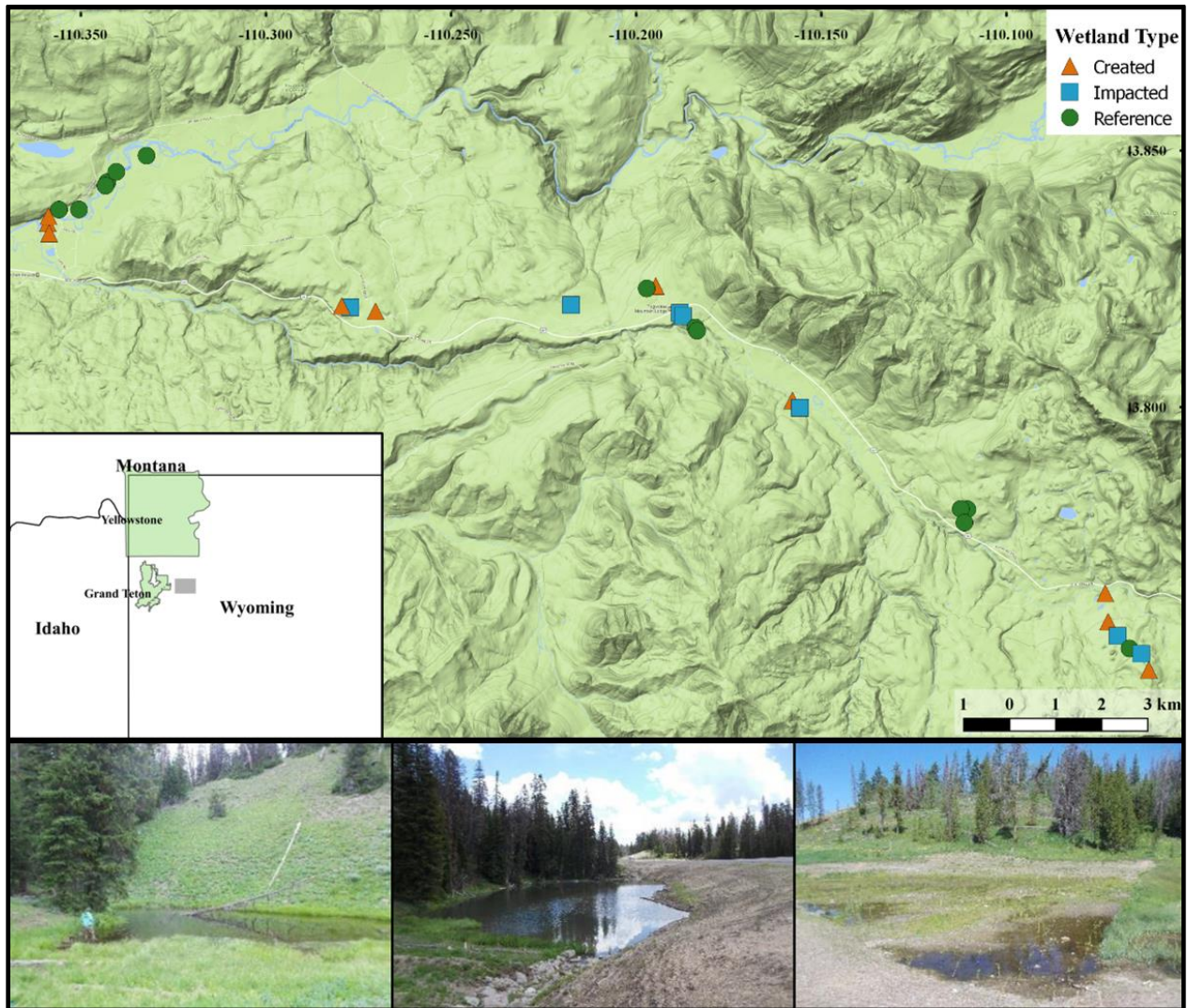
Figure 1. Locations of wetlands where invertebrates were sampled near Moran, Wyoming (inset) from 2013 to 2015 and photos of each wetland type (left to right: reference, impacted, created). Orange triangles represent created wetlands (n=10), blue squares represent impacted wetlands (n=7), and green circles represent reference wetlands (n=13). The white line is US Highway 26-287.
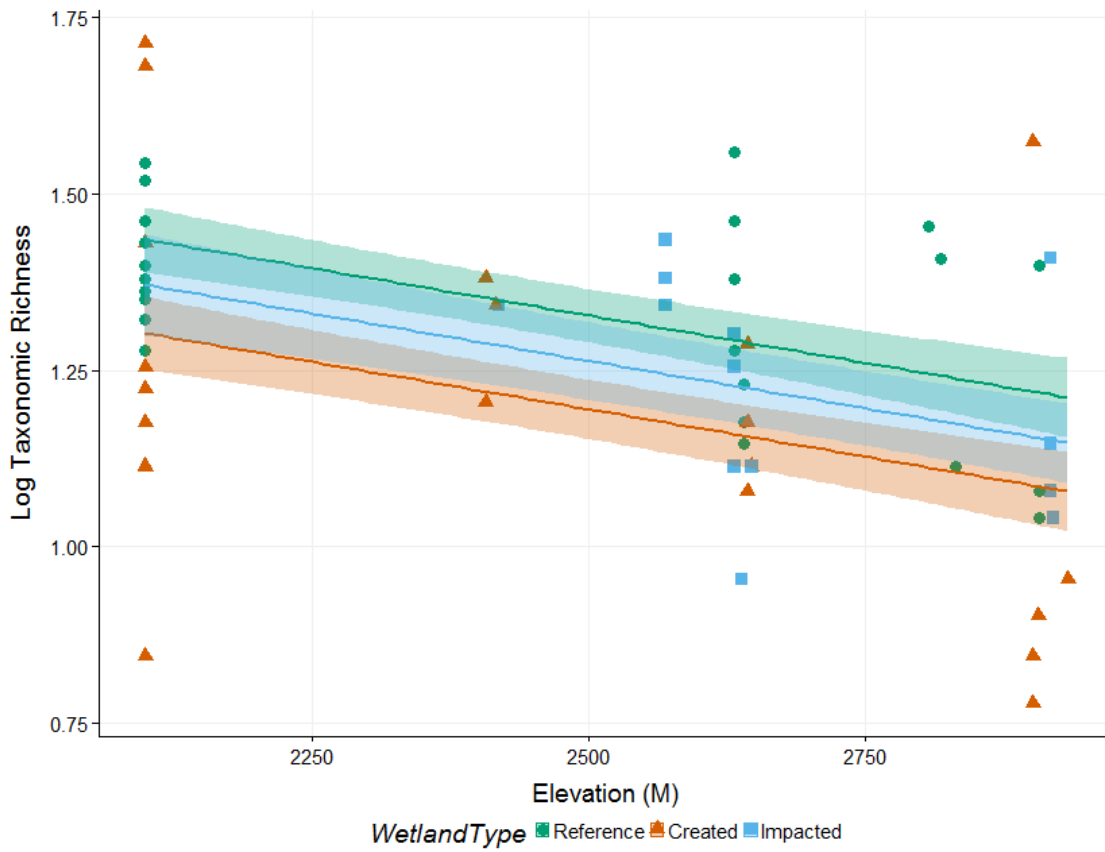
Figure 2. Estimated log taxonomic richness and standard error of invertebrates in reference, impacted, and created wetlands across elevation. Points represent richness in individual wetlands.
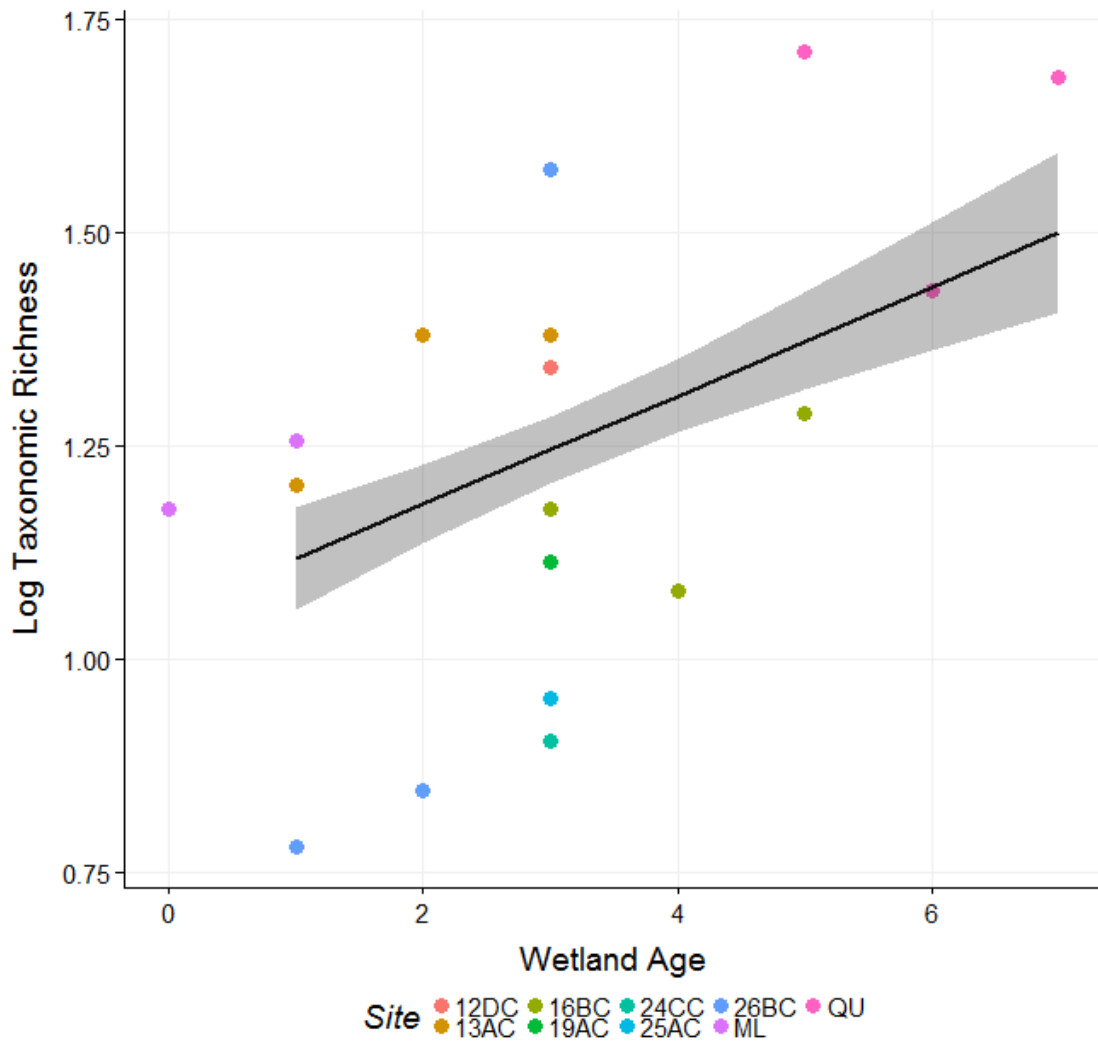
Figure 3. Relationship between log taxonomic richness of invertebrates in created wetlands and wetland age. Colors represent individual wetlands over multiple years. A quadratic effect of wetland age was evaluated but was not significant.
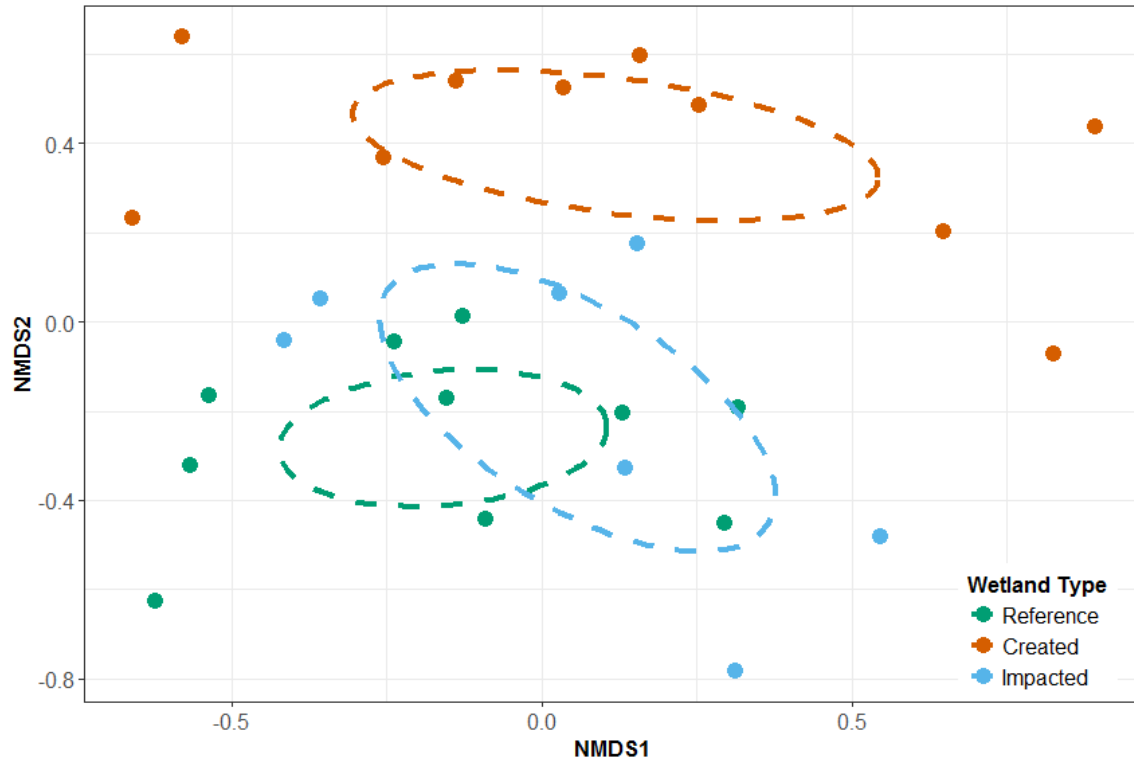
Figure 4: Non-metric multidimensional (NMDS) ordination of invertebrate community composition in created (orange), reference (green), and impacted (blue) wetlands (2015 only, stress = 0.21). Each point represents the community composition of invertebrates in a single wetland, where points that are closer together in ordination space have more similar community composition than points that are farther away from each other. Ellipses represent 95% confidence intervals around the mean axis score for each group.

APPENDIX 1: MACROINVERTEBRATE TAXA IDENTIFIED IN WETLAND SAMPLES

Taxonomic rankings retrieved [December, 16, 2017] from the Integrated Taxonomic Information System (ITIS) (http://www.itis.gov)

Kingdom Animalia, Phylum Arthropoda, Subphylum Crustacea
    Order Amphipoda
        Family Gammaridae
            Gammarus
        Family Hyalellidae
            Hyalella

Kingdom Animalia, Phylum Mollusca
    Class Bivalvia
        Family Pisidiidae
            Pisidium
    Class Gastropoda
        Family Lymnaeidae
            Lymnaea
        Family Physidae
            Aplexa
            Physa
        Family Planorbidae
            Armiger
            Gyraulus
            Helisoma
            Promenetus
        Family Valvatidae
            Valvata

Kingdom Animalia, Phylum Arthropoda, Class Insecta
    Order Coleoptera
        Family Dytiscidae
            Acilius
            Agabus
            Colymbetes
            Dytiscus
            Graphoderus
            Hydaticus
            Hydrotus
            Ilybius
            Laccophilus
            Laccornis
            Liodessus
            Oreodytes

    Rhantus
  Family Emidae
    Heterlimnius
  Family Gyrinidae
    Gyrinus
  Family Haliplidae
    Brychius
    Haliplus
  Family Helophoridae
    Helophorus
  Family Hydrophilidae
    Berosus
    Enochrus
    Hydrophilus
    Laccobius
    Tropisternus

Order Diptera
  Family Ceratopogonidae
  Family Chaoboridae
  Family Chironomidae
  Family Culicidae
  Family Dixidae
  Family Dolichopodidae
  Family Ephydridae
  Family Psychodidae
  Family Stratiomyidae
  Family Tabanidae
  Family Tipulidae

Order Ephemeroptera
  Family Baetidae
    Baetis
    Callibaetis
    Procloeon
  Family Caenidae
    Caenis
  Family Ameletidae
    Ameletus
  Family Siphlonuridae
    Siphlonurus

Order Hemiptera
  Family Belostomatidae
  Family Corixidae
  Family Gerridae
  Family Notonectidae

Order Odonata
    Sub order Anisoptera
        Family Aeshnidae
        Family Libellulidae
    Sub order Zygoptera
        Family Coenagrionidae
        Family Lestidae

Order Trichoptera
    Family Hydroptilidae
        Agraylea
    Family Leptoceridae
        Mystacides
        Ylodes
    Family Limnephilidae
        Ecclisomyia
        Hesperophylax
        Limnephilus
        Onocosmoecus
        Psychoglypha

Kingdom Animalia, Phylum Arthropoda, Class Collembola

Kingdom Animalia, Phylum Annelida, Class Clitellata
    Order Hirudinida
        Family Erpobdellidae
        Family Glossiphoniidae
        Family Hirudinidae
    Subclass Oligochaeta

Kingdom Animalia, Phylum Arthropoda, Class Arachnida
    Hydracarina

Kingdom Animalia, Phylum Cnidaria, Class Hydrozoa, Order Anthoathecatae
    Family Hydridae
        Hydra

Kingdom Animalia, Phylum Platyhelminthes, Class Rhabditophora
    Order Tricladida

CHAPTER 2: AMPHIBIAN DENSITY IN CREATED WETLANDS – SPECIES SPECIFIC RESPONSES TO WETLAND MITIGATION

ABSTRACT

Wetland construction is a common practice to replace natural wetlands lost due to anthropogenic activities. In light of recent and widespread amphibian declines, evaluating the ability of created wetlands to function as adequate replacement habitat has become a priority. A recent highway reconstruction project in northwestern Wyoming resulted in impacts to and the destruction of multiple natural wetlands. To mitigate this loss, the Wyoming Department of Transportation constructed new wetlands along the highway corridor. In 2015 and 2016, I measured habitat characteristics and conducted repeated counts of larvae of the barred tiger salamander *(Ambystoma mavortium)*, boreal toad *(Anaxyrus boreas)*, Columbia spotted frog *(Rana luteiventris)*, and boreal chorus frog *(Pseudacris maculata)* in created (n=10), impacted (n=7), and reference (n=10) wetlands. For each species, I analyzed larval counts using dynamic N-mixture models to estimate density, survival, and detection probability. As a complementary, independent estimate of abundance, I also conducted counts of Columbia spotted frog egg masses. Created wetlands were shallower, had smaller surface area, and had less aquatic vegetation than reference and impacted wetlands. Impacted wetlands did not differ from reference wetlands in measured habitat variables. Estimated densities of barred tiger salamander, boreal toad, and boreal chorus frog larvae were higher in created wetlands than in reference and impacted wetlands. In contrast, Columbia spotted frog larvae and egg masses were only observed in one created wetland but were common and occurred at high densities in reference and impacted wetlands. Created wetlands in my study area were almost all designed to have a temporary – intermediate hydroperiod and many dried partially or completely by the end of July in both study years, often resulting in partial or complete mortality of amphibian larvae, providing evidence that some created wetlands may be functioning as population sinks or ecological traps for amphibians. Conservation and management of native amphibians should take into account the life history requirements of all target species when creating and restoring wetlands.

Key Words: Amphibians, Constructed Wetlands, Greater Yellowstone Ecosystem, Dynamic N-mixture models

INTRODUCTION

Widespread wetland loss due to agriculture, development, and climate change has contributed to population declines across taxa (Gibbs 2011, Gallant et al. 2017). In recent decades, growing awareness of the importance of wetlands for wildlife has contributed to the passage of legislation protecting wetlands, including Section 404 of the Clean Water Act. Under Section 404, discharge of dredged or fill materials into waters of the United States, including most wetlands, is prohibited without a permit from the US Army Corps of Engineers. Today, the Corps' permitting process is largely guided by the 1989 executive policy of "no net loss" of wetlands and any loss of wetlands area must be mitigated by an equal or greater number of acres of gains, achieved either through wetland restoration or construction (Hough and Robertson 2008). In North America alone, over 3,000,000 ha of wetlands and freshwater ponds were created or restored over a 20 year period (Copeland 2010). What remains uncertain is the capacity of these created wetlands to replace natural wetland functions, including supporting a full host of native organisms (Moreno-Mateos et al. 2012).

Amphibians are one group of organisms that often depend on wetlands for survival and reproduction. The use of created and restored habitats by amphibians is important to managers and conservationists, as many amphibian species worldwide have experienced dramatic declines, with habitat alteration and destruction playing an important role (Stuart et al. 2004, Pounds et al. 2009). The biphasic life history and semi-permeable skin of amphibians make them sensitive to changes in both terrestrial and aquatic environments (Dunson et al. 1992). Created wetlands can be beneficial for amphibians, but results are often species specific and dependent upon specific habitat design features, such as hydroperiod (the length of time a wetland holds water each year), aquatic vegetation, landscape placement, and the presence of fish and other predators (Brown et

al. 2012). For example, Shulse and Semlitsch (2012) found that high amounts of vegetation cover, lack of fish, and presence of shallow-sloped littoral zones increased amphibian diversity in created wetlands in Missouri, but even in wetlands with desired features, some species were rarely encountered. Better understanding of wetland design features likely to increase the capacity of created and restored wetlands to support the full complement of native amphibians will result in better mitigation practices and wildlife policies.

Amphibians use a variety of wetland types ranging from temporary to permanent and wetland restoration faces the challenge of replacing realistic hydrologic variation. An ongoing problem in wetland mitigation has been the replacement of temporary wetlands with less complex, permanent, open-water ponds that do not function like the wetlands that were destroyed (Dahl 2011). Permanent ponds are vulnerable to invasion by fish and non-native predators such as bullfrogs, which can reduce survival of native amphibians and strongly alter community structure (Shulse et al. 2013, Rowe and Garcia 2014). Consequently, it is becoming common for mitigation plans to require construction of more complex temporary wetlands, which poses new challenges for wetland design (Lichko and Calhoun 2003, Calhoun et al. 2014). For instance, predicting the depth required to produce a specific hydoperiod is challenging due to variable soil characteristics and inter-annual variation in precipitation and groundwater table height. If dug too deep, wetlands will be permanent, risking predatory fish invasion. If too shallow, wetlands will dry before amphibian larvae are able to metamorphose. In the second scenario, mitigation wetlands have the potential to act as population sinks or ecological traps, luring amphibians to immigrate and breed, but resulting in catastrophic reproductive failure when wetlands dry. If reproductive failure occurs frequently, it has the potential to reduce growth rates of amphibian populations (Dimauro and Hunter 2002, Schlaepfer et al. 2002).

The effects of global climate change also complicate the design of temporary mitigation wetlands. Because small, isolated wetlands often rely on snowmelt, and summer precipitation to fill, they are particularly vulnerable to early drying during drought conditions (Brooks 2009, Matthews 2010). In the Greater Yellowstone Ecosystem (GYE), hotter, drier summers, increased evapotranspiration, earlier runoff, and decreased snowpack have been associated with earlier drying of natural wetlands (Sepulveda et al. 2015, Ray et al. 2016). These changes are likely contributing to population declines of all four species of amphibians that occur in the region (Hossack et al. 2015, Ray et al. 2016). In light of climate-related changes to and loss of natural wetlands, it is critically important to evaluate the capacity of created mitigation wetlands to function as refuges for amphibians and identify structural characteristics that promote reproductive success.

Four amphibian species occur in GYE: barred tiger salamanders *(Ambystoma mavortium),* boreal toads *(Anaxyrus boreas),* Columbia spotted frogs *(Rana luteiventris*), and boreal chorus frogs *(Pseudacris maculata)*. A fifth species, the northern leopard frog (*Lithobates pipens*), historically occurred in the area but appears to have been extirpated (Ray et al. 2014) and was not a part of this study. All four species require standing water for breeding, oviposition, and larval development, but spend the majority of their adult lives in the terrestrial environment surrounding breeding ponds.

Recent mitigation efforts in Wyoming provide an opportunity to evaluate differences between created, impacted, and reference wetlands. The Wyoming Department of Transportation created 38 wetlands between 2005 and 2014 to mitigate wetland impacts associated with the reconstruction of Highway 287 over Togwotee Pass in Wyoming between Moran and Dubois, WY. Created wetlands were excavated with heavy equipment down to the water table and

planted with a wetland seed mix and willow cuttings. While the wetlands were designed with a range of depths, most were designed to be shallow with temporary – intermediate hydroperiods. Impacted wetlands were those that sustained impacts from the road construction activities (i.e. modified banks, some filling, and erosion control) but were not completely destroyed. Reference wetlands were those that did not sustain impacts from road construction and were used as a baseline for comparison with created and impacted sites. While reference and impacted wetlands also ranged in depth, they were generally deeper than created wetlands and held water throughout the year.

My objective was to evaluate the capacity of created mitigation wetlands to support amphibian biodiversity. I accomplished this by comparing amphibian larval density in created and impacted wetlands relative to reference wetlands. While the four species studied often share breeding, foraging, and overwintering areas, they differ in several key life history traits that may influence their use of created wetlands. Unlike the three anuran species in the GYE that complete metamorphosis in a single season, tiger salamanders can complete metamorphosis in one season, overwinter as larvae, or retain larval characteristics as paedomorphic adults (Werner et al. 2004). Because the majority of created wetlands in my study area were designed to be temporary, I predicted that tiger salamanders would occur in lower densities in created wetlands because adults would select breeding sites that retain water throughout the year to provide ample time for larvae to metamorphose (Hossack et al. 2015). Similarly, Columbia spotted frogs are highly aquatic and generally breed in deep, permanent water bodies with abundant vegetation, so I expected that species to occur more frequently and in higher density in reference and impacted wetlands, rather than created wetlands (Hossack et al. 2013, Ray et al. 2016). In contrast to Tiger Salamanders and Columbia spotted frogs, boreal toads and boreal chorus frogs often breed in

ephemeral wetlands with warm, shallow water (Ray et al. 2016). Boreal toads have been

documented colonizing and breeding in new habitats immediately following disturbance such as

wildfire and pond construction (Pearl and Bowerman 2006, Guscio et al. 2007, Hossack et al.

2013). Therefore, I expected those species to occur in a high proportion of created wetlands, but

to be susceptible to catastrophic reproductive failure if wetlands dried prior to larvae

metamorphosis.

METHODS

Study area

In 2015 and 2016, I sampled all four species of amphibian larvae, counted Columbia

spotted frog egg masses, and measured habitat characteristics in 10 created wetlands, 10

reference wetlands, and 7 impacted wetlands in the Bridger-Teton National Forest in Wyoming

along highway 287/26 between the town of Moran and Togwotee pass, just east of Grand Teton

National Park, USA (43.828872, -110.355998; Fig. 1). Created wetlands were built by the

Wyoming Department of Transportation in formerly upland areas near the highway to mitigate

wetland loss from a road reconstruction project, and ranged in age from 2 to 10 years old (Table

1). To select focal wetlands, I first identified all created wetlands that held water in June 2015,

then I selected the impacted and reference wetlands nearest to each of these created wetlands.

Wetlands ranged in elevation from 2,100 to 3,050 m above sea level. Surrounding vegetation

was dominated by conifer forest at higher elevations (lodgepole pine [*Pinus contorta*], whitebark

pine [*Pinus albicaulis*], Engelmann spruce [*Picea engelmannii*], and Douglas fir [*Pseudotsuga

menziesii*]) and mixed sagebrush (*Artemisia spp.*) and grassland vegetation at lower elevations.

This area is characterized by long, cold winters with heavy snowfall and short, cool summers.

Wetlands generally fill from snowmelt between early May (lower elevations) and early June (higher elevations). April 1st snow water equivalent measurements from the top of Togwotee Pass were close to normal in both years of this study (99.54 and 99.07 percent of median in 2015 and 2016, respectively) (NRCS).

Sampling

Larval trapping

I sampled amphibian larvae using a combination of collapsible mesh and plastic minnow traps placed at 20 meter intervals around the perimeter of each wetland (range = 1 – 48 traps/wetland) (Nyman 2015). I left traps open for two consecutive 24-hour periods every 2 weeks during larval development (mid-June – late-July) and counted the number of each species of larval amphibian in each trap during each period. Larvae were identified to species and released. This sampling design resulted in data in the form of the robust design (Pollock 1982, Dail and Madsen 2011), with secondary occasions (consecutive days) closed to births, deaths, immigration and emigration, nested within primary periods (two-weeks) when the closure assumption was relaxed. Dates of primary periods differed among sites due to differences in timing of breeding and larval development across elevations. However, at all sites I began sampling as soon as free-swimming larvae were large enough to be trapped, and stopped when metamorphosis occurred or wetlands dried. To increase detection probability of species that may be less likely to enter traps, I also conducted a dip-net sweep 1 m out from each trap before checking that trap (Dodd 2010). Due to time limitations in 2015, I stopped trapping at a site if no amphibians of any species were encountered during the first two secondary sampling occasions. Even so, these wetlands were all revisited several times throughout the season and visually

surveyed to ensure that they were truly unoccupied. In 2016, I increased sampling effort so that there was a minimum of four sampling occasions at each wetland (two primary periods) two (with the exception of one site that dried after the first primary period). Two wetlands (one reference, one impacted) had very steep banks along a portion of their perimeter, making it impossible to trap the entire shoreline and leading to slightly larger inter-trap intervals at those wetlands. Counts from traps and sweeps were pooled for a single count from each wetland on each trapping day.

Egg mass Surveys

Columbia spotted frogs are the only amphibian species in this region that lay conspicuous egg masses that can be used as a reliable index of the number of breeding females in a population (Licht 1975). To provide a complementary measure of abundance, I counted Columbia spotted frog egg masses in both years by walking the entire shoreline and other shallow areas of each wetland. The egg masses float near the water's surface and are typically laid communally near the shore, making them easy to detect. To reduce counting errors, each egg mass was marked with a colored toothpick and a pin flag labeled with the date and count of egg masses for that date. I began surveying each wetland as soon as ice melted (late April/early May) and visited each wetland at least once per week until the count of masses did not change for two consecutive visits and there was no change in counts in neighboring wetlands (Hossack et al 2013b).

Habitat characteristics

I developed an *a priori* suite of environmental and design characteristics that could influence density of amphibians across all wetland types (Table 2). I measured total wetland area and wetted wetland area using the area estimation tool in a Garmin e-trex Global Position

System (GPS). I defined total wetland area as the high-water line or boundary of wetland creation disturbance (i.e., willow plantings in created wetlands). Wetted wetland area was the portion of the wetland that held water in early June. Elevation was also recorded from a GPS unit. I measured maximum depth of each wetland at the beginning of the summer. I sampled vegetation in late July, using a 1-m^2 quadrat every 80 meters along the wetland shore, both at 1 m and 5 m out from the shore. In each quadrat, I estimated percent cover of aquatic (emergent and submersed) vegetation. I also recorded presence of fish when they were detected.

Statistical Methods

I analyzed larval amphibian counts using dynamic N-mixture models implemented in the R package unmarked (Fiske and Chandler 2011). N-mixture models are hierarchical and use information from temporally and spatially repeated counts of unmarked animals to estimate detection and predict abundance (Royle 2004). The original single-season N-mixture model assumed that count y_{it} from site i on sampling occasion t was a binomial random variable dependent on detection probability p and total population size N at location i.

$$y_{it} \sim Binomial(Ni, p).$$

Population size N_i at location i was assumed to follow a Poisson distribution with mean λ,

$$N_i \sim Poisson(\lambda),$$

where N_i was assumed to remain constant over the sampling period (Royle 2004). The dynamic N-mixture model relaxes the closure assumption and allows abundance at site i to vary over time as a function of abundance at time t-1, S_{it} (the number of individuals that survive from time t-1 to

t and remain at site *i*) plus G_{it} (the number of individuals that were gained through recruitment or immigration at location *i* between time *t*-1 to time *t*). S_{it} is a function of abundance at the previous time step and apparent survival ω (Dail and Madsen 2011) and G_{it} is a function of the arrival rate γ and the abundance at time *t*-1,

$$S_{it} \sim Binomial(N_{i,t-1}, \omega)$$

$$G_{it} \sim Poisson(\gamma N_{i,t-1})$$

Where initial abundance at site *i* is estimated in the same way as in the closed model.

Because all amphibian species in my study area breed around the same time (Werner et al. 2004) and larvae are restricted to a particular wetland until metamorphosis, I fixed the recruitment parameter γ to zero in all my models. I modeled initial abundance using a zero-inflated Poisson (ZIP) distribution to account for the large number of true zeros arising from unoccupied sites (Wenger et al. 2008, Joseph et al. 2009). To account for different trap density among wetlands, I included an offset parameter of log(number of traps) on abundance, which changes the response variable from abundance to density (Kéry and Royle 2016). Because of data limitations, models that included covariates on apparent survival (ω) generally did not converge, so I assumed that ω remained constant for each species and year. Since trapping ceased when metamorphosis occurred, apparent survival should be analogous to true survival of the larval stage over a 2-week period.

I used a two-part process to identify the best model for each species. First, I set all parameters except detection probability to be constant and considered two models for detection: a) variable by primary period or b) constant over time. I expected that detection probability would vary over the course of the summer due to changes in activity as larvae develop. I ranked each model based on Akaike's Information Criterion (AIC) (Burnham and Anderson 2002).

Second, using the top detection model for each species and year, I examined differences in initial density between wetland types. After accounting for wetland type, I was also interested in whether additional environmental covariates helped to explain differences in initial density among wetlands. I started with a global model that included wetland type (constructed, impacted, reference), year, percent cover of aquatic vegetation, maximum depth, wetted wetland area, and elevation. I scaled all continuous explanatory variables by subtracting the mean and dividing by the standard deviation to improve model convergence. I checked for correlations between explanatory variables and did not include collinear variables in the same model (Pearson's r > 0.7) (Dormann et al. 2013). I performed backwards selection to identify the best model for each species and year, removing variables with the least partial significance until only significant variables remained ($p < 0.1$). I assumed that detection probability was constant for all individuals of a given species at time period t and that no individuals were double counted within a secondary session. I also assumed that the effects of wetland type and other covariates were consistent between years.

As with the larval count data, Columbia spotted frog egg mass counts contained many zeros, so I was unable to fit a mixed effect model to account for two years of sampling at each site. Instead, I analyzed differences in egg mass counts among created, impacted, and reference wetlands using a negative binomial generalized linear model (GLM) with the mean count for each site (rounded to the nearest integer) as the response variable.

RESULTS

I detected all four native amphibian species during my surveys. In 2015, there were a total of 109 tiger salamander larvae, 1290 boreal toad tadpoles, 372 boreal chorus frog tadpoles,

and 239 Columbia spotted frog tadpoles trapped over 108 trapping occasions at 25 wetlands. In 2016 there were a total of 68 tiger salamander larvae, 391 boreal toad tadpoles, 425 boreal chorus frog tadpoles, and 252 Columbia spotted frog tadpoles trapped over 134 trapping occasions at 27 wetlands. Naïve species richness (unadjusted for detection probability) over the whole study was highest in reference wetlands (mean = 2.00 species, range = 0 – 4 species), followed by impacted wetlands (mean = 1.57, range = 0 – 3 species) and created wetlands (mean = 1.30 species, range = 0 – 4 species).

Habitat characteristics

Created wetlands had smaller surface areas than reference and impacted wetlands and had lower mean percent cover of aquatic vegetation (Table 2). Created wetlands were also shallower than reference or impacted wetlands and in both years a majority (year one = 90%, year two = 80%) of created wetlands dried partially (i.e. at least one isolated pool dried completely) or completely by the end of July (Tables 1 and 2). No reference or impacted wetlands dried over the same time period. There were no major differences in habitat characteristics between reference and impacted wetlands. I detected fish in two impacted and one reference wetland, all of which were permanent and had a stream or river connection.

Tiger Salamanders

I detected tiger salamander larvae in 13 of 27 wetlands (3 created, 3 impacted, 7 reference). The top detection model included differences in detection based on primary period. Detection probability ranged from 0.10 to 0.33 with the highest detection probability in the third primary period (Table 3). The top model for density included significant effects of wetland type, elevation, and year, with created wetlands having the highest density of larvae, followed by

reference wetlands and impacted wetlands (Table 4, Figure 2). Elevation was positively

correlated with salamander density and estimated density was lower in year two than year one

(Table 4). Estimated 2-week apparent survival was 0.59 (SE = 0.25).

Boreal Toads

I detected boreal toads in 6 of 27 wetlands (4 created, 0 impacted, 2 reference). Because

of the low and uneven occupancy rates by this species across wetland types (i.e., no detections in

impacted wetlands), basic models that included wetland type did not converge. There were also

several outlier counts (year one: 910 and 135, year two: 185, mean count = 6.96) which I

replaced with the 95th quantile of non-zero data to improve model convergence (Zuur et al.

2010). All three of these extremely high counts were from one created wetland (Quarry [QU])

and likely reflect the often clumpy distribution of toad tadpoles along wetland margins. The top

detection model included an effect of primary period, with detection ranging from 0.19 to 0.46

(Table 3). Without considering wetland type, the top model for density included negative effects

of depth and wetland area and a positive effect of aquatic vegetation (Table 4, Figure 3).

Estimated density was higher in year two than year one. Apparent survival was not estimable

(confidence intervals ranged from 0-1). To describe relative density by wetland type, I

summarized the point estimates for density at each site and calculated the mean and standard

error for each wetland type (Figure 2). While these point estimates varied considerably, created

wetlands had by far the highest estimated mean density (22.50, SE = 4.38), followed by impacted

wetlands (1.12, SE = 0.34) and reference wetlands (4.68, SE = 1.28).

Boreal Chorus Frogs

I detected boreal chorus frogs in 17 out of 27 wetlands (6 created, 5 impacted, and 6 reference wetlands). The top detection model included an effect of primary period, with detection probability ranging from 0.32 to 0.62 (Table 3) and increasing over the summer. Detection in the 4th primary period was not estimated. The top model for density included significant effects of wetland type, depth, elevation, and year (Table 4, Figure 2, and Figure 3). Created wetlands had significantly higher larval densities than impacted and reference wetlands. Larval density increased with elevation and declined with maximum depth. Estimated density was lower in year two than year one. Estimated 2-week apparent survival was 0.51 (SE = 0.03).

Columbia Spotted Frogs

I detected Columbia spotted frog larvae in 9 of 27 wetlands (1 created, 3 impacted, and 5 reference wetlands). Detection probability varied by primary period and ranged from 0.19 to 0.80 and increased throughout the summer (Table 3). The top model for density included wetland type, along with negative effects of depth and wetland area and a positive effect of elevation (Table 4, Figure 5). Estimated initial density was highest in impacted and reference wetlands and was much lower in created wetlands (Figure 2). Estimated 2-week apparent survival was 0.58 (SE = 0.04).

Egg Mass Surveys

I found Columbia spotted frog egg masses in 9 of 27 wetlands (1 out of 10 created, 3 out of 7 impacted, and 5 out of 10 natural) (Table 5). Egg mass counts ranged from 0 to 49 per site. There were significantly more egg masses in reference wetlands (estimated mean = 7.45, SE = 5.56) than created wetlands (estimated mean = 0.20, SE = 0.21) but no difference in egg mass counts between reference and impacted wetlands (estimated mean = 7.43, SE = 6.95).

DISCUSSION

My results illustrate species specific responses to wetland creation in the southern GYE and highlight the challenges associated with constructing temporary – intermediate hydroperiod wetlands that support the full complement of extant amphibians. Created wetlands were shallower, smaller, and had less aquatic vegetation than reference wetlands, while impacted wetlands did not differ from reference wetlands in measured environmental variables. I used larval density of four species and counts of Columbia spotted frog egg masses as measures of potential amphibian reproductive success. Estimated densities of barred tiger salamander, boreal toad, and boreal chorus frog larvae were higher in created wetlands than in reference and impacted wetlands. In contrast, Columbia spotted frog larvae and egg masses were only observed in one created wetland but were common and occurred at high densities in reference and impacted wetlands. However, most created wetlands dried partially or completely by the end of July in both study years, often resulting in partial or complete mortality of amphibian larvae, setting up the possibility that some created wetlands may be functioning as population sinks or ecological traps for amphibians.

Species-specific responses to wetland creation

Consistent with other studies of amphibian use of created wetlands, I found species-specific responses to wetland creation (Brown et al. 2012). Tiger salamander, boreal toad, and boreal chorus frog larvae occurred at higher densities in created wetlands than in reference and impacted wetlands, suggesting that adults of these species may be preferentially selecting created wetlands for breeding over nearby reference and impacted wetlands. Tiger salamander larvae were detected in fewer created (naïve occupancy = 0.30) and impacted (naïve occupancy = 0.43)

wetlands than reference wetlands (naïve occupancy = 0.70), but estimated density of larvae was significantly higher in created wetlands than reference and impacted wetlands. This result suggests that the majority of created wetlands in my study area were not suitable for tiger salamanders, but those few created wetlands that were suitable promoted high densities. The three created wetlands where tiger salamanders were detected were relatively deep, perhaps because in cold climates like the GYE, tiger salamanders often require permanent water to overwinter as larvae before they metamorphose (Ray et al. 2016).

I detected boreal toads in relatively few wetlands, a pattern which is consistent with long-term monitoring in Yellowstone and Grand Teton National Parks (Hossack et al. 2015). Boreal toads have experienced population declines over large portions of their range, including within protected areas such as the Greater Yellowstone Ecosystem (GYE), and now occupy <2% of available breeding sites (Ray et al. 2016). Boreal toad larvae were detected in more created wetlands (naïve occupancy = 0.40) than reference wetlands (naïve occupancy = 0.12). Boreal toads were not detected in any impacted wetlands. Although I was unable to model boreal toad density by wetland type, density declined with increasing wetland depth and site-specific estimates indicated that boreal toads achieved high densities in created wetlands. Toads often respond positively to disturbances including wildfire and wetland construction and often select for warm, shallow water to breed in, a pattern that my data supports (Pearl and Bowerman 2006, Hossack et al. 2013).

Boreal chorus frogs were common across all wetland types. Naïve occupancy was 0.60 in created wetlands, 0.60 in reference wetlands, and 0.71 in impacted wetlands. Even so, as with tiger salamanders and boreal toads, estimated density of chorus frog larvae was significantly higher in created wetlands than reference and impacted wetlands and estimated density was

negatively correlated with maximum depth, supporting previous work showing that chorus frogs often breed in warm, shallow, ephemeral wetlands (Klaver et al. 2013, Ray et al. 2016).

In contrast to the other three amphibian species, Columbia spotted frog larvae and egg masses were only detected in one created wetland over the course of this study while they occurred commonly and at high densities in reference and impacted wetlands. Spotted frogs are one of the most highly aquatic amphibian species in the Greater Yellowstone Ecosystem and are most likely to breed in large, permanent wetlands with emergent vegetation (Hossack et al. 2015). Because Columbia spotted frogs lay conspicuous egg masses, I was able to use egg mass counts as a secondary measure of reproductive success for this species. Egg mass counts closely mirrored tadpole counts (i.e., I never found egg masses where we did not also find tadpoles), both of which showed higher occurrence and density in reference and impacted wetlands than created wetlands.

The single created wetland where I detected spotted frog reproduction (Quarry) is the second oldest created wetland in the study, and had time to develop the aquatic vegetation that provides crucial habitat for spotted frog breeding (Pearl et al. 2007). Even so, spotted frog egg masses and tadpoles were only detected in 2015 and at very low numbers. Quarry is also deeper than most of the other created wetlands, has abundant emergent and submersed aquatic vegetation and holds water throughout the summer months. All four species of amphibians were detected in Quarry, indicating that these design features (intermediate hydroperiod, shallow littoral zones, and abundant aquatic vegetation) may be an appropriate objective for wetland mitigation in this region. Supporting this, in Chapter 1, I found that Quarry also had the highest taxonomic richness of invertebrates of all the wetlands in this study.

Are created wetlands ecological traps?

Under the assumption that density of amphibian larvae reflects breeding habitat preferences of adult amphibians, my results provide evidence that some amphibian species may preferentially select created wetlands to breed in over nearby reference and impacted wetlands. In my study area, this pattern was most pronounced for boreal toads and boreal chorus frogs. After accounting for wetland type, density of both species was inversely correlated with depth, suggesting a preference for breeding in shallow, ephemeral wetlands wetlands (Hossack et al. 2015). Unfortunately, in both years of this study, over 80% of created wetlands dried partially or completely prior to metamorphosis, suggesting that created wetlands have the potential to be ecological traps (low quality habitats that are preferred over higher quality habitats) (Battin 2004). Even when created wetlands did not dry completely because of varied topography on the bottom of the wetland, they often formed multiple pools – effectively stranding and killing tadpoles even when only a portion of the wetland dried.

Temporary and intermediate hydroperiod wetlands are important for amphibians and many other wetland species because they are less likely to be invaded by predatory fish or non-native amphibian predators such as bullfrogs (Vasconcelos and Calhoun 2006, Shulse et al. 2013, Drayer and Richter 2016). However, due to inter-annual variation in precipitation and temperature, predicting what depth will produce a given hydroperiod is challenging. Created wetlands are more successful if they maintain a minimum hydroperiod corresponding to the life history requirements of target organisms. For example, all four species of extant, native amphibians in the GYE breed in the spring and require standing water until at least mid-July for larvae to metamorphose. We need to improve our ability to construct pools with intermittent hydroperiods (Kolozsvary and Holgerson 2016).

N-mixture models

This study demonstrates that N-mixture models are a promising tool for estimating abundance or density of larvae in isolated water bodies. To date, there have been few studies that have applied N-mixture models to estimate demographic parameters of amphibians and most of these have focused on counts of adults or metamorphs (Dodd and Dorazio 2004, Mazerolle et al. 2014, Strain et al. 2017). Instead, many authors use catch per unit effort or similar methods as a surrogate for abundance, or distill counts to presence-absence data, losing valuable information. Furthermore, relative to traditional mark-recapture methods, the count data required for N-mixture models are inexpensive and easy to collect.

The dynamic N-mixture models I used in this study are appealing due to their ability to incorporate covariates and detection probability into estimates of abundance, apparent survival, and recruitment. In my study, estimated survival over a 2-week period ranged from 0.51 for boreal chorus frogs to 0.59 for tiger salamanders. Because of the challenges associated with conducting mark-recapture surveys on amphibian larvae, these are among the first field-based larval survival estimates for these species in the literature (Biek et al. 2002). Unfortunately, because of the relatively small number of sites in this study, I was unable to incorporate covariates on the survival parameter in my N-mixture models. Even if I had, this survival term would not have accounted for mortality due to wetland desiccation, since we had to stop trapping when wetlands dried. One limitation to using the unmarked package to generate maximum likelihood parameter estimates from N-mixture models for areas with many true zeros (unoccupied sites) is that there is currently no way to model the zero-inflation parameter as a function of covariates. For most species and years, the zero-inflation parameter had wide CI's

that crossed zero, making it challenging to disentangle different effects of wetland type and environmental covariates on occupancy and abundance.

Conclusions

With the exception of Columbia spotted frogs, created wetlands in my study area supported breeding populations of most native amphibians including tiger salamanders, boreal toads, and boreal chorus frogs. Even so, premature drying of shallow created wetlands often lead to catastrophic reproductive failure, with potential detrimental population-level effects (Taylor et al 2006). Incorporating a variety of depths that include warm, shallow littoral zones into wetland design is good for amphibians, but managers should ensure that there are deeper areas where larvae can retreat to as wetlands dry over the course of the summer (Porej and Hetherington 2005, Petranka et al. 2007, Shulse et al. 2010). Building wetlands resistant to early drying is particularly important in light of expected climate change impacts to temporary and intermediate wetlands in the Intermountain West.

LITERATURE CITED

Battin, J. 2004. When good animals love bad habitats: Ecological traps and the conservation of animal populations. Conservation Biology 18:1482–1491.

Biek, R., W. C. Funk, B. a Maxell, and L. S. Mills. 2002. What Is Missing from Insights Amphibian Decline Ecological Sensitivity Analysis. Conservation Biology 16:728–734.

Brooks, R. T. 2009. Potential impacts of global climate change on the hydrology and ecology of ephemeral freshwater systems of the forests of the northeastern United States. Climatic Change 95:469–483.

Brown, D. J., G. M. Street, R. W. Nairn, and M. R. J. Forstner. 2012. A place to call home: Amphibian use of created and restored wetlands. International Journal of Ecology 1–11.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (2nd ed). Ecological Modelling. Volume 172.

C. Kenneth Dodd, J. 2010. Amphibian ecology and conservation. A Handbook of Techniques 556.

Calhoun, a. J. K., J. Arrigoni, R. P. Brooks, M. L. Hunter, and S. C. Richter. 2014. Creating Successful Vernal Pools: A Literature Review and Advice for Practitioners. Wetlands 34:1027–1038.

Copeland, C. 2010. Wetlands: An Overview of Issues.

Corn, P. S., B. R. Hossack, E. Muths, D. a Patla, C. R. Peterson, and A. L. Gallant. 2005. Status of amphibians on the Continental Divide: surveys on a transect from Montana to Colorado, USA. Alytes 22:85–94.

Dahl, T. 2011. Status and trends of wetlands in the conterminous United States 2004 to 2009. Washington, D.C.

Dail, D., and L. Madsen. 2011. Models for Estimating Abundance from Repeated Counts of an Open Metapopulation. Biometrics 67:577–587.

Dimauro, D., and M. L. Hunter. 2002. Reproduction of Amphibians in Natural and Anthropogenic Temporary Pools in Managed Forests. Forest Science 48:397–406.

Dodd, C. K., and R. M. Dorazio. 2004. Using Counts To Simultaneously Estimate Abundance and Detection Probabilities in a Salamander Community. Herpetologica 60:468–478.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, C. Mcclean, P. E. Osborne, B.

Reineking, B. Schröder, A. K. Skidmore, D. Zurell, and S. Lautenbach. 2013. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:027–046.

Drayer, A. N., and S. C. Richter. 2016. Physical wetland characteristics influence amphibian community composition differently in constructed wetlands and natural wetlands. Ecological Engineering 93:166–174.

Dunson, W. a, R. L. Wyman, and E. S. Corbett. 1992. A Symposium on Amphibian Declines and Habitat Acidification. Journal of Herpetology 26:349–352.

Fiske, I., and R. Chandler. 2011. Unmarked: An R package for fitting hierarchical models of wildlife occurence and abundance. Journal of Statistical Software 43:1–23.

Gallant, A. L., R. W. Klaver, G. S. Casper, M. J. Lannoo, A. L. Gallant, R. W. Klaver, G. S. Casper, and M. J. Lannoo. 2017. Global Rates of Habitat Loss and Implications for Amphibian Conservation Published by : American Society of Ichthyologists and Herpetologists (ASIH)

Gibbs, J. P. 2011. Wetland Loss and Biodiversity Conservation. Conservation Biology 14:314–317.

Guscio, G., B. R. Hossack, L. A. Eby, and P. S. Corn. 2007. Post-Breeding Habitat Use By Adult Boreal Toads (Bufo boreas) After Wildfire in Glacier National Park , USA. Herptelogical Conservation and Biology 3:55–62.

Hossack, B. R., M. J. Adams, C. a Pearl, K. W. Wilson, E. L. Bull, K. Lohr, D. Patla, D. S. Pilliod, J. M. Jones, K. K. Wheeler, S. P. McKay, and P. S. Corn. 2013. Roles of patch characteristics, drought frequency, and restoration in long-term trends of a widespread amphibian. Conservation biology 27:1410–20.

Hossack, B. R., W. R. Gould, D. A. Patla, E. Muths, R. Daley, K. Legg, and P. S. Corn. 2015. Trends in Rocky Mountain amphibians and the role of beaver as a keystone species. Biological Conservation.187:260–269.

Hossack, B. R., W. H. Lowe, and P. S. Corn. 2013a. Rapid Increases and Time-Lagged Declines in Amphibian Occupancy after Wildfire. Conservation Biology 27:219–228.

Hossack, B. R., W. H. Lowe, R. K. Honeycutt, S. A. Parks, and P. S. Corn. 2013b. Interactive effects of wildfire, forest management, and isolation on amphibian and parasite abundance. Ecological Applications 23:479–492.

Hough, P., and M. Robertson. 2008. Mitigation under Section 404 of the Clean Water Act: where it comes from, what it means. Wetlands Ecology and Management 17:15–33.

Joseph, L. N., C. Elkin, T. G. Martin, and H. P. Possingham. 2009. Modeling abundance using

N-mixture models: The importance of considering ecological mechanisms. Ecological Applications 19:631–642.

Kéry, M., and A. J. Royle. 2016. Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance, and species richness in R and BUGS. Volume 1. Academic Press, London.

Klaver, R. W., C. R. Peterson, and D. A. Patla. 2013. Influence of Water Conductivity on Amphibian Occupancy in the Greater Yellowstone Ecosystem. Western North American Naturalist 73:184–197.

Lichko, L. E., and a. J. K. Calhoun. 2003. An Evaluation of Vernal Pool Creation Projects in New England: Project Documentation from 1991-2000. Environmental Management 32:141–151.

Matthews, J. 2010. Anthropogenic climate change impacts on ponds: a thermal mass perspective. BIORISK – Biodiversity and Ecosystem Risk Assessment 5:193–209.

Mazerolle, M. J., A. Perez, and J. Brisson. 2014. Common reed (Phragmites australis) invasion and amphibian distribution in freshwater wetlands. Wetlands Ecology and Management 22:325–340.

Moreno-Mateos, D., M. E. Power, F. a Comín, and R. Yockteng. 2012. Structural and functional loss in restored wetland ecosystems. PLoS biology

Nyman, S. 2015. Evaluation of a new funnel trap for shallow water habitats used by the Oregon spotted frog (Rana pretiosa). Defining a New Ecological Baseline: Pacific Northwest Fauna and Flora in the Anthropocene: Society for Northwestern Vertebrate Biology and Northwest Partners in Amphibian and Reptile Conservation, Annual Metting. Portland, Oregon.

Pearl, C. A., M. J. Adams, and W. H. Wente. 2007. Characteristics of Columbia spotted frog (Rana luteiventris) oviposition sites in northeastern Oregon, USA. Western North American Naturalist 67:86–91.

Pearl, C. a., and J. Bowerman. 2006. Observations of Rapid Colonization of Constructed Ponds By Western Toads (Bufo Boreas) in Oregon, Usa. Western North American Naturalist 66:397–401.

Petranka, J. W., E. M. Harp, C. T. Holbrook, and J. a. Hamel. 2007. Long-term persistence of amphibian populations in a restored wetland complex. Biological Conservation 138:371–380.

Pollock, K. H. 1982. A Capture-Recapture Design Robust to Unequal Probability of Capture. Journal of Wildlife Management 46:752–757.

Porej, D., and T. E. Hetherington. 2005. Designing wetlands for amphibians: The importance of

predatory fish and shallow littoral zones in structuring of amphibian communities. Wetlands Ecology and Management 13:445–455.

Pounds, A., K. Masters, J. Collins, and M. Crump. 2009. Extinction in our times: global amphibian decline. Nature. Volume 462. Oxford University Press Inc., New York.

Ray, A. M., W. R. Gould, B. R. Hossack, A. J. Sepulveda, D. P. Thoma, D. A. Patla, R. Daley, and R. Al-Chokhachy. 2016. Influence of climate drivers on colonization and extinction dynamics of wetland-dependent species. Ecosphere 7.

Ray, A., A. Sepulveda, B. Hossack, D. Patla, and K. Legg. 2014. Using monitoring data to map amphibian breeding hotspots and describe wetland vulnerability in Yellowstone and Grand Teton National Parks. Park Science 31:112–119.

Rowe, J. C., and T. S. Garcia. 2014. Impacts of wetland restoration efforts on an amphibian assemblage in a multi-invader community. Wetlands 34:141–153.

Royle, J. A. 2004. N-Mixture Models for Estimating Population Size from Spatially Replicated Counts. Biometrics 60:108–115.

Schlaepfer, M., C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. Trends in Ecology & Evolution 17:22–27.

Sepulveda, A. J., M. T. Tercek, R. Al-Chokhachy, A. M. Ray, D. P. Thoma, B. R. Hossack, G. T. Pederson, A. W. Rodman, and T. Olliff. 2015. The shifting climate portfolio of the greater Yellowstone area. PLoS ONE 10.

Shulse, C. D., R. D. Semlitsch, and K. M. Trauth. 2013. Mosquitofish dominate amphibian and invertebrate community development in experimental wetlands. Journal of Applied Ecology 50:1244–1256.

Shulse, C. D., R. D. Semlitsch, K. M. Trauth, and A. D. Williams. 2010. Influences of design and landscape placement parameters on amphibian abundance in constructed wetlands. Wetlands 30:915–928.

Shulse, C., and R. Semlitsch. 2012. Testing wetland features to increase amphibian reproductive success and species richness for mitigation and restoration. Ecological Applications 22:1675–1688.

Strain, G. F., P. J. Turk, J. Helmick, J. T. Anderson, G. F. S. A, P. J. T. B, J. H. C, and J. T. A. D. 2017. Amphibian reproductive success as a gauge of functional equivalency of created wetlands in the Central Appalachians. Wildlife Research 44:354–364.

Stuart, S. N., J. S. Chanson, N. a Cox, B. E. Young, A. S. L. Rodrigues, D. L. Fischman, and R. W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306:1783–6.

Taylor, B. E., Scott, D. E. and Gibbons, J. W. (2006), Catastrophic reproductive failure, terrestrial survival, and persistence of the marbled salamander. Conservation biology, 20: 792–801.

Vasconcelos, D., and A. J. K. Calhoun. 2006. Monitoring created pools for functional success: a six-year case study of amphibian responses. Wetlands 26:992–1003.

Wenger, S. J., M. C. Freeman, and J. Wenger. 2008. Estimating Species Occurrence , Abundance , and Detection Probability Using Zero-Inflated Distrubutions. Ecology 89:2953–2959.

Werner, J. K., B. . Maxell, P. Hendricks, and D. L. Flath. 2004. Amphibians and Reptiles of Montana. Mountain Press Publishing Company, Missoula, MT.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3–14.

Table 1. Descriptions of wetlands surveyed for amphibians in 2015 and 2016. "Dried 2015" and "Dried 2016" indicate whether or not a wetland dried partially (partial, i.e. at least one isolated waterbody dried completely) or completely (yes) before the end of July (before tadpole metamorphosis was complete if tadpoles were present). "4-leggers detected" indicates whether or not metamorphs of any species were detected before wetland dried.

Site	Wetland Type	Year Created/ Impacted	Years Surveyed	Dried 2015?	Species detected 2015	4-leggers detected 2015?	Dried 2016?	Species detected 2016	4-leggers Detected 2016?
12DC	Created	2012	2015, 2016	Partial	PSMA	Y	Partial	PSMA	Y
13AC	Created	2012	2015, 2016	Partial	AMTI, PSMA	Y	Yes	AMTI, PSMA,	Y
16BC	Created	2010	2015, 2016	Yes	ANBO, PSMA	N	Partial	ANBO, PSMA	Y
19AC	Created	2012	2015, 2016	Partial	-	-	Yes	-	-
24CC	Created	2012	2015, 2016	Partial	-	-	Partial	-	-
25AC	Created	2012	2015, 2016	Partial	-	-	Partial	-	-
26BC	Created	2012	2015, 2016	No	-	-	Partial	-	-
ML	Created	2014	2016	Partial	NA	NA	No	ANBO, PSMA	
QU	Created	2008	2015, 2016	Partial	AMTI, ANBO, PSMA, RALU	Y	Yes	AMTI, ANBO, PSMA	N
SP	Created	2005	2016	Partial	NA	NA	No	AMTI, ANBO, PSMA	
12CI	Impacted	2011	2015, 2016	No	PSMA	Y	No	PSMA	N
15AI	Impacted	2008	2015, 2016	No	AMTI, PSMA, RALU	Y	No	PSMA, RALU	
17AI	Impacted	2008	2015, 2016	No	PSMA, RALU	Y	No	PSMA, RALU	Y
17BI	Impacted	2008	2015, 2016	No	AMTI, PSMA	Y	No	AMTI, PSMA	Y
19BI	Impacted	2008	2015, 2016	No	AMTI, PSMA, RALU	Y	No	-	-
25BI	Impacted	2009	2015, 2016	No	-	-	No	-	-
26AI	Impacted	2009	2015, 2016	No	-	-	No	-	-
16CR	Reference	-	2015, 2016	No	AMTI, PSMA	Y	No	AMTI, PSMA	Y
17DR	Reference	-	2015, 2016	No	PSMA	N	No	PSMA, RALU	Y
17ER	Reference	-	2015, 2016	No	PSMA, RALU	Y	No	AMTI, PSMA, RALU	Y
21AR	Reference	-	2015, 2016	No	-	-	No	-	-
21BR	Reference	-	2015, 2016	No	-	-	No	AMTI, PSMA	N
21CR	Reference	-	2015, 2016	No	AMTI		No		
25CR	Reference	-	2015, 2016	No	-	-	No	-	-
HE	Reference	-	2015, 2016	No	AMTI, ANBO, RALU	Y	No	AMTI, ANBO, RALU	Y
RW	Reference	-	2015, 2016	No	AMTI, PSMA, RALU	Y	No	AMTI, PSMA	Y
SD	Reference	-	2015, 2016	No	AMTI, ANBO, PSMA, RALU	Y	No	AMTI, PSMA, RALU	Y

Table 2. Physical habitat characteristics (mean [SD]) of wetlands surveyed for amphibians in 2015 and 2016 summarized by wetland type.

Variable	Created		Impacted		Reference	
	2015 (n=8)	2016 (n=10)	2015 (n=7)	2016 (n=7)	2015 (n=10)	2016 (n=10)
Wetland Area (m^2)	2644.7 (3768.83)		5377.71 (3637.66)		3678 (3773.19)	
Elevation (m)	2515.5 (342.21)		2678.14 (182.54)		2556.8 (329.63)	
Max depth (cm)	38.35 (25.62)	44.40 (34.16)	124.08 (45.59)	113.29 (32.91)	111.7 (35.81)	100.2 (31.27)
Aquatic vegetation (% cover)	24.07 (29.48)	27.29 (32.97)	46.43 (33.39)	70.43 (50.31)	49.39 (33.06)	60.72 (39.62)

Table 3. Estimated probability of detection and associated standard error (SE), 95% CI (lower, upper), z-score (z) and P-value (P>|z|) for each species and primary period.

Species	Primary Period	P(detection)	SE	Lower	Upper	z	P(>|z|)
Tiger Salamander	1	0.10	0.02	0.06	0.16	-8.13	0.00
	2	0.28	0.09	0.14	0.49	2.29	0.02
	3	0.33	0.25	0.05	0.82	1.21	0.22
	4	0.21	0.23	0.02	0.79	0.64	0.52
Boreal Toad	1	0.37	0.02	0.34	0.40	-7.53	0.00
	2	0.46	0.02	0.41	0.50	3.43	0.00
	3	0.19	0.02	0.15	0.24	-5.41	0.00
	4	0.32	0.13	0.13	0.60	-0.33	0.74
Chorus Frog	1	0.32	0.02	0.28	0.36	-8.84	0.00
	2	0.46	0.03	0.40	0.52	4.19	0.00
	3	0.62	0.06	0.49	0.73	4.44	0.00
	4	0.00	0.01	0.00	1.00	-0.10	0.92
Columbia spotted frog	1	0.20	0.02	0.15	0.25	-9.30	0.00
	2	0.42	0.04	0.35	0.49	6.37	0.00
	3	0.71	0.06	0.58	0.82	7.00	0.00
	4	0.81	0.14	0.43	0.96	3.16	0.00

Table 4. Coefficient estimates and associated standard error (SE), z-score (z) and P-value (P>|z|) from top model of larval density for each species.

Species	Covariate	Estimate	SE	z	P(>|z|)
Tiger salamander	Created (intercept)	1.82	0.29	6.30	0.00
	Impacted	-2.09	0.41	-5.13	0.00
	Reference	-1.48	0.22	-6.74	0.00
	Elevation	0.57	0.14	4.08	0.00
	Year 2	-0.66	0.23	-2.97	0.00
Boreal toad	(Intercept)	0.51	0.12	4.40	0.00
	Aquatic Veg	0.73	0.18	4.14	0.00
	Max Depth	-2.29	0.11	-21.29	0.00
	Wetland Area	-0.66	0.13	-5.00	0.00
	Year 2	0.37	0.14	2.59	0.01
Chorus frog	Created (intercept)	1.85	0.13	14.10	0.00
	Impacted	-0.87	0.22	-4.03	0.00
	Reference	-0.57	0.14	-4.08	0.00
	Max Depth	-0.57	0.10	-5.90	0.00
	Elevation	0.83	0.07	11.95	0.00
	Year 2	-0.44	0.10	-4.53	0.00
Columbia spotted frog	Created (intercept)	-3.42	1.12	-3.04	0.00
	Impacted	5.12	1.17	4.37	0.00
	Reference	4.72	1.12	4.23	0.00
	Max Depth	-0.58	0.18	-3.28	0.00
	Wetland Area	-0.30	0.11	-2.68	0.01
	Elevation	0.47	0.19	2.53	0.01

Table 5. Total number of egg masses counted at each wetland in 2015 and 2016 and mean and standard deviation of the number of egg masses in each wetland type.

| Site	Wetland Type	2015	2016
12DC	Created	0	0
13AC	Created	0	0
16BC	Created	0	0
19AC	Created	0	0
24CC	Created	0	0
25AC	Created	0	0
26BC	Created	0	0
ML	Created	0	0
QU	Created	3	0
SP	Created	0	0
12CI	Impacted	0	0
15AI	Impacted	21	24
17AI	Impacted	24	23
17BI	Impacted	0	0
19BI	Impacted	7	5
25BI	Impacted	0	0
26AI	Impacted	0	0
16CR	Reference	0	0
17DR	Reference	1	1
17ER	Reference	14	9
21AR	Reference	0	0
21BR	Reference	0	0
21CR	Reference	0	0
25CR	Reference	0	0
HE	Reference	39	30
RW	Reference	19	4
SD	Reference	37	9
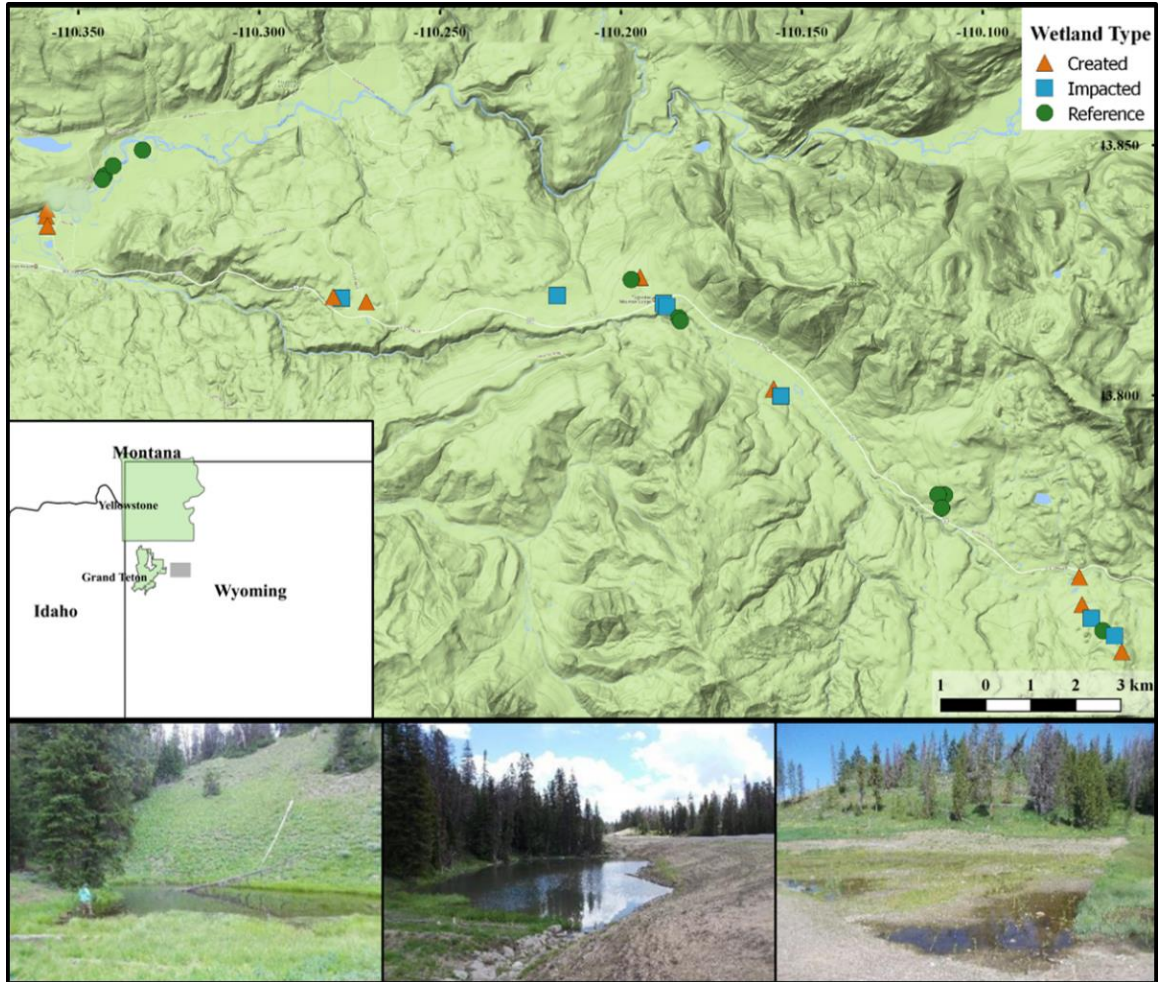
Figure 1. Locations of wetlands where amphibians were sampled near Moran, Wyoming (inset) from 2015 to 2016 and photos of each wetland type (left to right: reference, impacted, created). Orange triangles represent created wetlands (n=10), blue squares represent impacted wetlands (n=7), and green circles represent reference wetlands (n=10). The white line is US Highway 26-287.
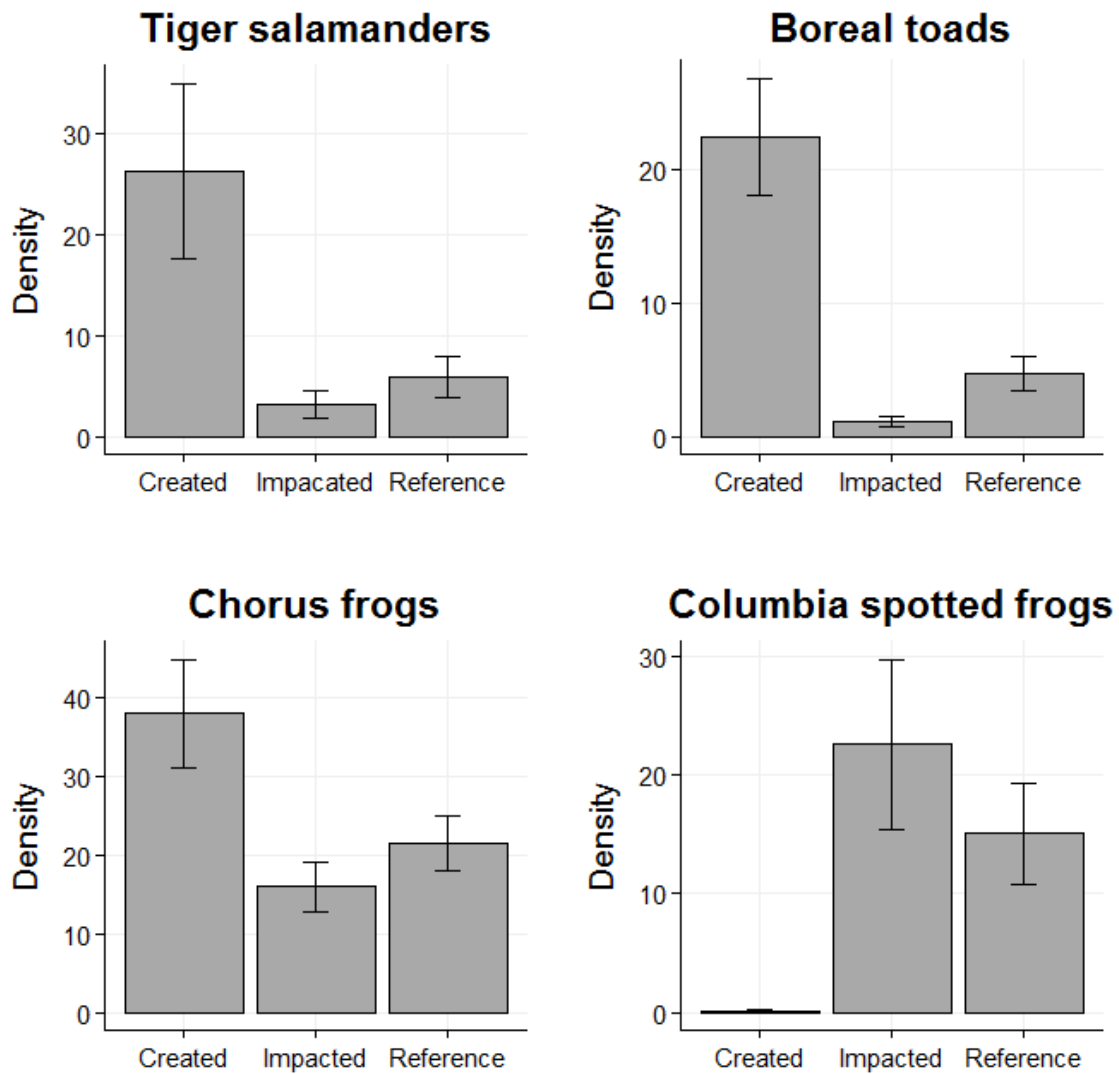
Figure 2. Estimated mean density (no. larvae/ trap area, +/- standard error) of larval amphibians by wetland type for each species. Note that for boreal toads, models that included wetland type did not converge, so the plot shows the mean calculated from the site-specific estimates of density.
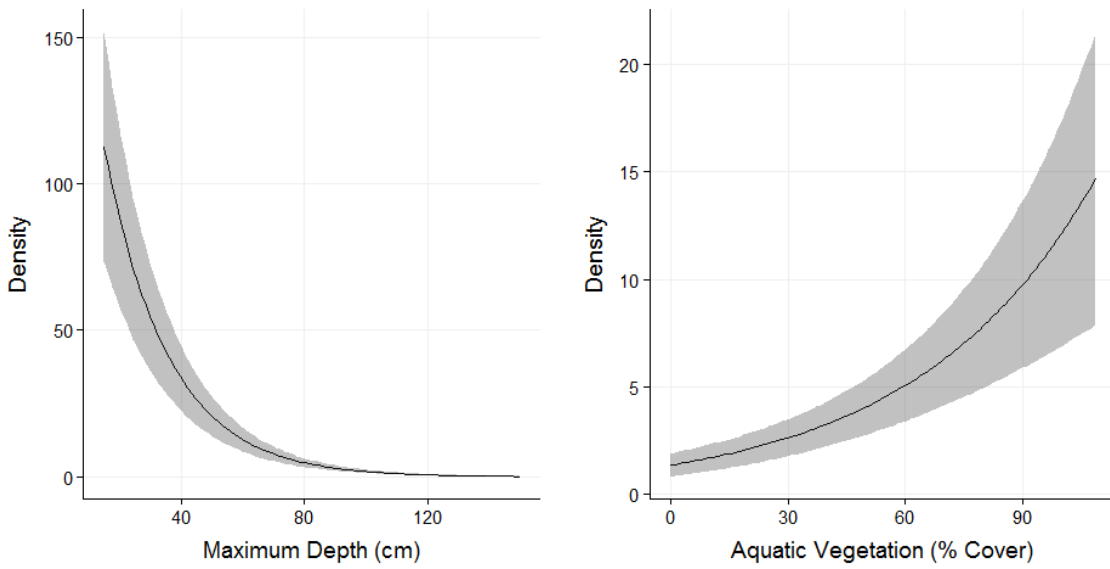
Figure 3. Estimated density (no. larvae/trap area) (+/- SE) of boreal toad larvae along a gradient of depth (left) and aquatic vegetation (right).
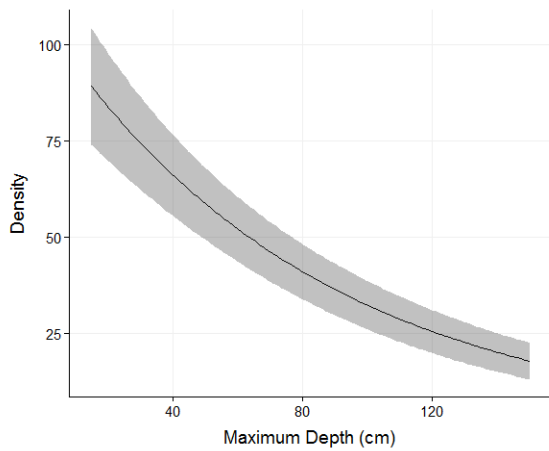

Figure 4. Estimated density (no. larvae/trap area) (+/- SE) of boreal chorus frog larvae along a gradient of depth.
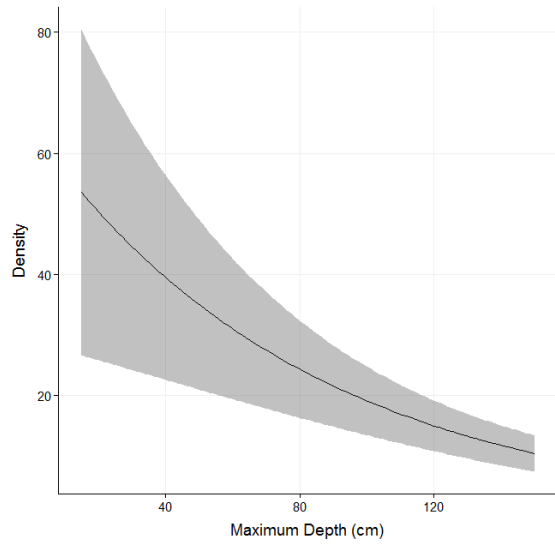
Figure 5. Estimated density (no. larvae/trap area) (+/- SE) of Columbia spotted frog larvae along a gradient of depth.