

5-15-2023

Evaluating Abiotic and Biotic Factors Affecting Plant Succession Processes at Malheur Lake

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EVALUATING ABIOTIC AND BIOTIC FACTORS AFFECTING PLANT SUCCESSION PROCESSES AT MALHEUR LAKE

A Thesis

Submitted to the Graduate Faculty
of the Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Master of Science

in

The School of Renewable Natural Resources

by

Beth Lauren Boos

B.S., University of Wisconsin Stevens Point, 2020

August 2023

ACKNOWLEDGEMENTS

First and foremost, I would like to thank my advisor Dr. Sammy King for his guidance, support, and encouragement throughout the project. I am also grateful to my committee, Dr. Andy Nyman, Dr. Richard Keim, and Dr. Tracy Quirk for extending their knowledge and time to this project. I would also like to thank Dr. Steve Midway and Dr. Drew Fowler for sharing their passions and for always welcoming questions and thought-provoking discussions.

This project would not have been possible without the support and contributions from the staff at Malheur National Wildlife Refuge. I am specifically in debt to Alexa Martinez, who was instrumental in my learning and success at every level on the refuge. I would also like to thank Rebecca Pickle for her contributions and dedication to completing my research when I could not be there. I am also thankful to the administrative staff, notably Suzanne McConnell, who was always willing to look for a solution to any problem.

I would also like to thank my collaborators, including High Desert Partnership, for their excitement and energy towards this project. In particular, I am grateful to Melissa Petschauer for her time and effort in the field. In addition, I want to thank Brenda Smith for always listening and being open to supporting the project in any way possible. I would also like to thank Cassandra Smith of USGS for her work and contributions to Malheur and my project through many conversations and brainstorming sessions even when it felt like we had an impossible task.

Words cannot express my thanks to my fellow lab mates in the Louisiana Cooperative Fish and Wildlife Research Unit. I cannot imagine the long days and unprecedented challenges without the aid and love of Aylett Lipford, Leah Moran, and Shannon Stemaly, whom I would move mountains to help in their respective journeys. I am immensely grateful to Kristi Buehler for her strength and assistance in every little thing that made my life easier. I would also like to

acknowledge the wonderful supportive graduate students at LSU, including but not limited to Katie Loesser, Garrett Rhyne, Alessandra Bresnan, and Abigail Greer for their constant troubleshooting, friendship, and shared laughs and tears.

I am also incredibly blessed to have friends and family supporting me along this journey from thousands of miles away. Thank you to my parents, Jay and Kathy, my siblings, Noah, Andrew, Katrina, and my brother in-law Brian for their love and understanding throughout the last few years. Lastly, thank you to my best friends who have heard every struggle and milestone and lifted me up without hesitation, Nathan Mueller and Sara Lavilla.

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ABSTRACT

Arid wetlands are diverse systems that provide habitat for a variety of flora and fauna, including stopover and breeding habitat for migratory birds. In the western United States, these wetlands support a network of stopover sites on the Pacific Flyway, and due primarily to wetland loss and alterations, these areas are becoming more isolated. Malheur Lake is a shallow endorheic lake in eastern Oregon that supported a robust emergent marsh throughout most of the 20th century. However, following large scale flooding in the 1980s, emergent vegetation was extirpated and has only reestablished in small patches. Our objective was to identify factors limiting vegetation establishment using a plant succession approach. We sought to answer three broad questions: (1) is the seedbank present and viable? (2) are conditions conducive for germination and survival of seedlings? and (3) how does a reduction in herbivory and wind-wave action affect existing vegetation growth? Utilizing a greenhouse experiment, we found that the seedbank is viable and contains the two most historically common robust emergents: hardstem bulrush (*Schoenoplectus acutus*) and broadleaf cattail (*Typha latifolia*). Seedlings of these species emerged at 94% and 80% of our seedbank samples in 2021 and 2022, respectively. In 2021, hardstem bulrush was detected at all field germination plots, broadleaf cattail was detected at 55% of plots, and alkali bulrush (*Bolboschoenus maritimus*) was detected at 55% of plots. In 2022, hardstem bulrush was detected at all plots, broadleaf cattail was detected at 5% of plots, and alkali bulrush was detected at 27% of plots. We recorded peak germination counts in mid to late July for both years followed by a decline that likely corresponded with drying soil. We also tested how a reduction of wind-wave action and herbivory affected vegetation expansion using exclosures. The results of this study indicate that vegetation establishment at Malheur Lake is not

limited by seedbank presence, and a combination of abiotic and biotic factors including soil moisture and herbivory may be limiting establishment of seedlings depending on lake conditions.

INTRODUCTION

Arid wetland systems vary across many dimensions including water sources, geomorphic setting, and hydroperiod (Euliss Jr et al. 1999) which affects community assemblages and distributions (Zedler 2000, Roshier et al. 2002) and complicates management and restoration actions. Paleohydrologic studies of arid wetlands emphasize the importance of understanding specific climatic conditions that sustained the system historically and comparing those to current conditions (Honke et al. 2019). This historical context provides an important link to explaining variation within systems, but there is increasing concern of how climate change will impact arid wetland systems in the future (Haig et al. 2019). Climate change is projected to decrease wetland abundance, area, and connectivity in regions where evapotranspiration exceeds precipitation (Larson 1995, Sofaer et al. 2016), and semi-arid and regions are expected to experience significant declines in water storage (Döll et al. 2020). Shifts in temperature and precipitation resulting from climate change will alter hydrological systems including snowpack melting and accumulation (Qian et al. 2015) which will affect annual hydrographs and challenge water managers (Haig et al. 2019). Anthropogenic climate change and natural variation in water availability threatens wetland connectivity and function in arid environments.

Arid wetlands that lack an outlet or downstream connectivity are classified as endorheic (terminal) wetlands, and these systems that are highly sensitive to hydrologic inputs and climate conditions. Commonly, these terminal wetlands tend to become saline as salts accumulate over time if the system lacks a flushing mechanism (Skrzypek et al. 2016). They are predominantly fed by snowmelt and precipitation, although groundwater can supplement these sources (Wang et al. 2022). These systems are present throughout the Great Basin, situated predominately in Nevada, Utah, Oregon, and California, where increasing annual temperatures and changes in

precipitation patterns have led to warmer and drier summers that reduce wetland availability and function (Snyder et al. 2019). Endorheic water bodies are highly affected by upstream withdrawals and local water budget decisions as evidenced by conditions at Lake Abert (Oregon), Mono Lake (California) and Great Salt Lake (Utah) (Ficklin et al. 2013, Moore 2016, Null and Wurtsbaugh 2020). In terminal arid wetlands, water variability and distribution create a gradient of salinity and/or soil moisture that can support wetland vegetation, and specific characteristics that affect hydrology and abiotic characteristics create unique environments to support biodiversity.

Arid systems provide habitat for a multitude of fauna, and both the local conditions and their spatial arrangement at broader scales impact habitat use (Plissner et al. 2000, Donnelly et al. 2020). In the western United States, wetlands, wet meadows, and riparian areas provide stopover sites that maintain migratory connectivity, and the impacts of wetland loss or alteration can be amplified because of its spatial location relative to other wetlands in the flyway (Gilmer et al. 1982, Donnelly et al. 2020). Direct anthropogenic effects on wetland availability have already disrupted wildlife habitats (Sofaer et al. 2016, Heintzman and McIntyre 2021). Avian species richness has declined in arid regions in response to climate conditions; declines of up to 40% have been observed in the Mojave Desert (Iknayan and Beissinger 2018). Shorebird populations, especially those dependent on saline water bodies, are threatened as critical habitats are lost to desiccation and increased salinization (Moore 2016). Water variability in arid wetlands provides a range of conditions for wildlife, but water stress has large scale implications on the future of these systems (Gingerich et al. 2022).

While climate change may affect hydrologic processes in arid wetlands, anthropogenic impacts from water withdrawals for urban and agricultural land use currently exceed climate

change impacts (Abbott et al. 2019, Null and Wurtsbaugh 2020). In the western United States, 85% of water use is for agricultural purposes (Richter et al. 2020), and there is often insufficient supply for agriculture and city demands (Sabo et al. 2010). The overallocation of water rights in the western United States has decreased aquifer recharge and increased water shortages (Castle et al. 2014). Agricultural lands can provide some wetland functions utilized by birds, but conversion of these private lands that were historically flooded to drip-irrigation or other land-use changes limits their availability and function for birds (Donnelly et al. 2021, Moulton et al. 2022). Increased consumptive water use and groundwater depletions further compromise ecosystem resilience (Herbert and Döll 2019, Donnelly et al. 2022), and groundwater recharge is expected to decline by 30-70% in arid regions (Döll and Fiedler 2008, Niraula et al. 2017). Arid regions typically also experience high evapotranspiration (ET) rates, which further restricts water availability (Mu et al. 2007, Wang and Ma 2016). Increasing frequency and duration of droughts have depleted both surface water and groundwater levels as farmers and cities race towards increased water scarcity, and aquifer storage loss threatens the resilience of humans and ecosystems alike (Sabzadeh and Shourian 2020, Gingerich et al. 2022, Song et al. 2022). Restoration of arid wetlands can reduce anthropogenic influence on habitat and water availability while increasing flyway connectivity.

Restoration of degraded wetlands benefits from a process-based approach where abiotic processes (e.g., hydrology, nutrient cycling, and energy capture) are examined to implement a dynamic approach that can adapt to the unpredictable nature of ecosystems (Whisenant 1999). The timing, volume, and quality of water available to wetlands can have significant impacts on plant and animal communities (Hemond and Benoit 1988, Euliss Jr et al. 1999, Zedler 2000, Roshier et al. 2002). Restoring natural hydrology to a wetland system can improve connectivity

and encourage desirable plant communities to establish (Gosselink and Mitsch 2011). Vegetative communities are often the target for restoration as they form the basis for food chains in most ecosystems and maintain ecosystem stability (Shen et al. 2018) and are used as indicators of habitat quality for numerous species (Morrison et al. 2012). Emergent vegetation provides cover for wildlife as well as breeding areas for native fishes and migratory waterbirds (Fournier et al. 2021). Vegetation also reduces eutrophication by holding nitrogen and phosphorus, which is of particular importance in agriculture dominated watersheds (Silvan et al. 2004). In addition, hydrophytic vegetation improves water quality by trapping sediment (Shoemaker et al. 2022) and reducing turbidity, although sedimentation decreases seedbank diversity (Peterson and Baldwin 2004). Vegetation can also act as a buffer for wind by reducing fetch; it is estimated that up to 40% of wave thrust can be reduced by grasses and vegetation (Donatelli et al. 2018, Donatelli et al. 2019). The loss of vegetative cover is often related to disturbance, which can be a natural or anthropogenic, and this can provide a natural catalyst for succession or inhibit germination and survival of desirable plant communities (Garnier et al. 2004, Bernhardt-Römermann et al. 2011). For these reasons, vegetative communities are used as indicators of habitat quality for numerous wildlife species (Johnson 2007).

The relationship between environmental conditions and species-specific germination requirements provides a guideline for restoration when plant succession processes are interrupted, and abiotic and biotic variables can inhibit these processes (Van Der Valk 1981). Perennial plants such as broadleaf cattail and hardstem bulrush can also expand asexually under stable water conditions (Frieswyk and Zedler 2006, Wilcox et al. 2018) unless processes are disrupted. Therefore, examining seed production, seed dispersal, seedbank viability, germination

requirements, and other biotic and abiotic factors in the system is necessary to enact successful restoration plans.

1.1. Plant Succession Processes

Wetland plants have two main strategies for seed production: sexual and asexual. Sexual reproduction occurs through pollination and fertilization of male and female gametes, whereas asexual reproduction originates from only one parent. Sexual reproduction relies on pollination, which is spatially variable, especially in the case of wind-pollination (Ahee 2014). In wetland plants, asexual reproduction occurs when an existing plant grows through a modified stem or root system. This is especially common with perennial emergent species, such as *Typha*, *Schoenoplectus*, and *Phragmites*, although these species can also reproduce sexually. There is very limited research available that dictates conditions necessary for these rhizomes to expand, although there is some evidence that depth of burial may be important in determining biomass accumulation (Chen et al. 2014). Research by Grace and Wetzel (1981) found evidence that a physiological trade-off occurs when an individual utilizes both sexual and asexual reproduction. This interaction can be adapted to support primarily vegetative reproduction, specifically in *Typha* species, especially when competition exists (Grace and Wetzel 1981). This reproductive strategy is highly beneficial for wetland emergent vegetation because it eliminates seed dispersal and germination as limiting steps to survival.

Seed dispersal mechanisms are not typically limiting in wetland systems because wind and water are prevalent as agents of dispersal, but genetic diversity can become a problem in isolated systems (Lozada-Gobilard et al. 2021). Connectivity within the system is important to increasing seedbank diversity, particularly in fragmented ecosystems (Tewksbury et al. 2002). Dispersal by wildlife is also common, and small seeds have higher dispersal distances, especially

following consumption by waterfowl (Soons 2006). Wind dispersal is not directionally limited and can be particularly important in increasing seedbank dispersal in areas with defined flow directions, although fragmentation and anthropogenic alterations can limit this capacity (Soons et al. 2005). Dispersal by water is more limited because connectivity is required, and it is typically more successful in riverine systems where floodplain connections exist (Soomers et al. 2013). Once a seed has been dispersed, there is a window of opportunity for germination to occur while the seed is still viable. Nabity and Hoagland (2006) examined seedbank samples from 14 agriculturally altered saline wetland systems and found limited evidence of any wetland species present after 50 years. Viability is species and environmentally specific, and there has been little research targeting this information.

Germination can be limited by biotic and abiotic factors, and conditions necessary for germination and seedling survival are typically narrower compared to the conditions required for mature plants (Martini et al. 2019, Ssali et al. 2019). Many emergent wetland macrophytes require a drawdown for establishment (Van Der Valk 1981), and this can occur naturally in arid systems. Drawdowns can be natural or anthropogenic; in this study, drawdowns are natural events and are completely unrelated to any type of management activity. Germination can further be limited by soil moisture (Van Der Valk et al. 1999), temperature (Kettenring and Galatowitsch 2011), salinity, (Maas and Hoffman 1977), and light availability (Jurik et al. 1994) among other factors. Sedimentation decreases germination percentages of wetland species with small-seeded species (*Typha*) failing to germinate when buried even 1 cm (Galinato and Van der Valk 1986). Endorheic basins are often subject to high sediments and nutrients, and anthropogenic modifications such as channelization increase erosion of riverine systems and increase sediment inputs. Numerous studies have been completed on germination requirements

for wetland plants; several studies have found that cold stratification increased germination rates of most wetland species (ShIPLEY and Parent 1991, Kettenring and Galatowitsch 2007, 2011). If conditions are not suitable for germination, a seed may enter dormancy until ideal growing conditions arise (Karssen 1982, Baskin and Baskin 1985). Additionally, survival of germinants can be influenced by herbivory (Fraser and Madson 2008), soil moisture (Kaplan and Muñoz-Carpena 2011), and competition (Leck 1989). If germination conditions are suitable and the seedling survives, it will expand and begin reproducing.

Once reproductive stages are reached, an individual is generally considered established. The survival of this individual can be impacted by herbivory, competition, and other disturbances (e.g., fire). Herbivores contribute to vegetation loss through grazing of aboveground biomass and digging of root and rhizomes (Johnson and Foote 1997, Jobe et al. 2022). Fish communities can also function as a hindrance to plant survival through herbivory or sediment disturbance (Lougheed et al. 1998, Pearson 2020). Wind-wave action can also lead to decreased light availability by disturbing sediments and can affect expansion of existing vegetation. Additionally, newly established plants are susceptible to stress in the dormant season, especially where ice scouring occurs (Hill and Johansson 1992, Pugh and Davenport 1997). Restoring vegetation in wetland systems is complex and requires examining every stage of plant establishment to identify limiting mechanisms.

In this study, I employed a process-based approach to understand factors limiting vegetation establishment at Malheur Lake in eastern Oregon. Malheur Lake is a large endorheic basin that during most of the 1900s supported an inland, deepwater marsh system dominated by robust emergent vegetation interspersed with open water and submergent plant communities (Duebbert 1969). This wetland system supported around 180,000 migratory waterfowl and other

waterbirds and was an important stopover and breeding area for many waterbird species (Annual Narrative, 1997). Harney Basin, the drainage basin terminating at Malheur Lake, is also recognized as a Key Shorebird Area (Service 2013). Following a prolonged period of deep flooding during the 1980s, vegetation cover was lost from Malheur Lake, and vegetation reestablishment and expansion has been limited to the periphery of the lake, compromising its habitat values. The mechanisms preventing vegetation establishment and expansion are unknown.

1.2. Research Objectives

I identified and tested specific mechanisms relating to the failure of vegetation recovery at Malheur Lake, Oregon. I examined the wetland seedbank and plant establishment and expansion processes for three vegetatively reproducing perennial emergent species (*Bolboschoenus maritimus*; *Schoenoplectus acutus*; *Typha latifolia*) that have a historical and current presence on the lake. Through our plant succession model, we identified three specific objectives:

- (1) Determine seedbank presence and viability for perennial emergent vegetation.
- (2) Evaluate abiotic & biotic factors that may be limiting germination and establishment of perennial emergent seedlings.
 - a. Specifically, evaluate the effects of salinity, volumetric water content, and soil temperature on germination.
 - b. Examine the effects of herbivory on perennial emergent seedling survival.
 - c. Analyze soil and water chemistry characteristics that may limit germination.
- (3) Assess how a reduction in herbivory and wind-action affects existing perennial emergent vegetation growth and expansion using exclosures.

METHODS

2.1. Study Area

Malheur Lake is situated within Malheur National Wildlife Refuge in Harney County, Oregon (approximately 43.3° N, 118.8° W; Figure 2). The refuge was established in 1908 by the United States Fish and Wildlife Service (USFWS) to preserve migratory waterfowl and colonial nesting bird habitat (Service 2013). Malheur Lake is a large, shallow, endorheic basin that experiences extreme water fluctuations in response to snowmelt from the Blue and Steen Mountain ranges located to the north and south, respectively (Hubbard 1975, Pearson 2020). On average it spans about 19,600 ha (32 km long X 19 km wide) with an average depth of 0.58 m and maximum depth of 1.26 m (Adjei et al. 2015). It is fed primarily by two rivers: the Donner und Blitzen (hereafter, Blitzen River) currently contributes approximately 55% inflow, and the Silvies River currently contributes approximately 28% inflow, with contributions from direct precipitation and Sodhouse Spring— although groundwater outflow is negligible (Hubbard 1975) at about 30000 m³/day (8900 acre-ft/yr.) (Garcia et al. 2022). Both rivers were historically considered flashy and experience wide fluctuations in discharge, sometimes even failing to connect to Malheur Lake (Piper et al. 1939). The lake is typically ice-covered during winter months. Water depth increases following snowmelt in late spring and gradually declines throughout the summer, and lake size and depth are affected by both snowpack and anthropogenic withdrawals, including agriculture. Although it is common for endorheic lakes to accumulate salts, United States Geological Service (USGS) studies, however, indicate relatively low salinities in Malheur which suggests regular removal of salts from the system. Specific conductance in the lake has measured between 300 to 3500 uS/cm, or about 0.14-2 PSU (Wood and Smith 2022).

Malheur Lake is situated within the Harney Basin, which consists of alluvial plains and playas covering approximately 1,357,000 hectares of eastern Oregon (Garcia et al. 2022). Harney Basin is characterized as a high desert ecosystem, approximate elevation 1280 m, and it features a wide range of air temperatures with average lows around 3 °C and average highs around 30 °C during the summer months. Harney, Malheur, and Mud Lake are the three dominant playas within the Harney Basin, and surface peat deposits up to 0.75 m were recorded at the latter two lakes in the early 1900s (Piper et al. 1939). The Narrows Pedon, which is on the northwest side of the lake (43° 20' 34.00", 118° 53' 41.99"W), is characterized as a calcareous, frigid Typic Halaquept (National Cooperative Soil Survey). Malheur Lake receives the dominant inflows from the basin, and surplus drains into Mud and Harney lakes; Harney Lake serves as the terminus of the basin when these lakes connect (Figure 2). Harney basin receives less than 25 cm of precipitation annually and is characterized by low humidity and high evaporation (Fusté and McKenzie 1987). Additionally, strong winds are common in this region, especially between March-June (Piper et al. 1939).

The basin was formed by volcanism, glaciation, and erosion processes dating back to the Quaternary Period. Alluvium and lake deposits filled the valley, and geologists concluded that the formation of Harney Basin occurred after an extrusion of basalt dammed Malheur Gap, cutting off the basin's outlet (Duebbert 1969, Dugas 1998). Groundwater movement varies within the basin depending on strata, and it is believed that sand and gravel deposits function as recharge areas for the unconfined aquifer. Historically, depth to the groundwater table was observed between 2.5-4.3 m beneath Malheur Lake, although it may be nearer to the land surface at river inlets (Piper et al. 1939). However, irrigation consumption has increased dramatically since those observations; maximum surface water volume reached 408,600 m³/day (121,000

acre-ft/yr.) in 2017, and groundwater irrigated fields peaked around 270,000 m³/day (80,000 acre-ft/yr.) between 2014-2018 (Beamer and Hoskinson 2021). Water use and natural variation within the basin over the last century have contributed to increased water stress for humans and wildlife within the region.

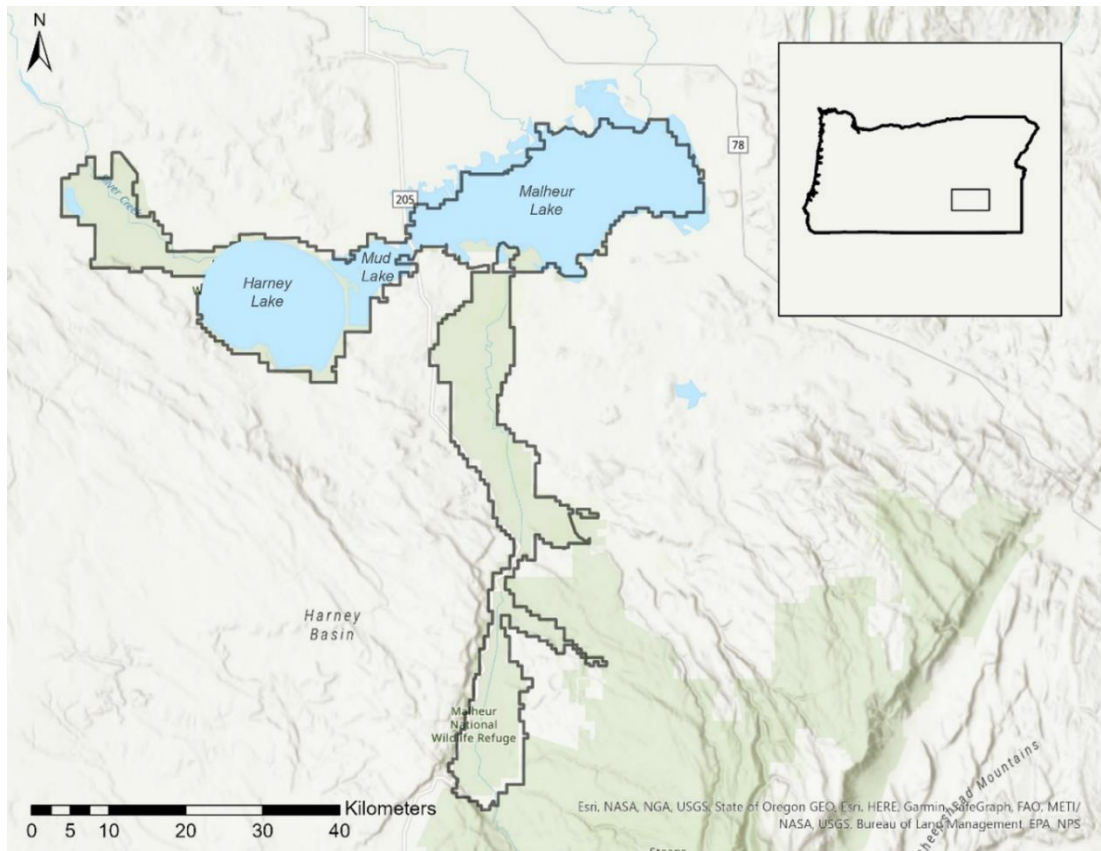


Figure 2. Map of Malheur National Wildlife Refuge boundaries.

Historic lake area is highly varied over geologic time, and in the last century it has seen lows of 500 hectares (ha) to highs around 30,000 ha (Dugas 1998, Pearson 2020). The lake was almost completely dry in 1889, and historical records suggest that the lake may have been relatively small prior to 1864 (Piper et al. 1939). In the early 1930s, low riverine inputs reduced the lake to less than 200 hectares, and desiccation continued until the following spring (Piper et al. 1939). Variability in snowmelt and climate conditions have led to frequent drawdowns in mud-flat regions where vegetation may be able to establish (Piper et al. 1939, Van Der Valk

1981). Piper et al. (1939) note that water altitude on the lake is affected by the rate of inflow, the intensity of wind, and the disposition of ‘tules’ (emergent vegetation). Malheur Lake supported a productive emergent marsh throughout much of the 1900s, but prolonged, deep multi-year flooding occurred in the 1980s eradicating Malheur’s emergent vegetation from the central reaches of the lake, leaving surviving vegetation only along the periphery of the lake (Pearson, 2020). The lake currently exists in a turbid state, and the specific mechanisms inhibiting vegetation have not been identified. With little vegetation to slow wind, high winds often alter hydrology on a daily and even hourly basis (Figure 3). The fetch, the length of water over which wind can blow without any obstruction, is currently as long as 14 kilometers (~8.7 miles). Predominant winds from the southwest often push the water to the north end of the lake, which reduces and even eliminates water retention in the southwest area of the lake for short periods of time. This natural variation in water depth and location supports a dynamic wetland system albeit sparsely vegetated.



Figure 3. Example of seiche effects over 15 hours in June of 2021 (north open germination set; 43.309552, -118.826130). This illustrates a common occurrence in the summer months along the periphery of the lake as winds can shift water quickly.

Malheur Lake's location and unique resources presents an ecologically important system that supports an incredible diversity of bird fauna. In the 1960s, it produced 15,000 ducks and 1,000 Canada geese annually (Duebbert 1969). Dabbling duck production in the 1990s averaged between 10,000 to 16,000 annually, whereas diving duck production averaged between 2,000 to 6,000 annually (1997 Annual Report). In addition to nesting and breeding habitat, Malheur Lake also functions as a migration stopover site on the Pacific Flyway. Between the years of 1957-1965, migratory waterfowl numbers averaged 400,000 ducks, 75,000 geese, and 3,500 swans annually (Duebbert 1969). Refuge surveys from 1997 presented a decline in spring migration observations with around 180,000 migratory waterfowl (Annual Narrative, 1997). The lake also provides habitat for colonial waterbirds including Double-crested Cormorants (*Phalacrocorax auratus*), American White Pelicans (*Pelecanus erythrorhynchos*), and Caspian Terns (*Hydroprogne caspia*). The number of nesting pairs of colonial waterbirds declined from around 1500 in the late 1980s to below 500 in the late 1990s (Annual Narrative, 1997). Low water levels from 2020-2022 also decreased breeding success dramatically. Airboat surveys and aerial surveys in 2020 observed no evidence of breeding on Tern Island (M.A. Martinez, personal communication, February 2, 2023). However, in low water years, shorebirds utilize the lake for breeding and as stopover grounds; Harney Basin is recognized as a Key Shorebird Area (Service 2013). The most prevalent shorebirds observed include Long-billed Dowitcher (*Limnodromus scolopaceus*), American Avocet (*Recurvirostra americana*), Dunlin (*Calidris alpina*), and Willet (*Tringa semipalmatus*) (Annual Narrative, 1997).

The Malheur Lake system also supports Redband trout (*Oncorhynchus mykiss* spp.), which is listed as a species of concern through the Endangered Species Act of 1973. This population is genetically unique due to the closed basin system, and the Oregon Department of

Wildlife and Fisheries (ODFW) is predominantly concerned with water quality, water quantity, and habitat quality. Drought plays a significant role in this population's survival, and arid climates are susceptible to increased frequency and duration of drought through anthropogenic and natural climate change (Jonsson and Jonsson 2009).

2.2. System Modifications

In addition to the increased surface and groundwater irrigation described above, the Malheur Lake system has experienced several anthropogenic modifications. Irrigation ditches were constructed to divert water from the Blitzen River beginning in the late 1800s, and center pivot irrigation has increased throughout the region in the last several decades (Gingerich et al. 2022). The Blitzen River was channelized from Bridge Creek Canal to Krumbo Lane in 1907-1913 (Figure 5), and channel incision was documented upstream of the channelization. Bank sloughing is also evident along the Blitzen. Previously, this portion of the river was slow moving and meandered throughout the floodplain (Piper et al. 1939). The construction of weirs throughout the river has also promoted channel erosion (Salant et al. 2010). Additionally, common carp (*Cyprinus carpio*), hereafter 'carp', were introduced into the system in the late 1800s, and a large population exists within the current Malheur Lake system (Pearson 2020).

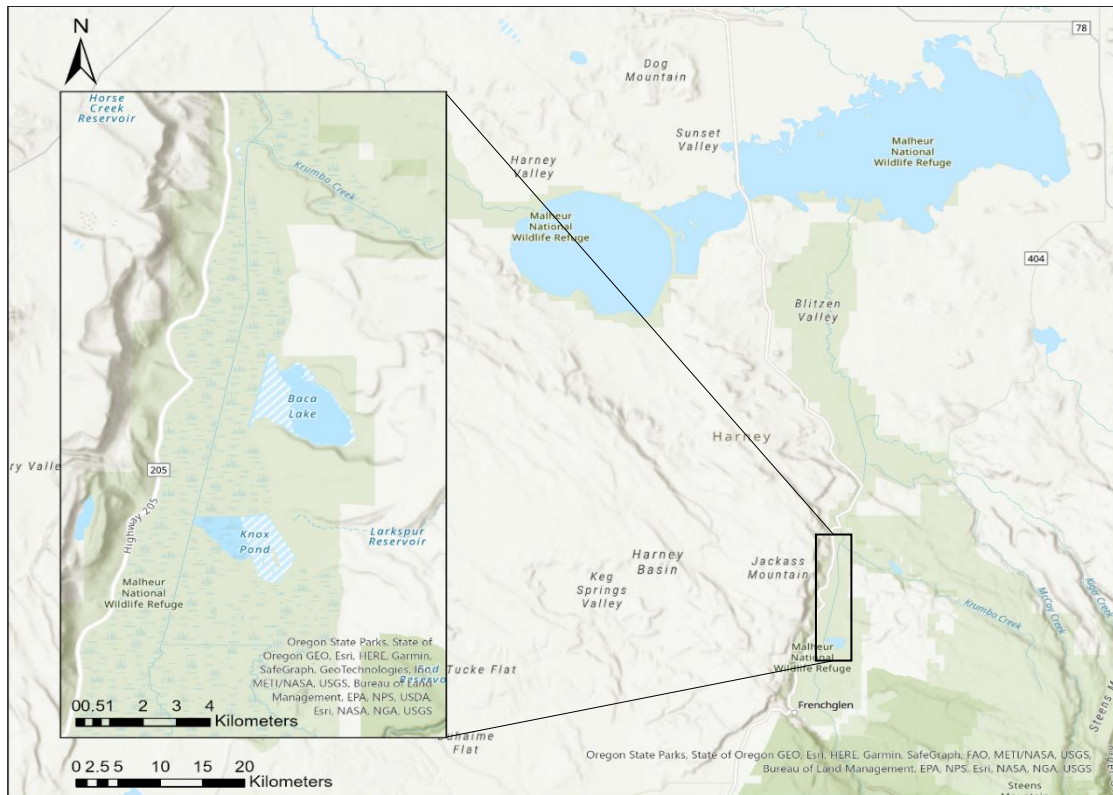


Figure 4. Channelized portion of the Blitzen River on Malheur NWR.

2.3. Previous Research and Management Actions

While restoration of vegetation has been a goal for refuge managers to reduce wind fetch, stabilize sediments, and improve bird habitat, there has been little progress. Spencer (1994) conducted surveys across six transects to evaluate recruitment on Malheur Lake. The emergent seedlings did not survive when water levels receded, although there were no indicators of drought stress on germinants. Additional research has targeted reductions and removal of invasive common carp to reduce turbidity and reestablish vegetation. Pearson (2020) conducted model simulations of carp removal below 50 kg/ha. Pearson's study ultimately determined that removal and management of carp must be paired with a broad systems approach for long-term success including wind reduction, vegetation expansion, and nutrient load reduction.

Refuge biologists began addressing vegetation restoration directly by introducing a pilot study in 2020. They constructed 4.8 m x 4.8 m plots using a combination of hog panel, hardware

cloth, and t-posts to observe vegetation responses. Refuge managers were primarily interested in vegetation establishment in Unit 4 because emergent vegetation is robust along the periphery of this section of the lake, so the pilot exclosures were set up within that region (Figure 5).

Hardware cloth was placed on the hog panels to restrict juvenile carp from the plots. Some exclosures were set up around existing vegetation clumps, while others were placed around bare soil patches. Throughout the growing season (May-August 2020), in some plots, they observed increased germination of perennial emergent and annual plants within the bare soil plots compared to areas directly outside the exclosures. They also noted a potential reduction in herbivory (seedhead consumption) for the exclosures around existing vegetation clumps.

These results were encouraging, but variability in presence of seedlings and low stem densities in most plots raise questions about processes limiting plant germination and establishment. We could not experimentally test all phases of plant succession, but we used this model to identify the most relevant questions for further analysis based on previous management actions and lake conditions. Although limited research has been done to establish vegetation lifespan, propagule longevity, and establishment requirements for each wetland species, we can infer based on historic conditions and observations of the species to apply van der Valk's Gleasonian approach to vegetation restoration.

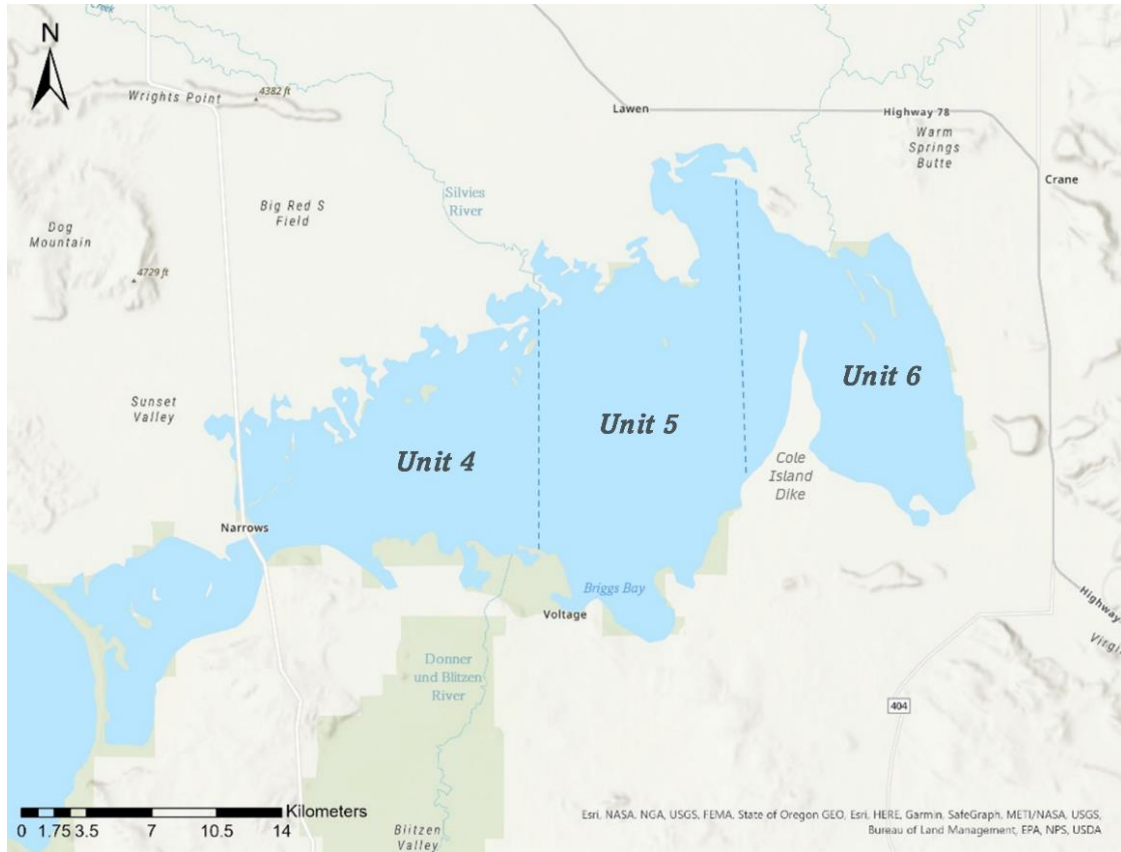


Figure 5. Malheur Lake divided into management units 4, 5, and 6.

2.4. Perennial Emergent Vegetation Species

Three perennial, vegetatively reproducing species that commonly occurred on the lake prior to the 1980 floods and continue to survive in limited regions presently. These species are hardstem bulrush (*Schoenoplectus acutus*), broadleaf cattail (*Typha latifolia*), and alkali bulrush (*Bolboschoenus maritimus*) (Figure 6). Based on previous observations of these species, all require a drawdown to germinate (Van Der Valk 1981).

Initial surveys of the lake provided an insight into the presence of these species on the lake. Alkali bulrush, typically a pioneer species, tolerates high salinity and basic pH, which suits conditions at Malheur when water levels are low (Kettenring 2016). This species is prevalent in saline wetlands that are flooded in the spring and early summer, and it tolerates late season drought and high pH (Ljevnaić-Mašić et al. 2020). However, the species has not expanded or

produced high density coverage in the lake. It is currently limited to the western portion of Unit 4 and can rarely be seen in the southern portion of Unit 5. Broadleaf cattail stands commonly occur in the southern portion of Unit 5. *T. latifolia* germination requirements include high temperatures (35°C), low oxygen concentrations, and prolonged sunlight exposure (Bonnewell et al. 1983). *Typha spp.* often proliferate rapidly in systems with anthropogenic disturbances (Newman et al. 1998). *T. latifolia* locally adapts to salinity concentrations in many cases, and it commonly survives in salinity ranges of 0-8 ppt (Freeland et al. 2020). Cattail germinants can be found throughout Unit 4 and the southern portion of Unit 5 during the early growing season, but historically they have not been able to establish and survive in Unit 4 (G. Ivey, personal communication, August 5, 2021). Hardstem bulrush occurs in all units of the lake. Flooding and inundation decrease survival of seedlings due to oxygen depletion and cause mortality for *Schoenoplectus spp.* due to low carbon storage (Sloey et al. 2016). Additionally, Sloey et al. (2016) found that *S. acutus* responded negatively to prolonged flooding and may require air exposure for a minimum of 40% of the day. Specific salinity tolerance for *S. acutus* is unknown, but this species commonly persists in saline environments. At Malheur, this species is currently established along the periphery of the lake, but there are especially dense areas in the western portion of Unit 4 and the southern portion of Unit 5. It can also be found dispersed in patches east of Cole Island Dike in Unit 6 (Figure 4).

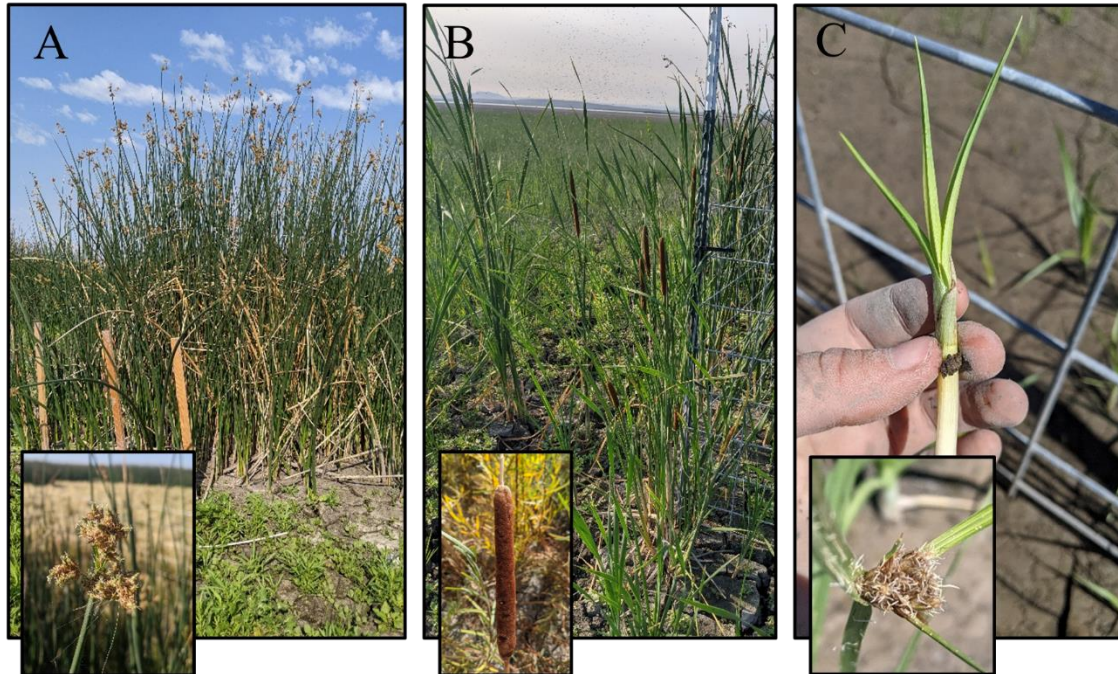


Figure 6. Common vegetatively reproducing perennials found on Malheur Lake (a) *Schoenoplectus acutus*, (b) *Typha latifolia* Broadleaf Cattail, and (c) Alkali Bulrush *Bolboschoenus maritimus*.

2.5. Soil and Water Analysis

To evaluate potential effects of abiotic characteristics within the soil (salinity, pH, nutrients, metals, soil texture), I used a 4-inch PVC soil core to collect samples from three locations on the lake (Figure 7). At each location, the samples were split by depth: 0-30 cm and 30-60 cm. Each sample was placed in a Ziplock bag and stored in a freezer until lab analyses. Samples were analyzed using Mehlich 3 (macronutrient and micronutrient) tests and flood tests (A.1) by the Soil Testing and Plant Analysis Laboratory at Louisiana State University. We also utilized National Cooperative Soil Survey (NCSS) data to explain lake chemistry dynamics.



Figure 7. Soil samples from Unit 4 (left) and Unit 5 (right) taken for analysis.

Additionally, I collected five, 50 mL water samples for nutrient and metal testing (A.2). Sample sites included Malheur Lake (2), Blitzen River, Silvies River, and a greenhouse water sample. Samples taken from the lake were collected from areas deep enough that soil inclusion would not bias the results, but samples were not filtered. Water samples were processed by the Wetland Biogeochemistry Analytical Services (WBAS) Laboratory within the Department of Oceanography and Coastal Sciences at Louisiana State University.

2.6. Seedbank Presence and Viability

To determine the presence and spatial variability of the seedbank, we initially conducted a visual survey of the lake to identify gross differences in abiotic conditions and environmental settings by periodically evaluating morphological attributes of soil cores and noting differences in vegetation composition. Based on this information, a stratified random sampling design was used to randomly distribute sampling plots within broadly recognizable features. These features include inlets of tributaries and areas with distinct soil structure and texture.

At each site, an Eckman Dredge (15.2 cm x 15.2 cm x 15.2 cm) was used to collect three samples (Art's Manufacturing & Supply Inc. American Falls, ID). A minimum volume of 1570 cm³, as determined by Hutchings 1986, was collected for each sample. In 2021, Units 4 and 5 were targeted for intensive sampling. Fifteen sites within these units were selected to extract soil samples. An additional two sites outside these units were selected to include the inlet of the Blitzen River and an area on the north end of the lake with a distinct blocky soil structure. In 2022, additional samples were taken from previously unsampled regions in Units 5 and 6 to test seed bank presence throughout the lake. The same methodology was followed as described for the first season, and we collected 3 samples each from 10 new sites for a total of 30 samples.

Thus, over our two field seasons, we collected 3 samples from 27 sites, resulting in 81 samples (Figure 8).

These samples were transported to a greenhouse where the samples were spread on 1-2 cm of perlite in an aluminum foil pan (20 x 20 x 4 cm) with drainage holes. Each pan was randomly assigned a position on a bench with all pans being equidistant from adjacent pans (Figure 9). The bench was constantly flooded at 2 cm to provide moisture while preventing pan inundation (Elsey-Quirk and Leck 2015). Greenhouse temperatures ranged approximately 20-40°C during the growing season. Samples were supplementally watered every 2-3 days to maintain field capacity conditions, and they were checked for new germinants at this time. Once the plant could be identified, it was recorded and removed to prevent crowding. We were predominantly interested in the presence of perennial emergent vegetation (hardstem bulrush, broadleaf cattail, and alkali bulrush), but all species were identified and recorded. Samples that could not be identified were sent to the Oregon State University Herbarium to identify. For some annuals, reproductive stages were never reached, and we could only identify to genus or family.

We expected that maintaining a constant water level throughout the year would provide moisture necessary for wetland vegetation to germinate. Providing adequate moisture was meant to facilitate the germination of perennial emergent vegetation species. These conditions replicated a drawdown in soils which is necessary for these species to germinate while providing enough moisture to fulfill plant requirements.

2.6.1. Data Analysis

I calculated summary statistics for both years of the greenhouse experiment. I also calculated the percent success of our perennial emergent target species by sampling location. The lack of replication between years did not allow for strict comparisons between years, although to

examine a potential relationship, I selected nine sites from 2021 and four sites from 2022 that were close in proximity (within 3 square kilometers) and performed a simple linear regression (Figure 10). We also classified each site into a broad region: North, South, East, and West to compare potential gaps in seed dispersal and seedbank presence using an Analysis of Variance and Tukey's post hoc comparisons (Figure 11). Average richness and the Shannon Diversity Index (SDI) were calculated for all samples and species detected (Hu et al. 2022).

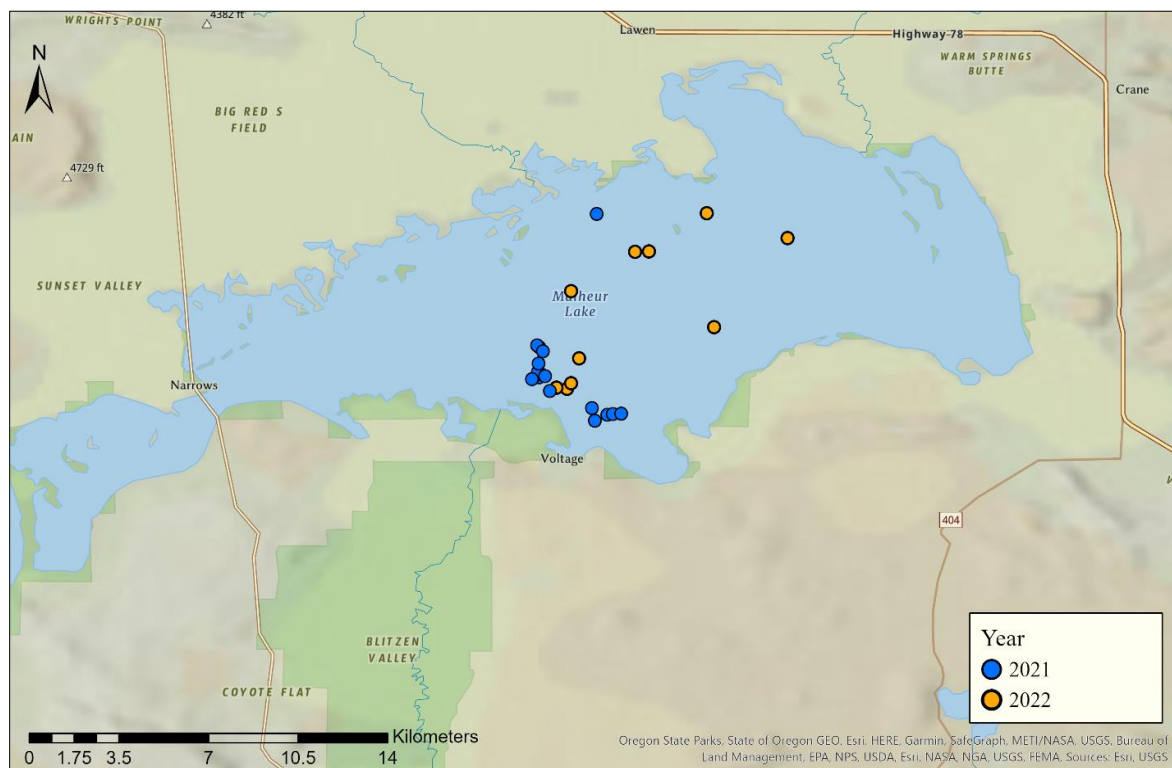


Figure 8. Locations of soil sample sites with sampling year designated by color. Seventeen sites were sampled in 2021 (blue) and ten sites were sampled in 2022 (orange).



Figure 9. Greenhouse sample set up in 2021. Greenhouse plastic was used to maintain the 2-3 cm waterbed.

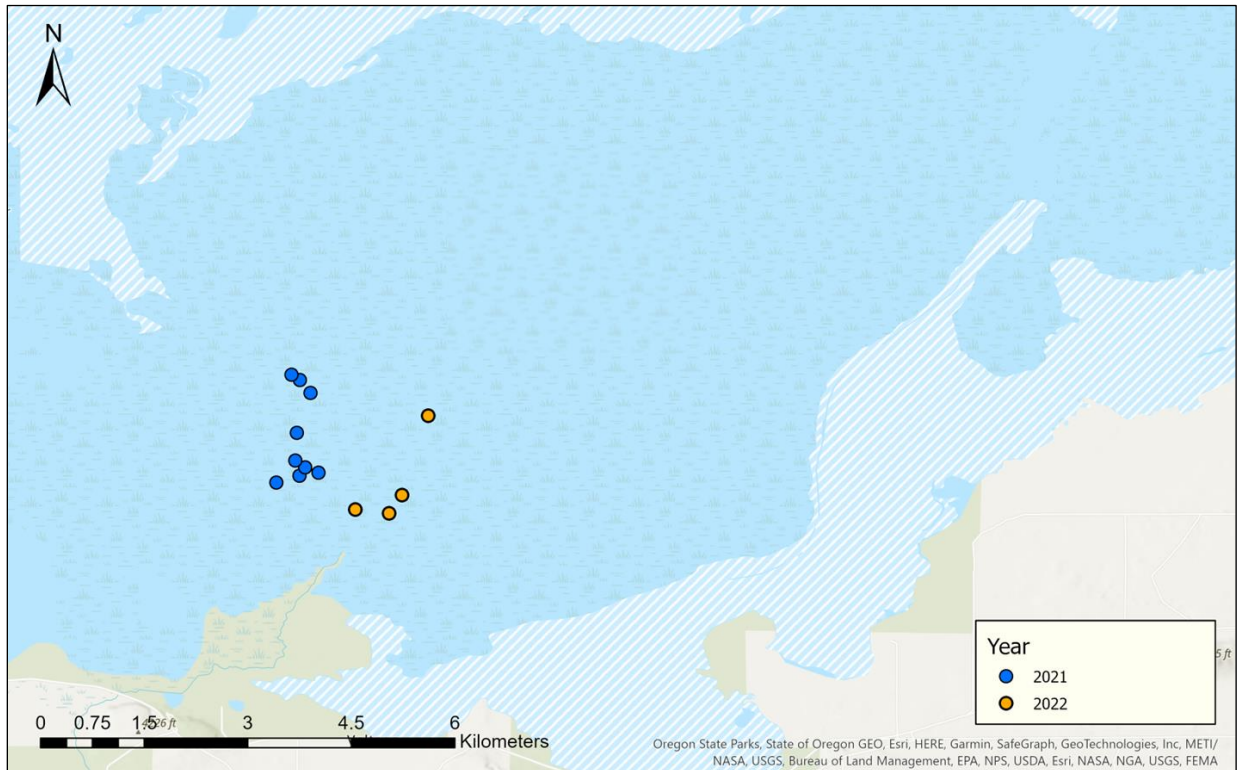


Figure 10. Sites selected for comparison between years in the western region of the lake.

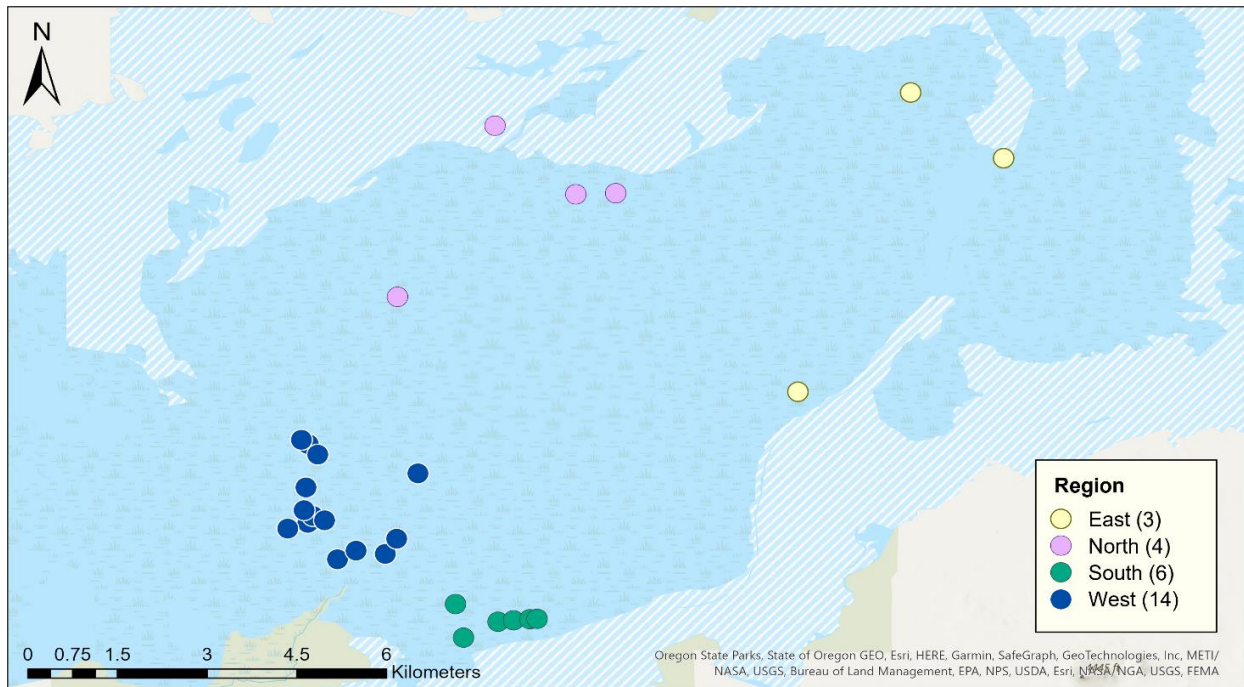


Figure 11. Greenhouse sample locations classified by region.

2.7. Examining Germination Conditions on the Lake

2.7.1. Exclosure Construction

To evaluate germination in the field, I established germination exclosures (G-exclosures) within three broad regions of Unit 4: South, Central, and North (Figure 12). G-Exclosures are a designated area that excludes herbivory through a physical barrier. In each of these regions, I constructed three sets of 4.8 m x 4.8 m² G-exclosures consisting of: 1 control (t-posts only) and 1 hog panel exclosure with hardware cloth covering (Figure 13). There were 9 controls and 9 hardware cloth G-exclosures constructed across the three regions. I assumed that water depth would increase from the current shoreline towards the perceived center of the lake. Along this transect line, three germination sets were constructed at varying water depths: Shallow (1 cm), Mid (5 cm), and Open (7 cm). There was no existing vegetation inside exclosure sites at the time of set up.

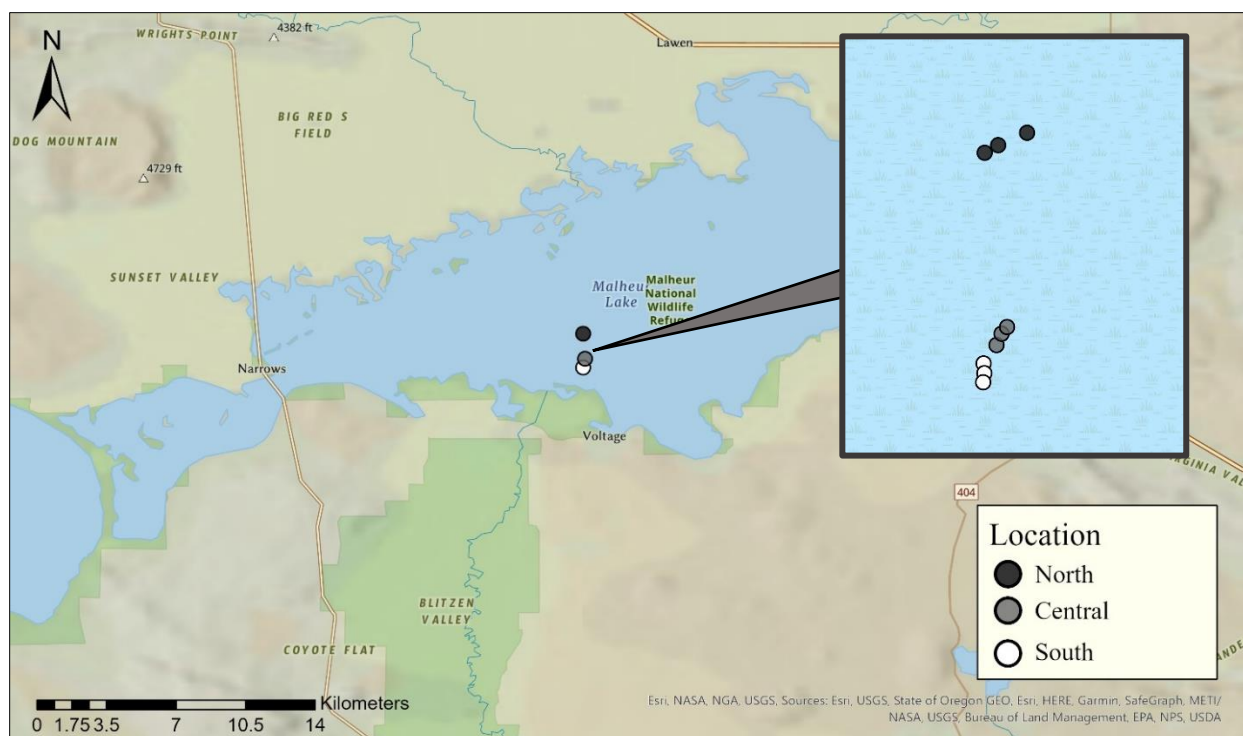


Figure 12. Germination enclosure locations by site. Each dot represents a hardware cloth enclosure and a control.



Figure 13. Set up of germination enclosures at Malheur Lake in 2021 in the southern region (left) and the northern region (right).

2.7.2. Growing Season Measurements

From May 2021- September 2021 and June 2022 – Sept 2022, weekly water levels were measured at all G-exclosures. On a bi-weekly basis (every two weeks), I counted and identified new germinants and seedlings. Additionally, instantaneous volumetric water content (I-VWC), salinity, and soil temperature at the surface were recorded bi-weekly (ProCheck and Teros 12 sensors; METER group Inc., Pullman, Washington). In saturated wetland soils, VWC ranges approximately 50-60% depending on sediment and organic matter concentrations, and these values can also be indicative of oxygen availability. In 2022, I also measured these variables at a depth of 10-15 cm. Initially, I counted all germinants within the entire 4.8 m x 4.8 m G-exclosure, but this method became unfeasible due to the large number of germinants observed throughout the growing season in 2021. Thus, I terminated this procedure and established three 1 m x 1 m plots within each enclosure to count and identify germinants starting in September 2021. For data analysis purposes, all measurements were converted to counts per square meter.

2.7.3. Germination Transect

Based on previous refuge conditions and Landsat images in the winter of 2021, I suspected that our 2022 field season would continue to exhibit drought and low water levels. To evaluate the effects of soil moisture on germination, I created a new transect to accommodate these drought conditions. Sampling plots were randomly placed every 125-150 m along a perceived moisture gradient in Unit 4 toward the lake center (Figure 14). Fifteen plots were set up on this transect in June 2022, and six data loggers were distributed at transect plots to measure continuous volumetric water content (C-VWC), salinity, and soil temperature every fifteen minutes (Figure 15; ZL6 Advanced Cloud Data Logger; METER group Inc., Pullman, Washington). Each data logger had two Teros 12 Sensors at depths of 2-5 cm and 50-55 cm.

There was no existing perennial emergent vegetation in these sites at the time of set up. Each site had three 1 m by 1 m plots that were monitored and evaluated in the same methods as described for the G-exlosures.



Figure 14. Set up of germination transect plots in 2022. Colored flags were used to mark 1 m x 1 m plots in each plot. Six sites had data loggers (left) and 9 sites had no data logger (right).

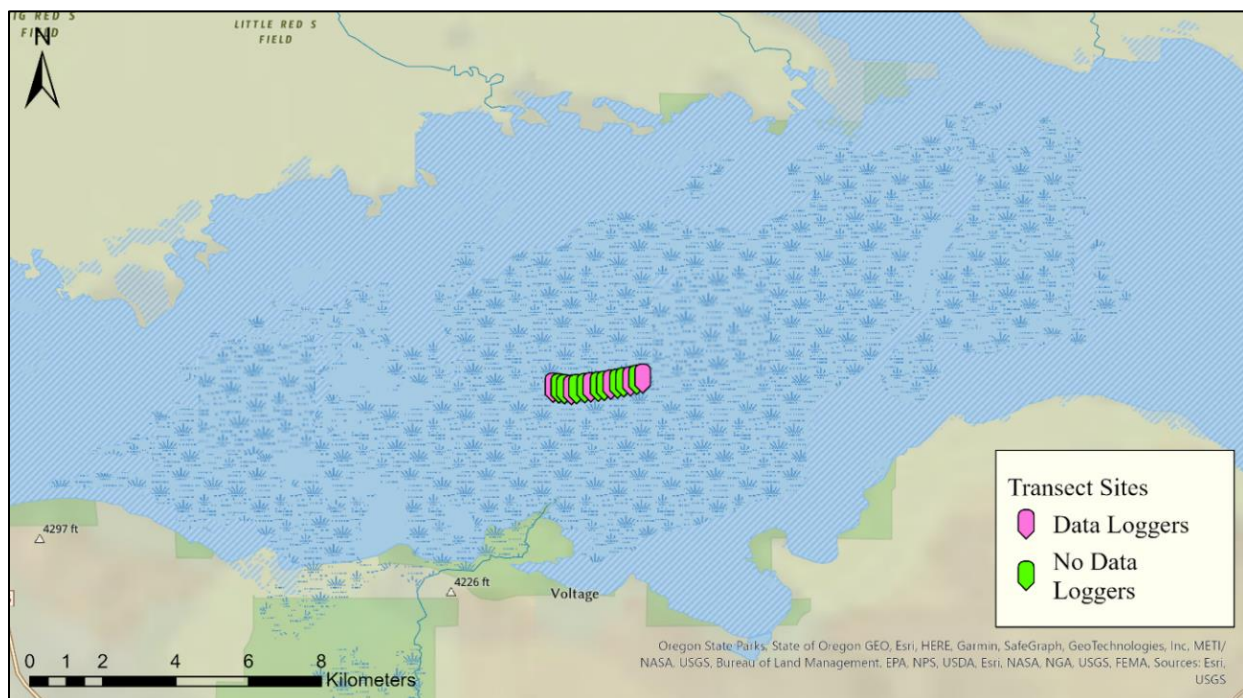


Figure 15. Germination transect locations by site along a 1.8 km transect towards the perceived center of the lake. Site 1 is the western-most site, and site 15 is the eastern-most site.

2.7.4. Data Analysis

Apparent mortality was calculated as the difference between sampling events when counts declined. Apparent new germinants were calculated as the difference between sampling events when counts increased. Because we sampled every two weeks, we cannot ascertain precise numbers of new emergence and mortality, but these variables represent the minimum amount of flux between weeks which assists in assessing our predictors' effects on germination and survival of seedlings. A Poisson Regression model was used to assess the relationships of I-VWC, salinity, and soil temperature on the number of new germinants and seedlings for perennial emergent vegetation species. In addition, I added a binomial predictor of flooding presence that indicated if the site had been flooded the previous week. Response variables in these models included new germinant and seedling counts, apparent mortality, and apparent new germinants. Apparent mortality and apparent new germinants models were fitted for transect data because of the flux in counts combined with variation in water levels that could be analyzed. Generalized linear models were fitted with site as a random effect for each independent variable in 2021 and 2022. High correlation coefficients were observed between variables; therefore, I completed a Principal Component Analysis (Jolliffe 2002) to find the best-fit model. Independent variables, including I-VWC, salinity, soil temperature, and depth, were centered and scaled for analysis. All combinations of these variables were fitted to multivariate generalized linear models, and I compared the model Akaike information criterion (AIC) values to determine the model that explained the most variance.

2.8. Hardstem Bulrush Expansion

To determine the effects of herbivory and wind-wave action on expansion of hardstem bulrush, exclosures were constructed in Units 4 and 5 (Figure 16). Initially, I surveyed the lake for areas with at least three large clumps of hardstem bulrush exclosures as these areas are believed to have a higher potential of success due to the increased presence of existing vegetation and potential protection from the predominant wind direction. In May 2021, exclosures (4.8 m X 4.8 m) were established along an elevation gradient. Each exclosure was centered around existing clumps of hardstem bulrush that had a width and length between 1.5-2 meters. Nine sites were chosen for either herbivory (H-exclosures) or wind exclosures (W-exclosures). Various exclosures types were constructed using hog wire panels, hardware cloth, plastic sheet panels, and/or T-posts (Figure 17). In total, we constructed 9 controls, 9 hog wire exclosures, 6 hardware cloth exclosures, and 3 hog wire with sheet panel exclosures. Additionally, four exclosures were fitted with trail cameras to identify any potential herbivores; these were checked monthly. Two of these were placed in the southern portion of Unit 5 (Briggs Bay), while the other two were placed in Unit 4.

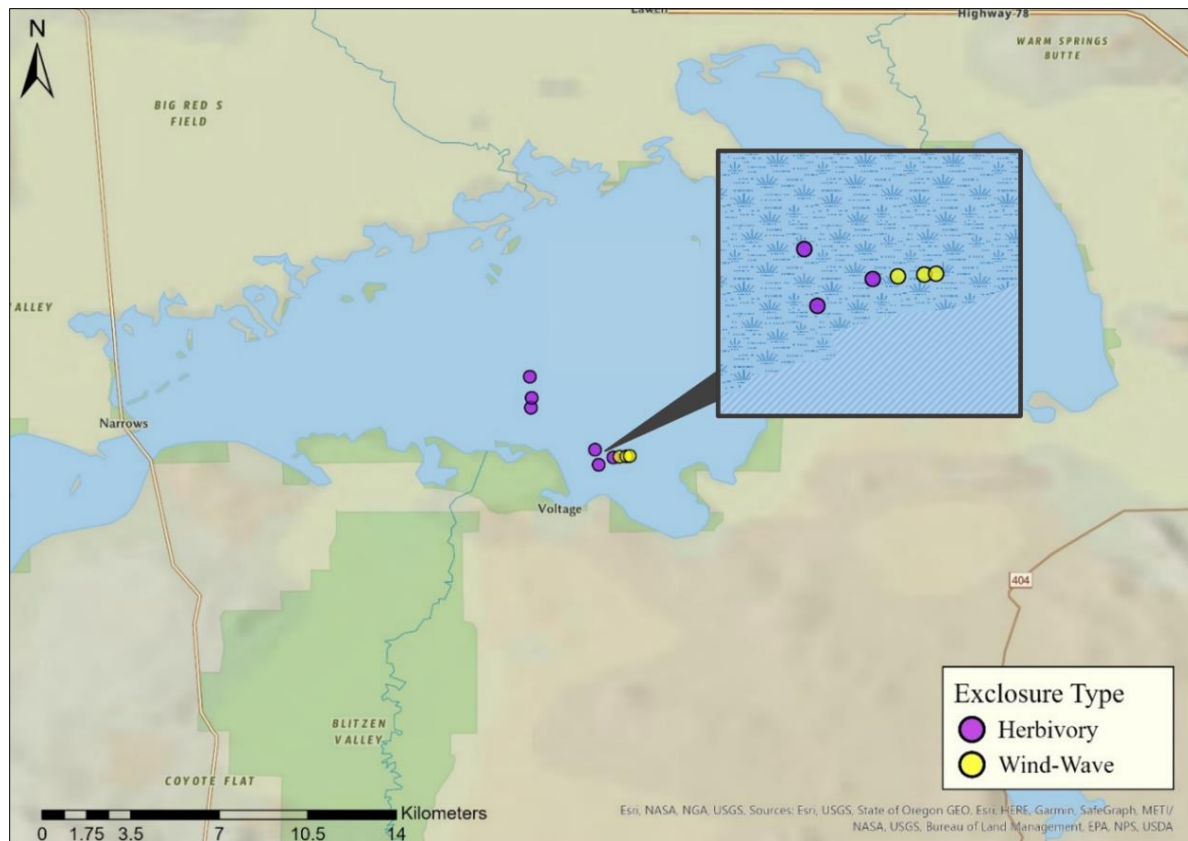


Figure 16. Exclosure locations by type. Each dot represents three constructed exclosures. For H-Exclosures (purple), this includes a control, hog panel exclosure, and hardware cloth exclosure. For W-Exclosures (yellow), this includes a control, hog panel, and hog panel with plastic sheet panel barriers.



Figure 17. Example set up of exclosures in 2021. A hog wire panel exclosure (left) with wooden stakes marking rhizomes and a hog panel with wind barriers (right) that blocked the predominant wind direction from the southwest.

2.8.1. Herbivory Exclosures (H-Exclosures)

Six sites were chosen for an analysis of the effects of herbivory on vegetation establishment. These were distributed evenly in Unit 4 and Unit 5. At each site we constructed three exclosure types: hog panel only (6), hog panel with hardware cloth (6), and t-posts with no panels (6). The hog panel and hog panel with hardware cloth exclosures were both used to examine a reduction in herbivory. The t-post exclosure was included as a control for the site.

2.8.2. Wind Exclosures (W-Exclosures)

Three sites were selected for analysis of reduction in wind-wave action; these were constructed in the southern region of Unit 5 (Briggs Bay). At each site we constructed three exclosure types: hog panel only (3), hog panel with sheet panels barriers (3), and t-posts controls with no panels (3). Hog panel with sheet panel barrier exclosures were tested as a wind-reduction technique. The sheet panels were constructed to protect from the predominant wind direction from the southwest. The hog panel only exclosures were an additional type of control where we excluded the potential influence of adult carp from biasing our results. T-post ‘exclosures’ were included as controls.

2.8.3. Growing Season Measurements

To track overall growth of each vegetation clump, three measurement windows were designated at the beginning, middle, and end of the growing season following exclosure set-up in May of 2021. These measurements were completed in both 2021 and 2022 field seasons. The beginning season measurement occurred in the last week of May or the first week of June, the mid-season measurement occurred in mid to late July, and the end of season measurement occurred at the end of September for each year. First, we identified and measured the longest diameter possible for each clump, and from there we took three additional diameters of the

clump every 45°, totaling four diameters. The azimuth of each diameter was recorded to repeat for future measurements. Second, we set out wooden stakes parallel with the furthest standing shoot so that we could monitor rhizome expansion throughout the growing season. A maximum of 10 stakes were set out for each exclosure to try and capture this growth. These stakes were placed during the pre-season measurements each year, and they were moved to mark growth during the mid-season measurement. Lastly, we recorded a visual estimate of vegetation surface area coverage (%) within the exclosure.

Each week, water levels were measured at each exclosure. Bi-weekly (every two weeks), we recorded instantaneous salinity, volumetric water content, and soil temperature (ProCheck and Teros 12 sensors; METER group Inc., Pullman, Washington). We also recorded evidence of herbivory (missing seedheads, tracks inside exclosures) and surface area coverage (%) of the vegetation clump on a biweekly basis.

2.8.4. Data Analysis

Using the four diameters, we were able to construct an approximate area of each vegetation clump throughout the growing season. Using these areas, we calculated the growth (in square meters) between each measurement event. We subset the exclosures by location and growing season (May-July; July-September) to compare expansion rates between exclosure types (hog panel, hardware cloth, control, hog panel with barriers). Analysis of variance was performed for all exclosure types in 2021 and 2022.

RESULTS

3.1. Soil and Water Analysis

3.1.1. Soil Analysis

Calcium extractable salts ranged between 6900-12000 ppm (Table 1). The pH of the system is slightly alkaline, ranging from 6.95-8.65 at our sampled sites (Table 1). The flood test revealed a notable difference in sodium concentrations, with low concentrations observed at Unit 5 North. Flood test salts ranged from 600-2400 ppm, and conductivity ranged between 0.94-3.78 dS/m. Soil textures from depths of 0-60 cm were fine sandy loams and silt loams (Figure 18).



Figure 18. Soil textures at depths 0-60 cm.

Table 1. Soil analysis results from Flood Test (top) and Mehlich Extractable Salts (bottom).

Site Identification		Flood Test								OM Test
Site	Depth	Ca, ppm	Cl, ppm	Cond., dS/m	Mg, ppm	Salts, ppm	SAR	Na, ppm	S, ppm	% OM
Unit 5, South	0-30 cm	68.37	4.24	0.94	22.92	604.16	3.45	129.09	71.62	>5.5
Unit 5, South	30-60 cm (1)	83.12	10.93	1.24	24.18	794.88	4.6	185.14	112.37	>5.5
Unit 5, South	30-60 cm (2)	79.92	14.31	1.77	23.66	1134.08	4.8	190.05	121.62	>5.5
Unit 5, North	0-30 cm	114.74	37.67	3.78	42.09	2417.92	0.13	6.37	296.6	>5.5
Unit 4	0-30 cm	143.77	12.61	1.91	52.17	1222.4	4.7	258.94	218.87	>5.5
Unit 4	30-60 cm	45.64	8.97	1.08	16.22	689.92	4.54	140.21	37.77	1.71

Site Identification		pH, Mehlich Extractable Salts								
Site	Depth	pH	P, ppm	K, ppm	Ca, ppm	Mg, ppm	Na, ppm	S, ppm	Cu, ppm	Zn, ppm
Unit 5, South	0-30 cm	6.95	22.47	536.54	7728.95	1845.00	740.21	231.43	3.93	4.48
Unit 5, South	30-60 cm (1)	7.92	35.49	555.24	8271.10	1604.82	948.34	375.47	7.53	5.1
Unit 5, South	30-60 cm (2)	7.95	51.95	497.97	7844.00	1134.84	659.27	146.31	8.23	2.03
Unit 5, North	0-30 cm	8.65	110.48	1816.15	11875.65	2724.04	766.99	382.98	6.89	3.26
Unit 4	0-30 cm	7.86	18.22	657.90	10281.18	2601.7	884.71	381.21	8.14	4.1
Unit 4	30-60 cm	8.32	21.5	316.92	6983.10	1385.31	589.12	54.73	6.05	1.39

3.1.2. Water Analysis

Water chemistry analysis confirmed the lake is a freshwater basin. Chloride concentrations were 0.83 mg/L in the Blitzen River and 2.18 mg/L in the Silvies River (Table 2). Concentrations in Malheur Lake were on average higher at 1.01 and 88 mg/L compared to Blitzen River samples (Table 2). Nutrient analysis categorized the lake as eutrophic (Xu et al. 2015, Qi et al. 2022); total phosphorus (persulfate) was 0.48 and 0.72 mg/L in lake samples (Table 2). The pH of the lake has ranged historically between 7.5-9 (Duebbert 1969, Fusté and McKenzie 1987).

Table 2. Anion and nutrient water chemistry results from WBAS laboratory. *b.d. = below detectable limit.

	Fluoride	Chloride	Sulfate	Nitrate	Phosphate	TN as N	TP as P
Sample Locations	F- mg/L	Cl- mg/L	SO ₄ mg/L	NO ₃ mg/L	PO ₄ mg/L	persulfate mg/L N	persulfate mg/L P
Malheur Lake 1	b.d.*	1.01	0.977	0.628	0.155	1.53	0.48
Malheur Lake 2	1.00	88	217	0.769	0.447	6.34	0.72
Blitzen River	b.d.	0.83	0.817	0.177	b.d.	0.64	0.21
Silvies River	b.d.	2.18	3.76	b.d.	b.d.	0.28	0.23
Greenhouse	b.d.	5.21	8.68	5.33	b.d.	1.39	0.23

Sample Locations	Al mg/L	B mg/L	Ba mg/L	Ca mg/L	Cd mg/L	Co mg/L	Cr mg/L	Cu mg/L	Fe mg/L
MDL**	0.038	0.015	0.008	0.003	0.008	0.008	0.009	0.009	0.007
Malheur Lake 1	0.470	0.0	0.0	24.4	0.00	0.00	0.00	0.00	0.399
Malheur Lake 2	0.000	3.04	0.0	15.8	0.00	0.00	0.00	0.00	0.004
Blitzen River	0.648	0.034	0.0	10.8	0.00	0.00	0.00	0.00	0.649
Silvies River	0.000	0.077	0.0	32.5	0.00	0.00	0.00	0.00	0.016
Greenhouse	0.000	0.092	0.0	16.0	0.00	0.00	0.00	0.00	0.000
	K mg/L	Mg mg/L	Mn mg/L	Na mg/L	Ni mg/L	Pb mg/L	Si mg/L	V mg/L	Zn mg/L
MDL**	0.1	0.002	0.001		0.01	0.035	0.012	0.006	0.006
Malheur Lake 1	2.75	9.37	0.01	10.5	0.00	0.00	19.7	0.008	0.00
Malheur Lake 2	52.6	31.7	0.00	323.0	0.00	0.00	27.6	0.098	0.00
Blitzen River	1.74	5.10	0.01	7.52	0.00	0.00	16.0	0.011	0.00
Silvies River	3.94	9.02	0.01	15.3	0.00	0.00	21.9	0.000	0.00
Greenhouse	5.44	6.32	0.00	18.6	0.00	0.00	31.3	0.011	0.146

3.2. Seedbank Presence and Viability

Our greenhouse could not be temperature regulated, so we compared mean and maximum temperatures in Burns, Oregon between years and found no significant difference ($p = 0.436$; $p = 0.118$) (A.3).

In 2021, we detected 12 plant species in the seedbank experiment (A.4). The average richness per sample, including all annual and perennial plants, was 5.03 ± 0.22 species (A.5).

Common annual species found include Nettleleaf Goosefoot (*Chenopodium murale*), False

Pimpernel (*Lindernia dubia*), Red Sorrel (*Rumex acetosella*), and Yellowcress (*Brassicaceae rorippa*) (Figure 19). Hardstem bulrush and broadleaf cattail were detected at 94% of the sites (A.6). No broadleaf cattail was found in samples from one northern region sample site, and no hardstem bulrush was detected at one southern region site (Figure 20).

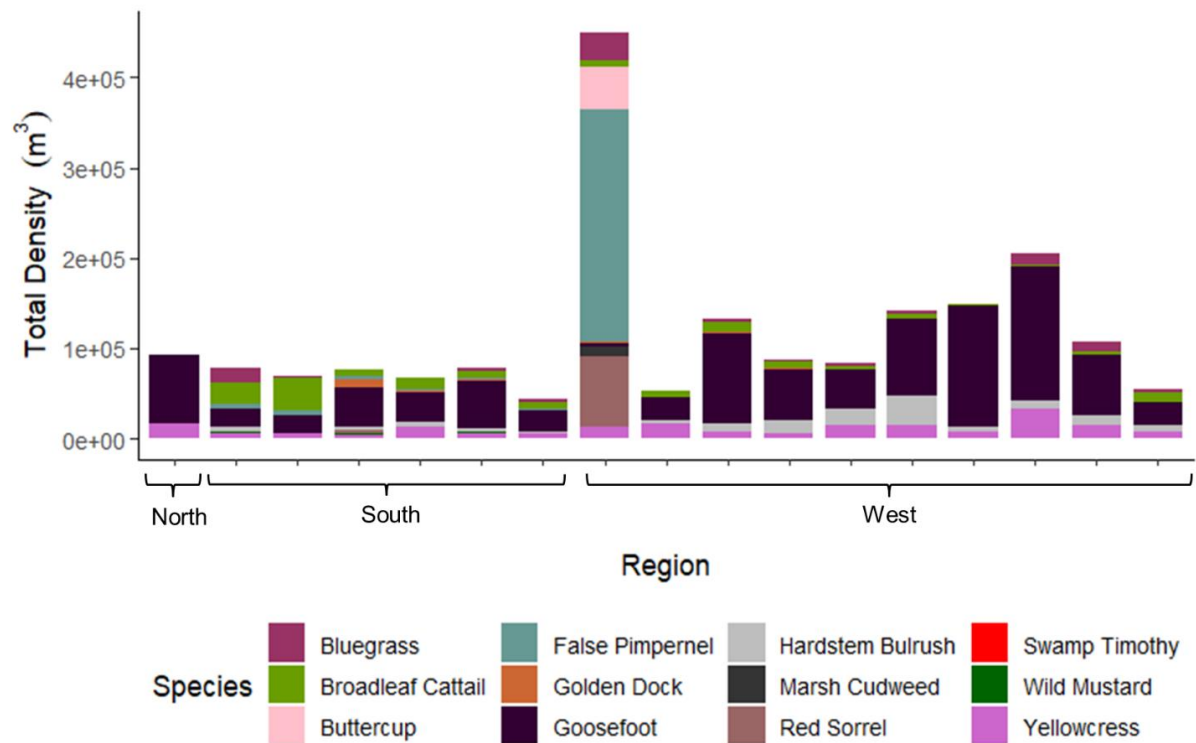


Figure 19. Seedbank density of 2021 greenhouse samples per cubic meter.

In 2022, we detected 12 plant species in the greenhouse experiment (A.7). The average richness for these sites was 3.76 ± 0.29 species (A.8). The most common annual species detected were Nettleleaf Goosefoot, Red Sorrel, and Bluegrass (*Poa spp.*)(Figure 21). Hardstem bulrush was detected at 80% of the sites; Several sites in the north-central portion of the lake did not support hardstem bulrush. Broadleaf cattail was detected at 80% of the sites, but none was detected at two sites in the north-central portion of the lake (Figure 22). One site in the northern portion of the lake was the only site that did not detect any perennial emergent species.

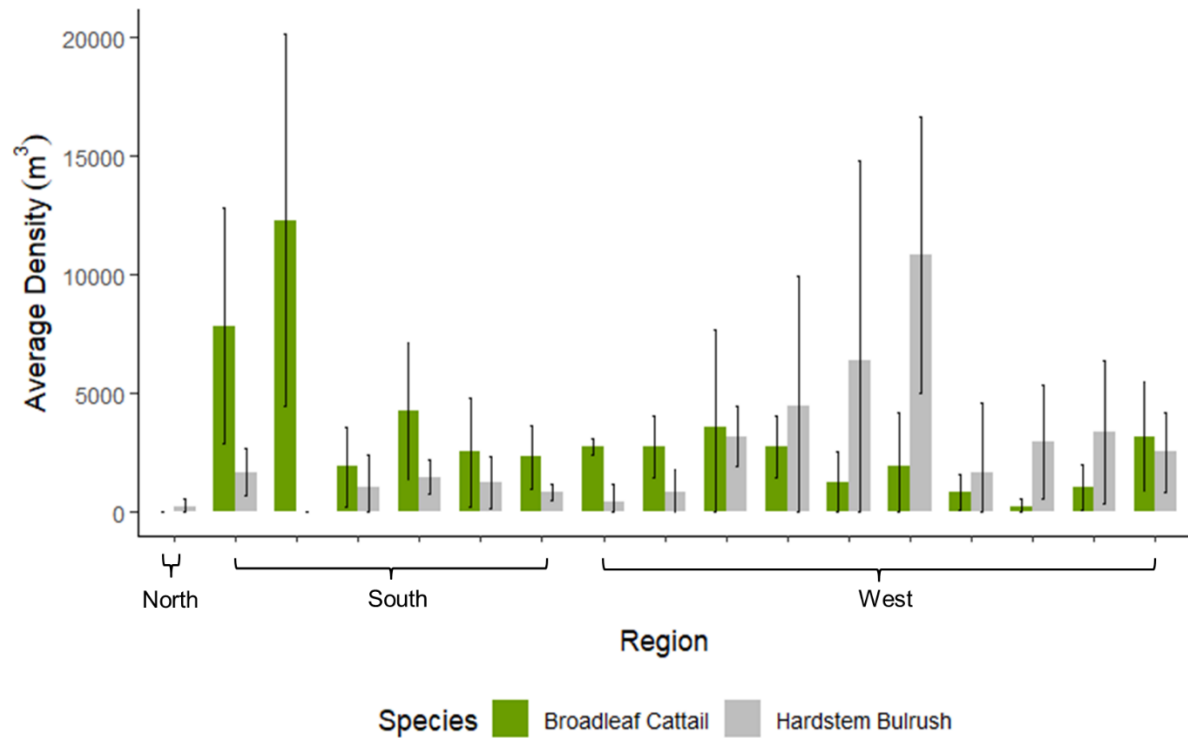


Figure 20. Average density of perennial emergent species in 2021 greenhouse experiment. Error bars represent one standard deviation.

The average number of hardstem bulrush ($p = 0.210$) and broadleaf cattail ($p = 0.061$) did not differ between years for our subsample of locations in close proximity (Figure 23). Although the sample size was small relative to the size of the lake, the presence of robust emergents in all samples suggest that the seedbank is likely not the limiting factor for vegetation establishment.

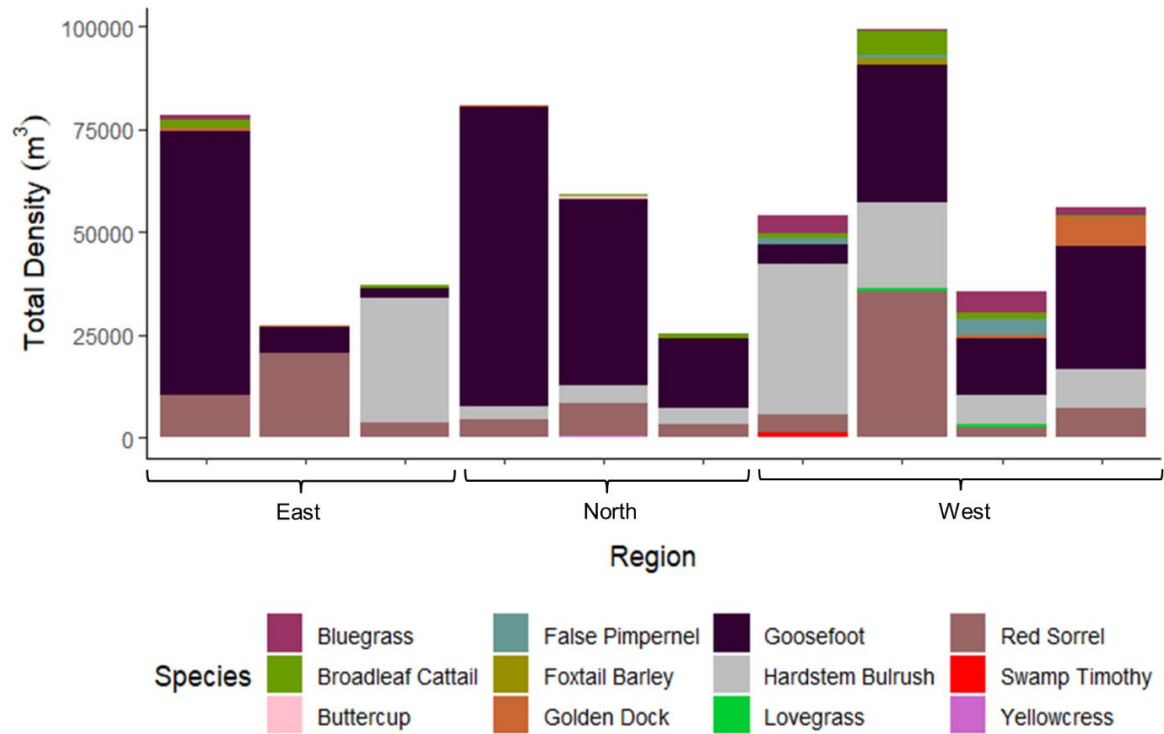


Figure 21. Seedbank density of 2022 greenhouse samples.

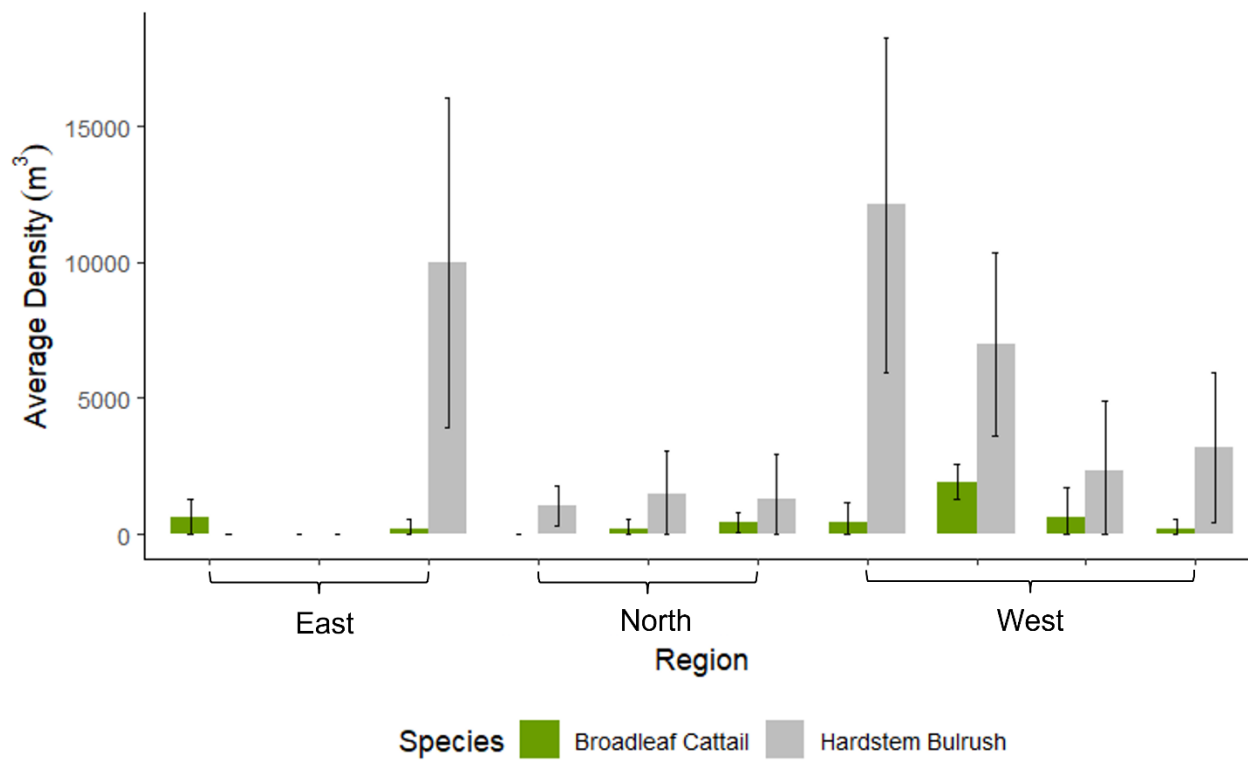


Figure 22. Average density of perennial emergent species in 2022 greenhouse experiment. Error bars represent one standard deviation.

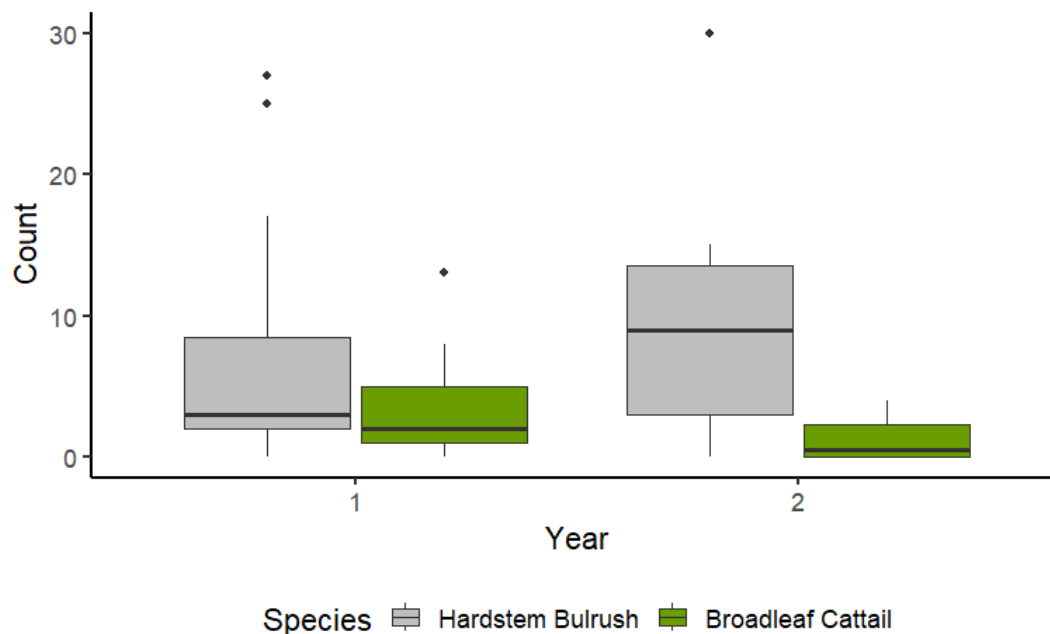


Figure 23. Comparison of perennial emergent vegetation detections between years using western region samples.

We also compared seedbank diversity (Figure 24) and richness (Figure 25) by region.

Seedbank diversity was greatest in the southern region (1.30 ± 0.07) compared to western sites (1.02 ± 0.06 ; $p = 0.04$), eastern sites (0.60 ± 0.01 ; $p < 0.001$), and northern sites (0.592 ± 0.10 ; $p < 0.001$). The western region had higher diversity than the East ($p = 0.01$) and North regions ($p = 0.004$). Similarly, species richness was greater in the South and West Regions. Species richness in the southern region (5.61 ± 0.001) exceeded both the eastern region (2.67 ± 0.19 ; $p = 0.003$) and the northern region (3.0 ± 0.27 ; $p = 0.004$). There was no difference detected between the South and West regions, but the western region also had higher diversity compared to the eastern ($p = 0.01$) and northern regions ($p = 0.02$).

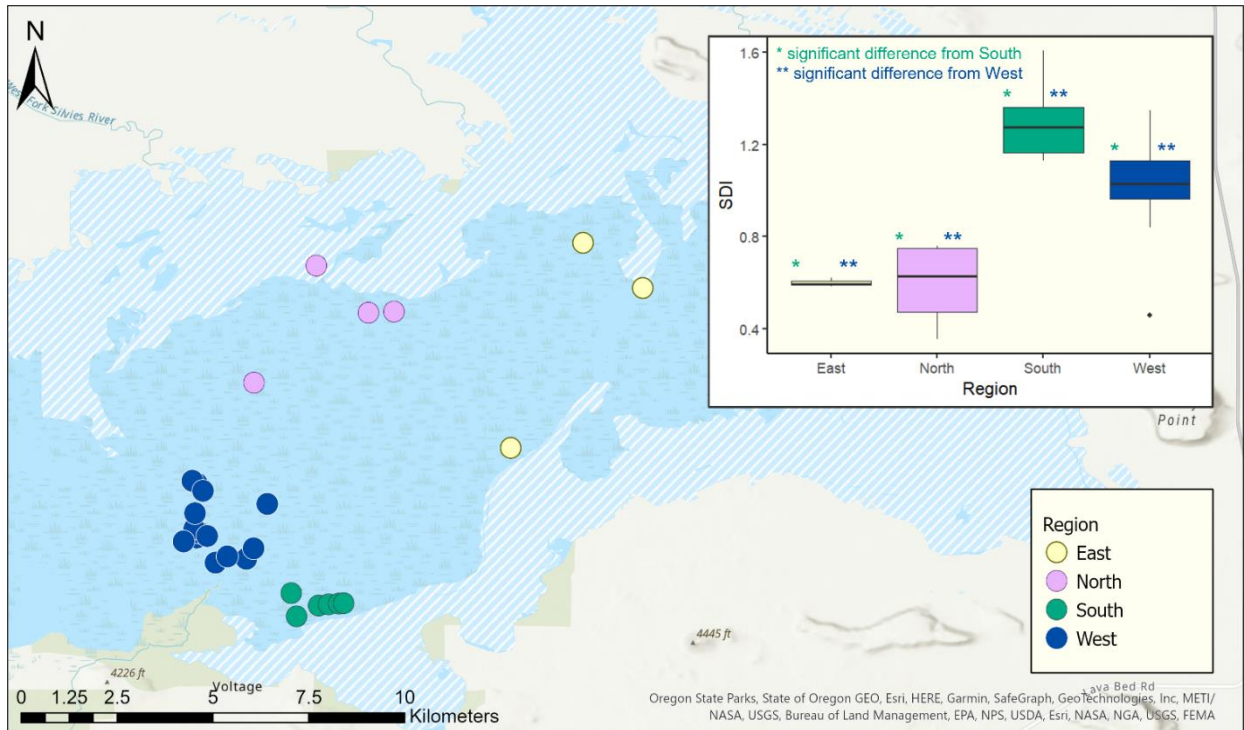


Figure 24. Comparison of diversity by region; sites were combined from 2021 and 2022.

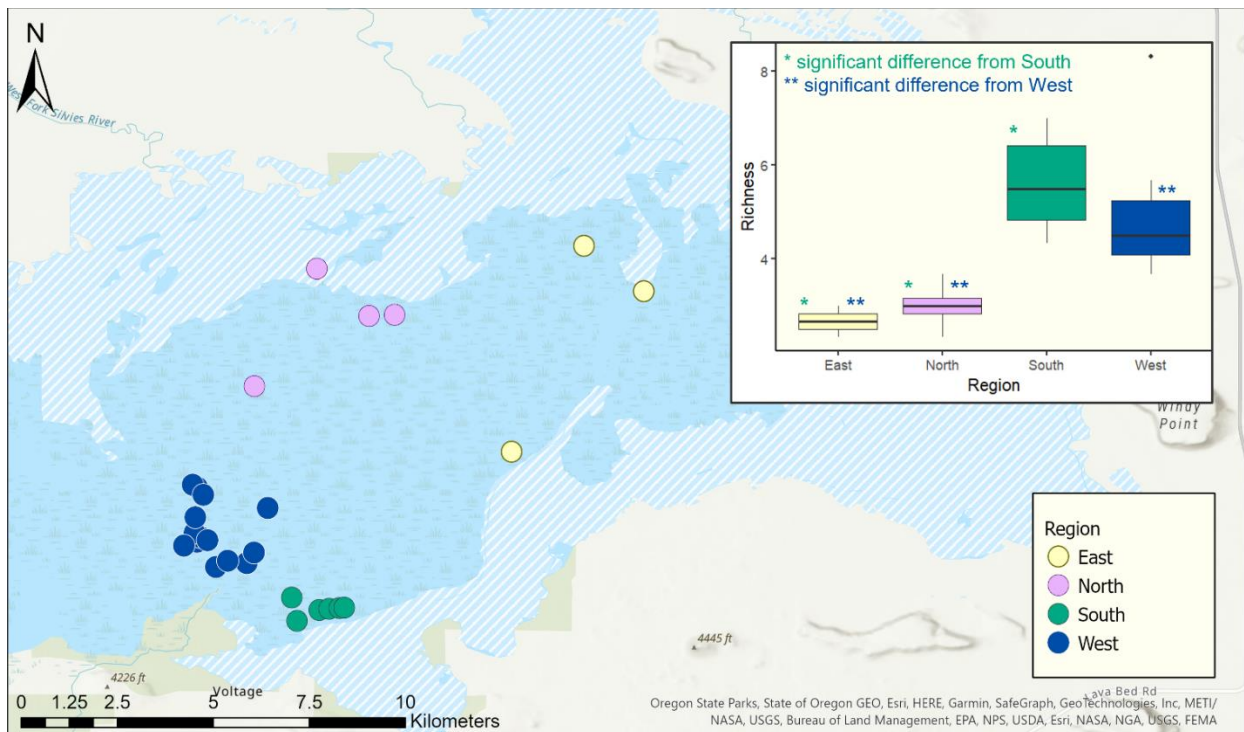


Figure 25. Comparison of richness by region; sites were combined from 2021 and 2022.

3.3. Germination Conditions on the Lake

In 2021, five species were identified in germination exclosures, including alkali bulrush, hardstem bulrush, and broadleaf cattail. Mean peak density was 504 ± 571 for all seedlings. Hardstem bulrush was the most prolific species detected. The maximum densities occurred in mid to late-July, and the central region of exclosures experienced the greatest emergence of germinants. In 2022, seventeen species were identified in germination exclosures, including the aforementioned species, although densities of broadleaf cattail and alkali bulrush were lower than 2021 densities. Most of the species detected in 2022 are not considered facultative wetland species, and some are even noxious weeds (foxtail barley and Canada thistle). Exclosures were dominated by annual species in 2022, especially red sorrel (*Rumex acetosella*), nettleleaf goosefoot (*Chenopodium murale*), and alkali aster (*Symphyotrichum frondosum*). Mean peak density of seedlings was 1.1 ± 1.05 and occurred in mid- July for most exclosures.

Abiotic conditions were monitored at exclosure plots in both years. Both years saw steep declines in Instantaneous-VWC in late July and early August (Figure 26). Temperature was higher during the beginning of the growing season in 2022, reaching up to 35 °C (Figure 27) while salinity was higher during the 2021 growing season (Figure 28). There was a positive relationship detected between salinity and volumetric water content for both years (Figure 29). In 2021, mean salinity was $0.217 \text{ ppt} \pm 0.18$ and ranged between 0.007-1.1 ppt. Peak salinity timing varied by exclosure location. Mean I-VWC was $22.02 \pm 9.57\%$ and ranged between 5.4-38.5%. Mean temperature was $17.98 \pm 5.30 \text{ }^{\circ}\text{C}$ and ranged between 10.2 – 24.8 °C. In 2022, mean salinity at the surface was $0.307 \pm 0.188 \text{ ppt}$ and values ranged between 0-1.15 ppt. Mean salinity at 10-15 cm was $0.307 \pm 0.216 \text{ ppt}$ and ranged between 0.006-1.17 ppt. Peak salinity values occurred in late June and early July. Mean I-VWC at the surface was $15.6 \pm 10.12\%$ and

ranged between 2.7-45.1%. Mean I-VWC at 10-15 cm was 28.4 ± 11.16 % and ranged between 7.8- 46.4%. Mean temperature at the surface was 22.1 ± 6.40 °C and ranged between 10.7-24.00 °C. Mean temperature at 10-15 cm was 22.4 ± 6.66 °C and ranged between 11.3- 33.8 °C.

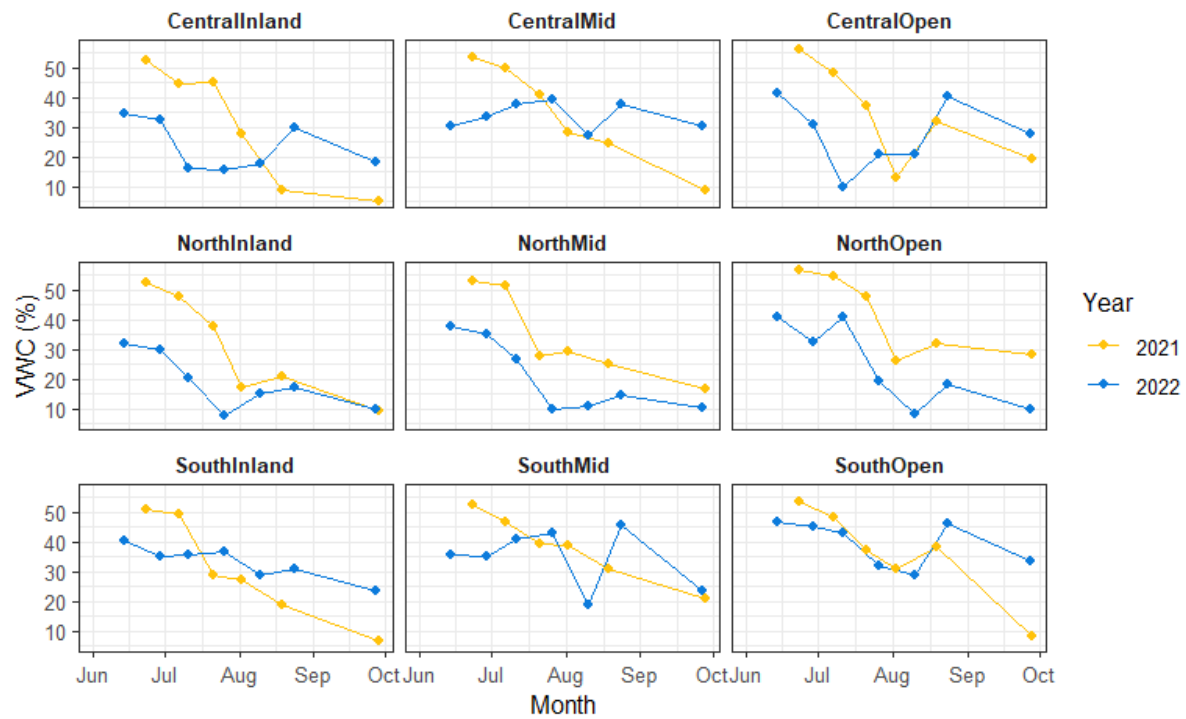


Figure 26. I-VWC (%) at germination enclosure sites in 2021 compared to 2022.

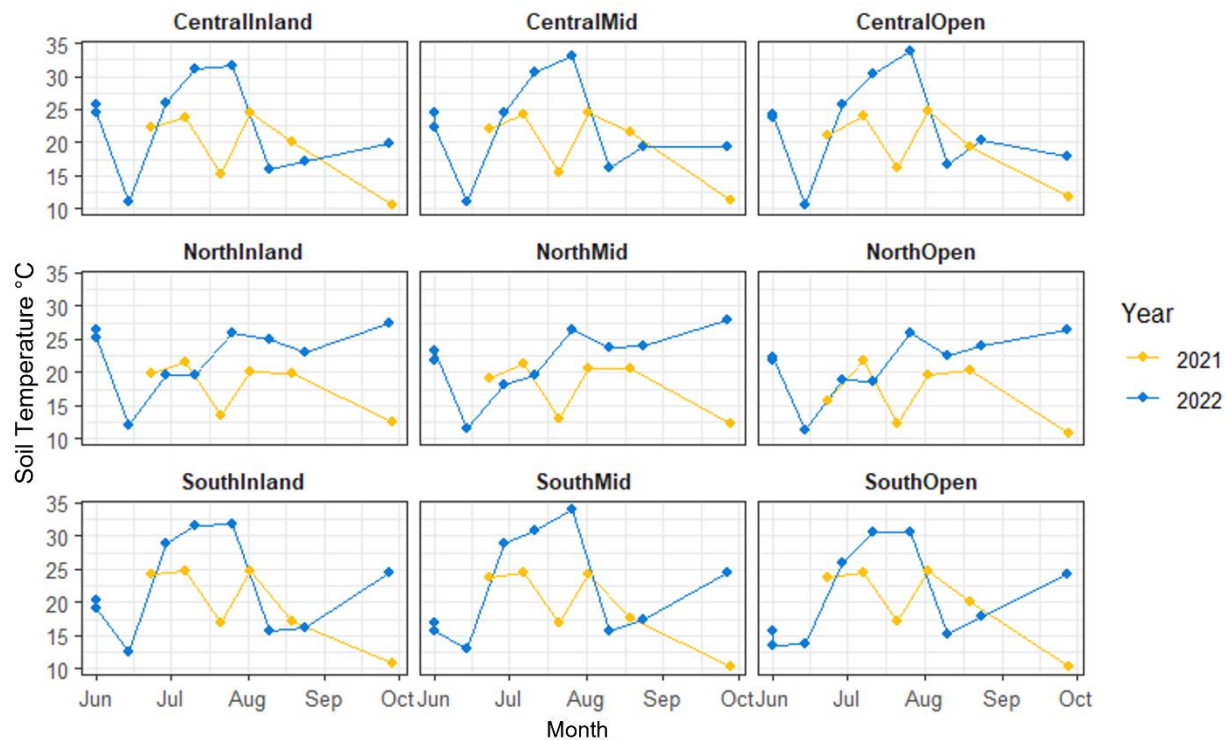


Figure 27. Surface soil temperature at germination enclosure sites in 2021 compared to 2022.

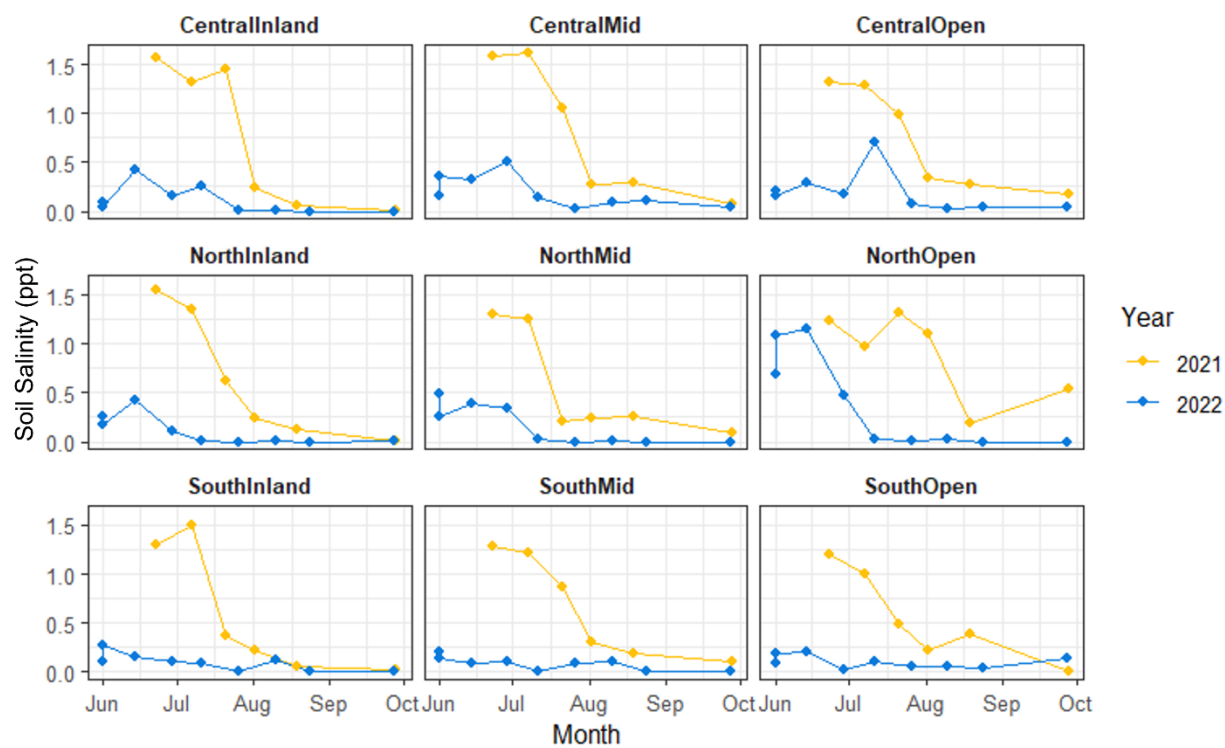


Figure 28. Surface salinity at germination enclosure sites in 2021 compared to 2022.

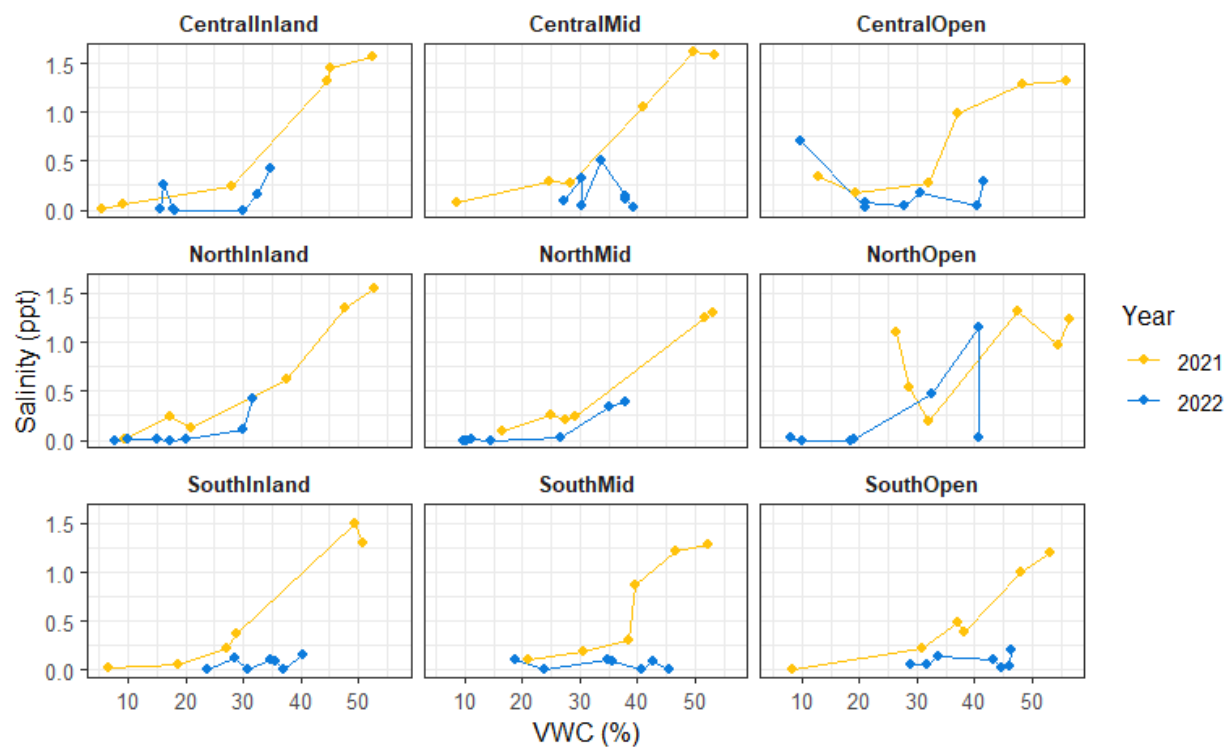


Figure 29. Relationship between salinity and I-VWC between years.

3.3.1. Germination Exclosure Results

Hardstem Bulrush

In 2021, hardstem bulrush germinants germinated in all 18 sample plots, with peak germination occurring in mid to late July (Figure 30). Hardstem bulrush was more abundant in controls (peak averages [m^2]: 6.31 ± 1.37) than in hardware cloth exclosures (peak averages [m^2]: 5.45 ± 0.92) (average difference: 0.085 ± 0.027) ($p = 0.0014$). Increasing water depth was also found to decrease germination counts ($p = 2\text{e-}16$). Additionally, germination counts were greater with higher soil temperatures ($p = 0.01$), but germination counts did not differ according to salinity ($p = 0.289$) or I-VWC ($p = 0.767$). The soil temperature predictor model explained the most variance between independent predictor models (Table 3). Correlation coefficients between predictors were too high to utilize multiple predictors in models ($\text{corr.} > 0.5$), so a PCA was performed for salinity, I-VWC, soil temperature, and date in 2021 (Figure 31). We used the

resulting PC1 and PC2 values, which accounted for 95% of the variance, to find the best model (Table 4). The model that explained the most variance included PC1, PC2, and water depth as predictors (Table 5).

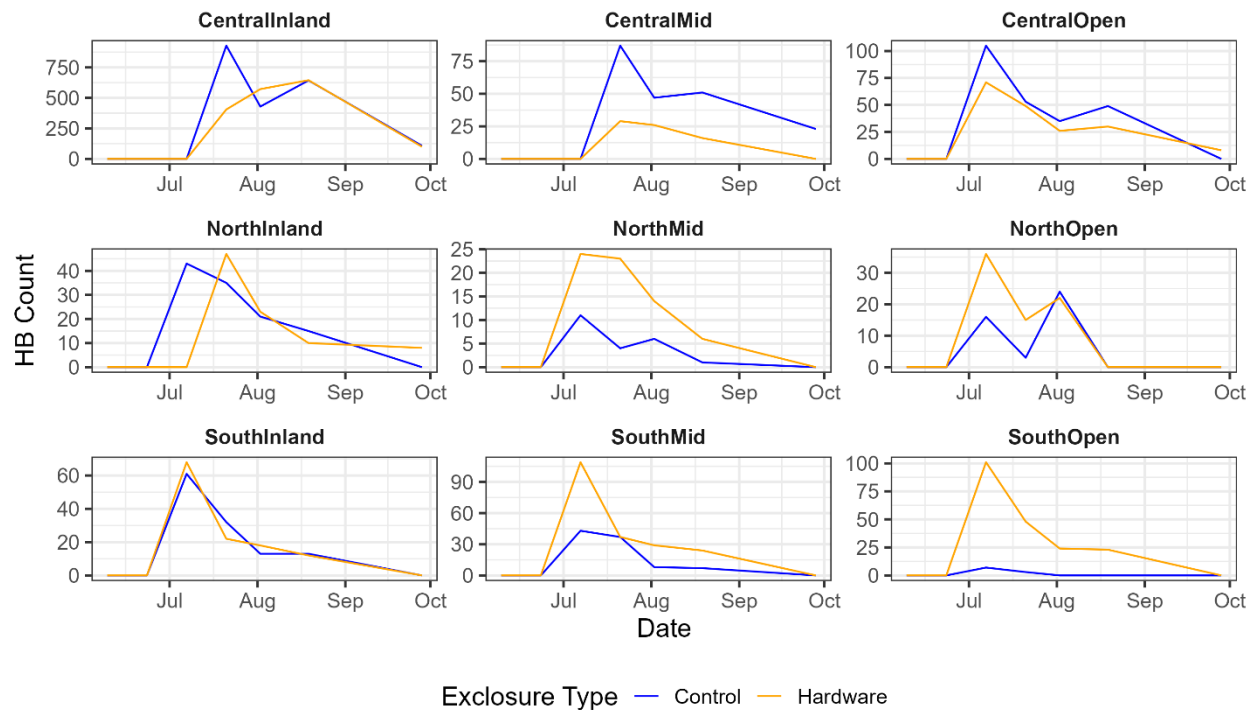


Figure 30. Hardstem bulrush counts by exclusion site for controls and hardware cloths. Note the difference in scales as “CentralInland” had extremely high germinant counts in 2021 with over 500 germinants observed in both the control and hardware cloth exclusion.

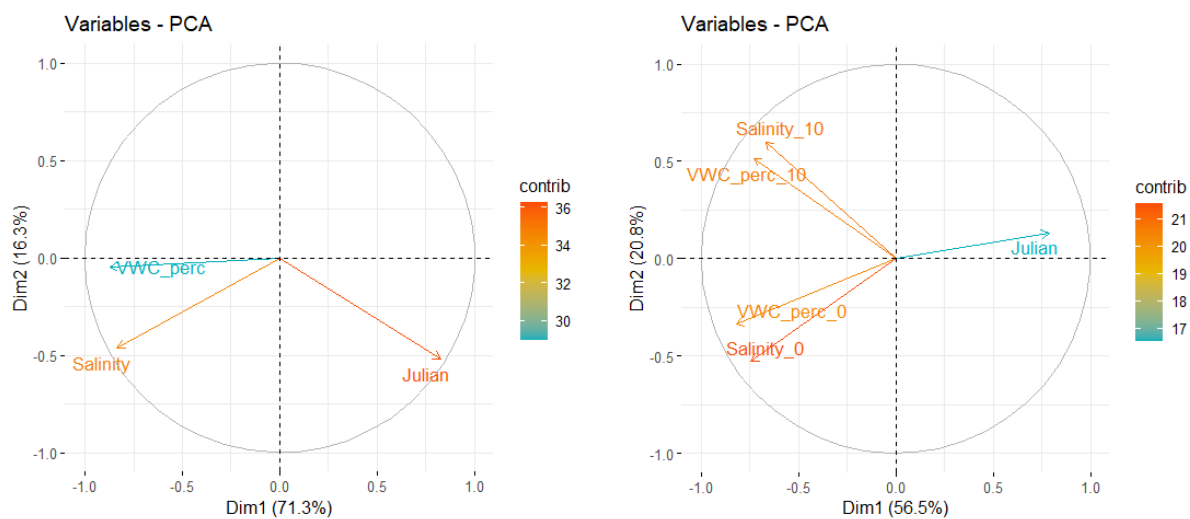


Figure 31. PCA visualization of correlated predictors in 2021 (left) and 2022 (right) germination exclusions. These predictors include salinity, Julian date, and I-VWC.

In 2022, hardstem bulrush germinants at all 18 sample plots. The number of germinants of hardstem bulrush was once again greater in in controls (peak averages [m²]: 7.89 ± 5.1) than in hardware cloth exclosures (peak averages [m²]: 10.11 ± 7.26) (average difference: $0.224 + 0.0585$; $p = 0.0001$). Additionally, the number of germinants were higher with increased salinity at the surface (average difference: $1.245 + 0.3932$; $p = 0.0015$) and greater I-VWC at the surface (average difference: 0.021 ± 0.0087 ; $p = 0.016$). Salinity at a depth of 10-15 cm ($p = 0.0984$) and I-VWC at 10-15 cm depth ($p = 0.682$) had no effect on the number of germinants. Soil temperature at either depth had no effect on the number of germinants at the surface ($p = 0.958$) or at a depth of 10-15 cm ($p = 0.488$) (Table 6). We performed a PCA with salinity, I-VWC, and date as correlated predictors for 2022 (Figure 22). The first two principal components explained 77% of the variance, and those components combined with surface soil temperature as predictors resulted in the best model (Table 7; Table 8).

Table 3. Single predictor models for hardstem bulrush in 2021.

Predictor	K	Estimate	Std. Error	Pr (> z)	AIC	Delta AIC
Temperature	5	0.06366	0.69375	0.00611	7057.506	0
Salinity	5	0.2583	0.2436	0.289	8331.839	1274.333
I-VWC	5	-0.001361	0.004598	0.767	8402.69	1345.183
Depth	5	-71.1774	0.002801	<2e-16	9016.904	1959.397

Table 4. Principle Components for 2021 collinear predictors (salinity, I-VWC, soil temperature, and date).

	PC1	PC2	PC3	PC4
Standard deviation	1.7642	0.8232	0.34434	0.30237
Proportion of Variance	0.7781	0.1694	0.02964	0.02286
Cumulative Proportion	0.7781	0.9475	0.97714	1

Table 5. Multi-predictor models for 2021 including PC 1 & 2 as predictors and water depth as independent predictor.

Model Name	K	Estimate	Std. Error	Pr (> z)	AIC	Delta AIC
PC1	7	-2.0805	0.0816	0.0108	6752.28	0
PC2		0.1211	0.0150	7.06e-16		
Depth		-2.8252	72.1245	0.9688		
PC1	6	-0.2055	0.0837	0.0141	6815.23	62.94
Depth		-2.8500	50.5165	0.9550		
PC1	6	-0.1794	0.0646	0.00549	6824.64	72.36
PC2		0.1278	0.0150	<2e-16		
PC1	5	-0.1726	0.0651	0.00765	6895.11	142.82
PC2	6	0.1568	0.0478	0.0010	7192.44	440.16
Depth		-2.6430	46.6201	0.9548		
PC2	5	0.1763	0.0546	0.00125	7224.23	471.95
Depth	5	-68.2667	0.00289	<2e-16	7301.51	549.22

Table 6. Single predictor models for hardstem bulrush in 2022.

Predictor	K	Estimate	Std. Error	Pr (> z)	AIC	Delta AIC
I-VWC (surface)	5	0.0027	0.00284	0.3400	1295.16	0.00
Temp (10-15 cm)	5	-0.0081	0.01160	0.4880	1297.18	2.03
Salinity (10-15 cm)	5	0.8862	0.53630	0.0984	1297.79	2.64
I-VWC (10-15 cm)	5	-0.0213	0.00273	7.98e-15	1305.87	10.72
Salinity (surface)	5	1.2450	0.39320	0.00154	1335.57	40.41
Temp (surface)	5	0.0201	0.00460	5.19e-6	1460.57	165.42

Table 7. Principle Components for 2022 PCA including collinear predictors date, salinity at surface, I-VWC at surface, salinity at depth, and I-VWC at depth.

	PC1	PC2	PC3	PC4	PC5
Standard deviation	1.6812	1.0187	0.70477	0.64558	0.47154
Proportion of Variance	0.5653	0.2076	0.09934	0.08335	0.04447
Cumulative Proportion	0.5653	0.7728	0.87218	0.95553	1

Table 8. Multi-predictor models following PCA analysis for hardstem bulrush in 2022 including PC1 & PC2 and temperature as predictors.

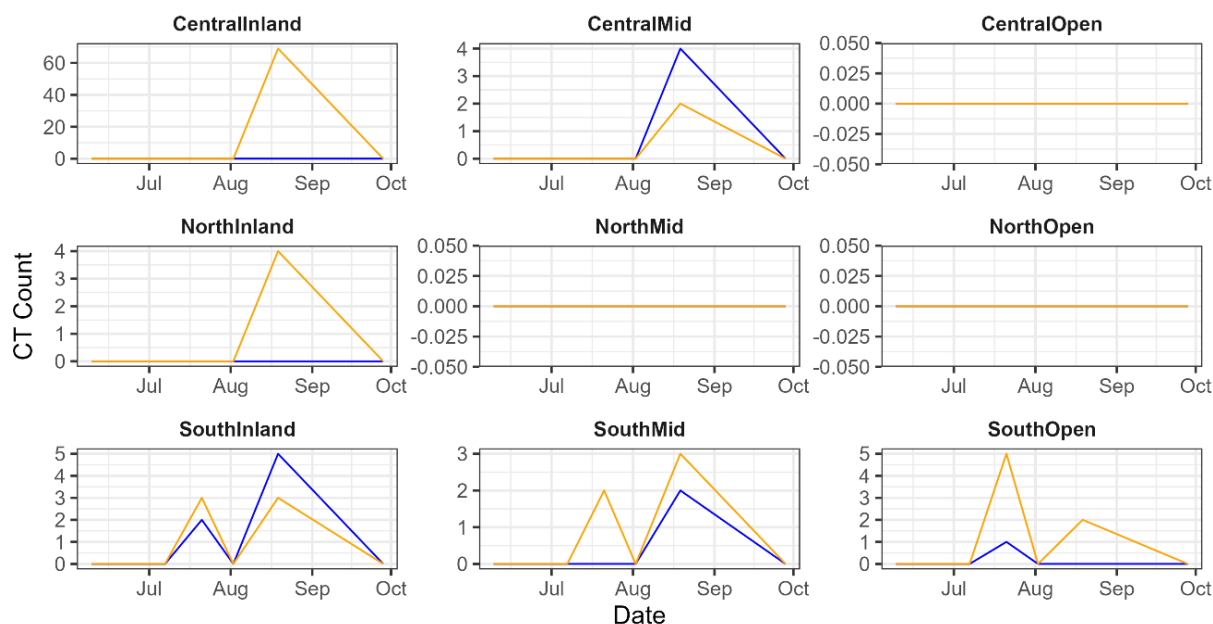
Model Name	K	Estimate	Std. Error	Pr (> z)	AIC	Delta AIC
PC1	7	-0.2022	0.0519	9.79e-5	1126.8	0
PC2		-0.2549	0.0423	1.64e-9		
Temp		0.0967	0.0324	0.00284		
PC1	6	-0.1783	0.0505	0.00042	1133.65	6.85
PC2		-0.3163	0.0373	<2e-16		
PC2	5	0.1369	0.1776	0.441	1142.16	15.36
PC1	6	-0.2497	0.0527	2.14 e-6	1160.89	34.09
Temp		0.1913	0.0289	3.34e-11		
PC1	5	-0.2129	0.0508	2.78e-5	1202.86	76.05
Temp	5	-0.00713	0.0175	0.684	1298.91	172.1

Broadleaf Cattail

In 2021, broadleaf cattail germinants were recorded at 55% of plots (Figure 32).

Broadleaf cattail was more abundant in hardware cloth enclosures (peak averages [m²]: 0.414 ± 0.10) (average difference: 1.894 ± 0.2867) ($p = 3.97e-11$) compared to controls (peak averages [m²]: 0.05 ± 0.01). Additionally, germinant counts were greater with decreasing I-VWC (average difference: 0.039 ± 0.0018) ($p = 2e-16$) and decreasing salinity (average difference: 1.945 ± 0.684) ($p = 0.0044$), but germination counts did not differ according to soil temperature ($p = 0.235$) or water depth ($p = 0.992$) (Table 9). Principle component analysis was performed as described for 2021 above, and water depth was an additional independent variable in models. The predictors in the best performing model were the first two principal components; water depth did not improve the model (Table 10).

In 2022, we observed broadleaf cattail at 5% of sites, and only eleven broadleaf cattail were recorded during the field season, which does not provide a large enough sample size to analyze the effects of our independent variables.



Enclosure Type — Control — Hardware

Figure 32. Broadleaf cattail counts by enclosure site for controls and hardware cloth enclosures. Note the difference in scales as “CentralInland” had extremely high germinant counts in 2021 with over 500 germinants observed in both the control and hardware cloth enclosure.

Table 9. Single predictor models for broadleaf cattail in 2021.

Predictor	K	Estimate	Std. Error	Pr (> z)	AIC	Delta AIC
Salinity	5	-1.945	0.6838	0.0044	430.81	0
I-VWC	5	-0.0390	0.00182	<2e-16	440.44	9.63
Temp	5	0.0213	0.0208	0.306	546.89	116.08
Depth	5	-2.5911	262.2196	0.9921	581.07	150.26

Table 10. Multi-predictor models following PCA analysis for broadleaf cattail in 2021 including PC1 & PC2 and water depth as predictors.

Model Name	K	Estimate	Std. Error	Pr (> z)	AIC	Delta AIC
PC1	6	0.5559	0.2508	0.0267	393.226	0.000
PC2		1.6815	0.2243	6.57e-14		
PC1	7	0.5549	0.2512	0.0272	395.503	2.277
PC2		1.6808	0.2244	6.93e-14		
Depth		-1.730	284.5135	0.9951		
PC2	5	0.6645	0.5178	0.1993	455.149	61.923
PC2	6	0.6422	0.4156	0.122	457.256	64.030
Depth		-1.9976	1030.0242	0.998		
PC1	5	0.1745	0.0016	<2e-16	495.770	102.544
PC1	6	0.1758	0.1258	0.162	497.802	104.576
Depth		-2.023	241.8820	0.993		
Depth	5	-2.6369	256.0000	0.9918	548.358	155.132

Alkali Bulrush

In 2021, alkali bulrush was detected at 55% of plots (Figure 33). Alkali bulrush was more abundant in hardware cloth enclosures (peak averages [m²]: 0.232 ± 0.03) compared to controls (peak averages [m²]: 0.154 ± 0.02) (average difference: 0.477 ± 0.212) ($p = 0.025$). Germinant counts were higher with increasing temperature (average difference: 0.189 ± 0.0016) ($p = 2e-16$), but counts did not differ according to I-VWC ($p = 0.280$), water depth ($p = 0.9902$) or salinity ($p = 0.085$) (Table 11). A principal component analysis was performed as described for 2021 above, and the best model included only the second principal component as a predictor (Table 12).

In 2022, alkali bulrush was detected at 27% of plots, but only five alkali bulrush were detected. This sample size was not sufficient to analyze the effects of our independent variables.

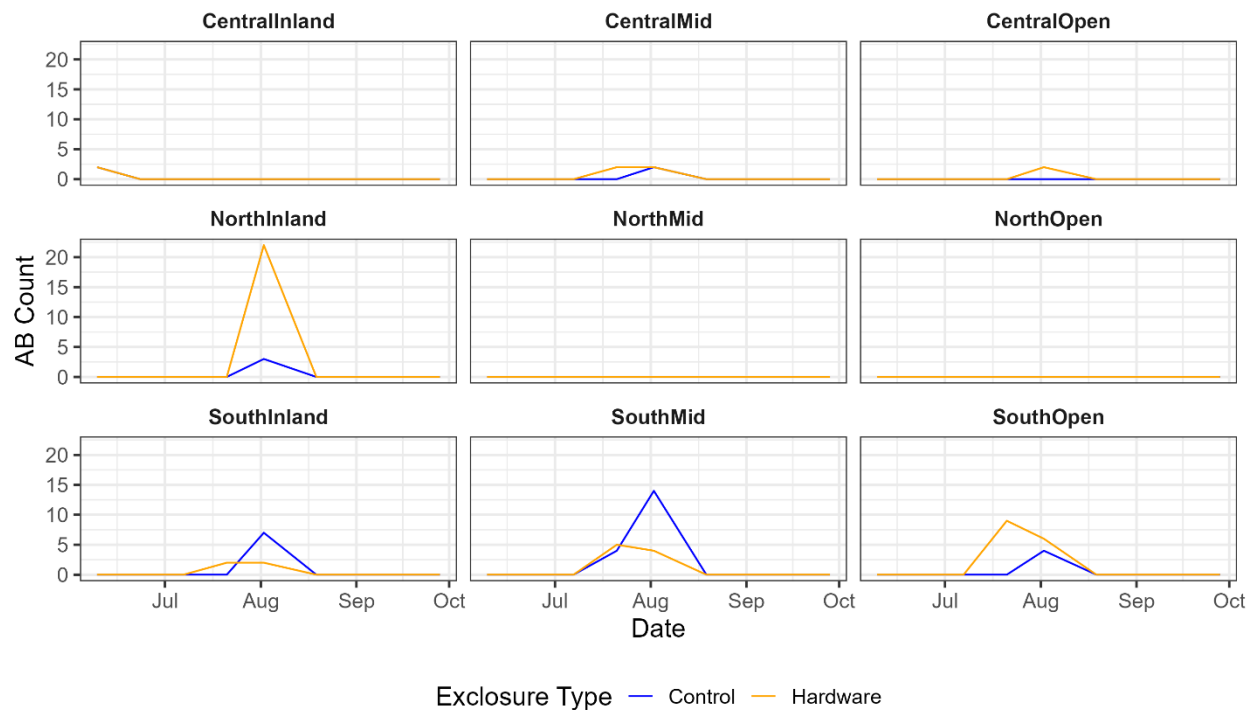


Figure 33. Alkali bulrush counts by enclosure site for controls and hardware cloths in 2021.

Table 11. Single predictor models for alkali bulrush in 2021.

Predictors	K	Estimate	Std. Error	Pr (> z)	AIC	Delta AIC
Temp	5	0.1887	0.0016	< 2e-16	365.53	0
Salinity	5	-0.8231	0.4779	0.085	401.43	35.9
I-VWC	5	-0.0211	0.0196	0.280	409.51	43.98
Depth	5	-2.4713	200.8240	0.9902	435.41	69.88

Table 12. Multi-predictor models following PCA analysis for alkali bulrush in 2021.

Models	K	Estimate	Std. Error	Pr (> z)	AIC	Delta AIC
PC2	5	1.7734	0.6301	0.0049	294.094	0.000
PC2	6	1.7630	0.6318	0.0053	296.312	2.218
Depth		-2.5023	261.3829	0.9924		
PC1	6	0.0692	0.0018	<2e-16	301.165	7.071
PC2		1.4553	0.0018	<2e-16		
PC1	7	0.0635	0.0018	<2e-16	303.424	9.330
PC2		1.4542	0.0018	<2e-16		
Depth		-1.1878	0.0018	<2e-16		
PC1	5	0.0700	0.0017	<2e-16	387.587	93.492
Depth	5	-2.9100	297.3788	0.9922	388.530	94.436
PC1	6	0.0628	0.1393	0.652	389.630	95.536
Depth		-1.9146	564.8436	0.997		

3.3.2. Transect Plots

At transect sites in 2022, I identified 11 species, including hardstem bulrush and broadleaf cattail. Hardstem bulrush was the most prolific perennial emergent wetland species, and high densities of foxtail barley, red sorrel, and nettleleaf goosefoot were also recorded. Mean peak density of seedlings was 112.5 ± 51.7 , and peaks occurred in mid to late-July for most sites. Peak seedling densities in most plots occurred when soil moisture was between 40-55%, and once soil moisture was 30% or less, there were never more than 10 seedlings in a plot (Figure 34). A soil moisture threshold could not be identified due to the relative extremes detected along the transect, but constant inundation did not support germination.

Transect sites experienced more varied abiotic conditions due to seiche and wind effects. Mean salinity was 0.79 ± 0.62 ppt and ranged between 0-2.8 ppt. Mean I-VWC was $40.8 \pm 17.9\%$ and ranged between 4.2- 58.7%. Mean temperature was 19.2 ± 4.52 °C and ranged

between 9.6- 27.1 °C (Figure 35). The transect design allowed for a variety of moisture regimes among transect sites that allowed us to better evaluate the effects of volumetric water content and water depth on germination of hardstem bulrush compared to our germination exclosures (Figure 34). Sites 1-5 were never flooded during the field season, and they experienced peak counts in mid-July. Sites 6-7 only had water at the time of set up, and peak germination and seedling counts occurred in late June and early July with counts declining rapidly in the next few weeks. Sites 8,9, and 11 were flooded (2-7 cm) until mid-July when hardstem bulrush emerged and quickly declined. Sites 10 and 12 experienced similar conditions of flooding (2-8 cm) until drawdown in mid to late-July. At least one reflooding event occurred in late August (<0.1 cm), and only 1 germinant was observed at site 12 throughout the growing season whereas site 10 peaked at 29 hardstem bulrush detections. Sites 13-15 did not drawdown until late July, and they experienced more reflooding events observed from seiche effects. Depth of flooding ranged from 6-20 cm in the early growing season (May-July), and reflooding occurred at 1-3 cm following the drawdown in late July. There was a small window for germinants and seedlings to persist at these sites because of the depth of water and associated turbidity. Individual predictors had varying effects on the response variables (Table 13). Increasing temperature and increasing water depth had negative effects on germination, and increasing I-VWC had a positive effect on germination overall.

Alkali bulrush was not detected at any transect site, and broadleaf cattail was only detected three times. We were not able to determine the effects of our abiotic predictors on these two species.

Table 13. Summary of individual response variables for germination transect.

Response Variable	Temperature	Water Depth	Salinity	I-VWC	Flooding (binomial)
Counts	Increasing temperature decreased counts	Increasing depth decreased counts	No effect	Increasing VWC increased counts	No effect
Apparent New Growth	Increasing temperature decreased new growth	Increasing depth decreased new growth	No effect	Increasing VWC increased new growth	No effect
Apparent Mortality	Increasing temperature increased mortality	No effect	No effect	No effect	Flooding in the last week decreased apparent mortality

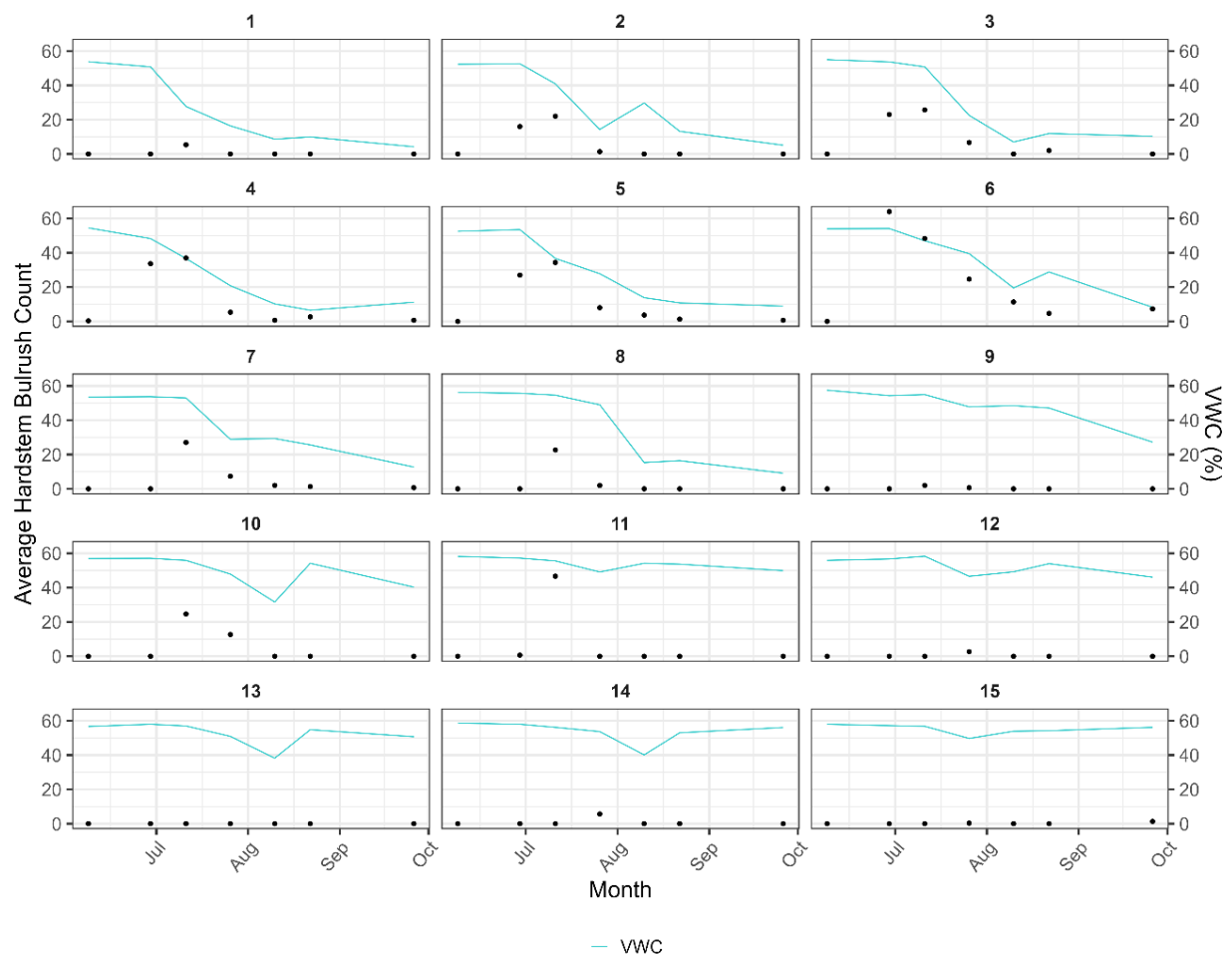


Figure 34. Transect hardstem bulrush counts (per m³) and I-VWC in 2022.

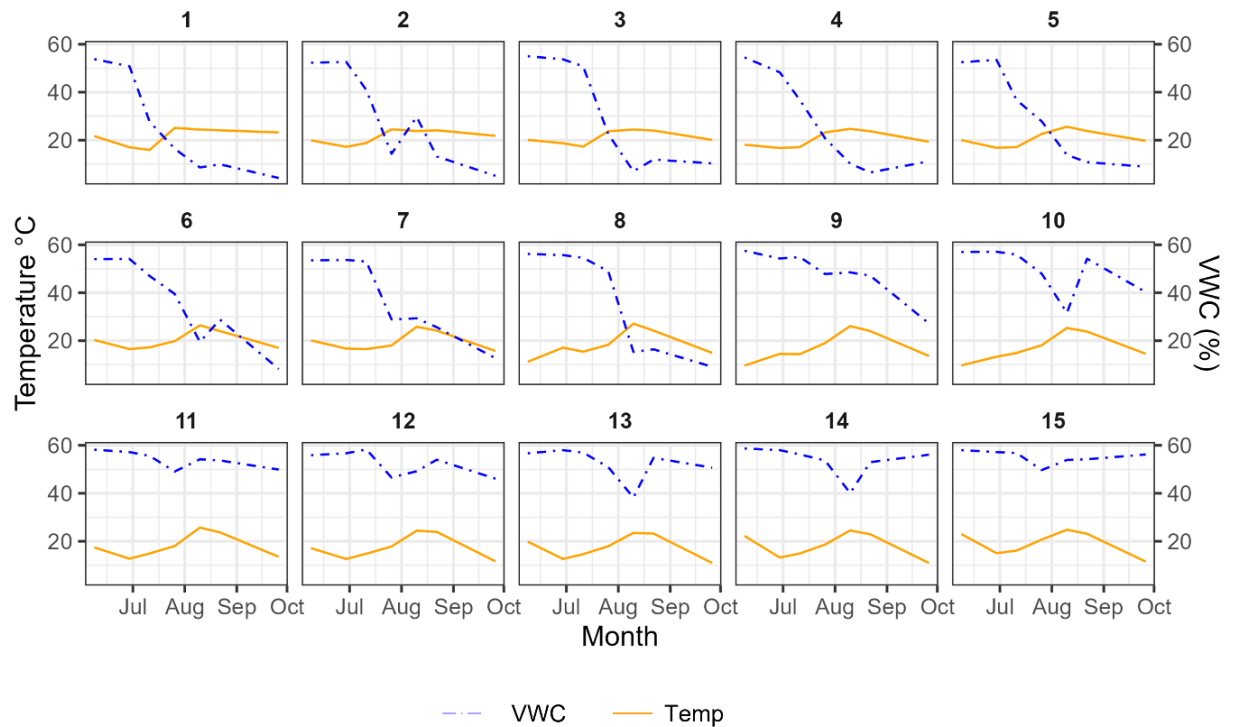


Figure 35. Transect temperature and I-VWC relationship.

There was a positive relationship identified between salinity and volumetric water content. In most freshwater basins, freshwater inflows dilute salts. However, in our system the salinity levels increased with volumetric water content. This may be due to high evaporation and evapotranspiration rates in the system that allowed for precipitated salts to be subject to high winds (A.9). The movement of water across the lakebed and subsequent evaporation deposits salts throughout the lake. The relationship between salinity and time helps confirm this conclusion as transects 9-15 experienced regular flooding events that coincide with salinity increases (Figure 36). Transects 1-8 saw salinity decline over the field season as those sites decreased in volumetric water content. This indicates that the salts were either dispersed through wind or that lake inputs are more saline than groundwater inputs. The relationship between volumetric water content and salinity was site specific, and it is likely that the interaction of wind action or groundwater inflows affects these values (Figure 37).

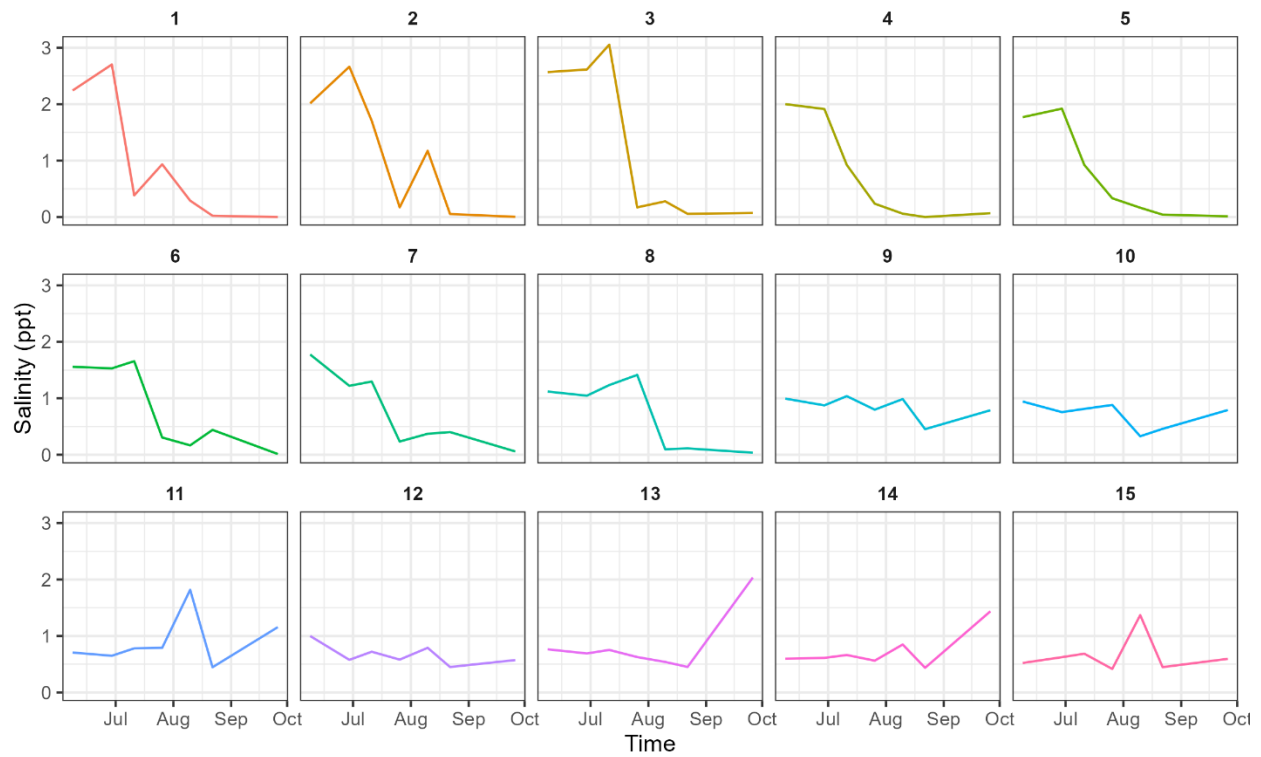


Figure 36. Salinity over time for each transect site in 2022.

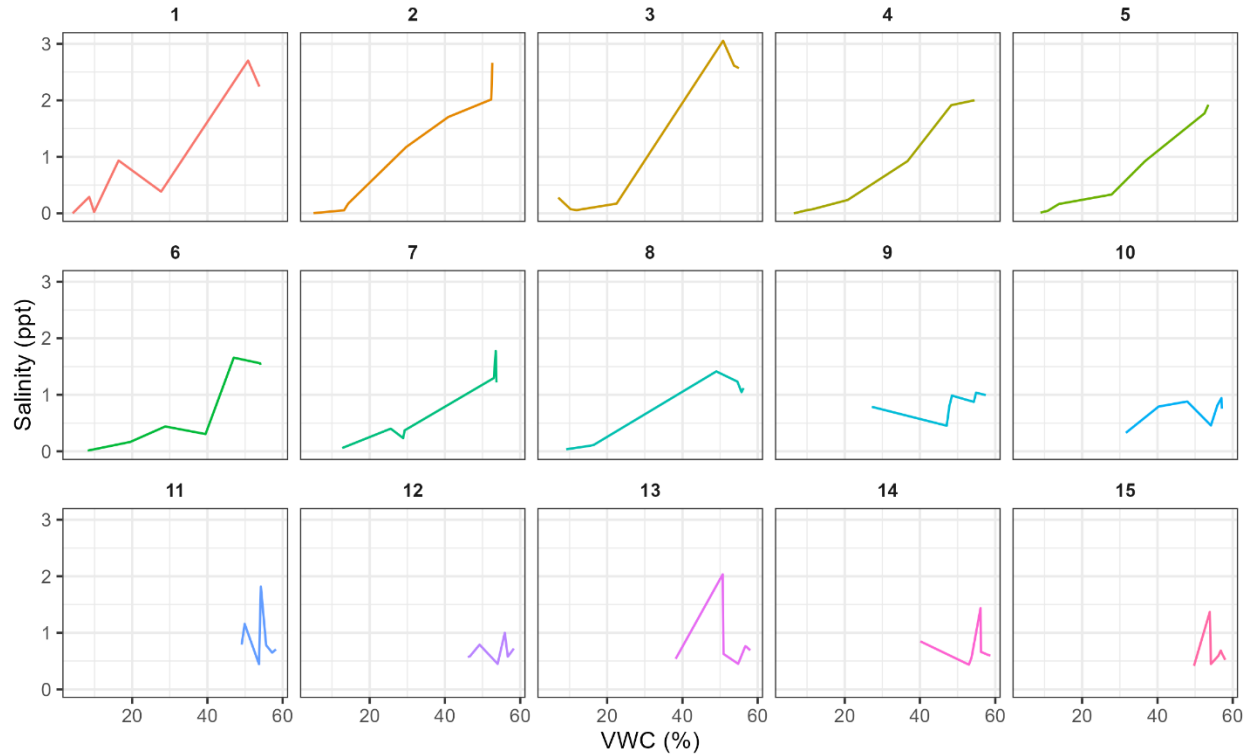


Figure 37. Salinity and I-VWC relationships by transect number for 2022.

Hardstem Bulrush

I observed germination events occurring at low depths (<1 cm) or following drawdowns. Although seedlings could survive flooding events, the emergence of new germinants did not occur when depths exceeded 2 cm. Sites that experienced initial drawdowns in mid-July saw an immediate response in germinant emergence, but counts declined dramatically in the following weeks.

Germination counts were affected by I-VWC, temperature, and water depth. The number of germinants was greater with increasing I-VWC (mean difference = 0.0376 ± 0.0176 ; $p = 0.033$). Additionally, decreasing temperature increased the number of germinants (mean difference = 0.2296 ± 0.055 ; $p = 3.38e-5$) while increasing water depth decreased the number of germinants (mean difference = 1.067 ± 0.463 ; $p = 0.021$). Salinity and flooding were not found to significantly affect germination at transect sites ($p = 0.520$; $p = 0.471$).

After plotting correlation between predictors, we determined that correlations greater than 0.5 exhibit collinearity that exceeds acceptable limits to use within the same model. The predictors with high correlation include Julian date, I-VWC, flooding (binomial), and salinity. We performed a PCA with these predictors (Figure 38). The remaining independent variables that did not exhibit collinearity were soil temperature and water depth. The first two principal components explained 85.6% of the variance (Table 14). We extracted these values to include in Poisson Regression models.

Hardstem bulrush presence or absence (binomial model) was used as a response variable. Individual predictor models revealed the probability of hardstem bulrush presence decreased with increasing water depth (mean difference = -0.559 ± 0.258 ; $p = 0.03$). Soil temperature, I-VWC, salinity, and flooding had no effect (Table 15). The best performing multi-predictor model included the first principal component, soil temperature, and water depth as predictors (Table 16).

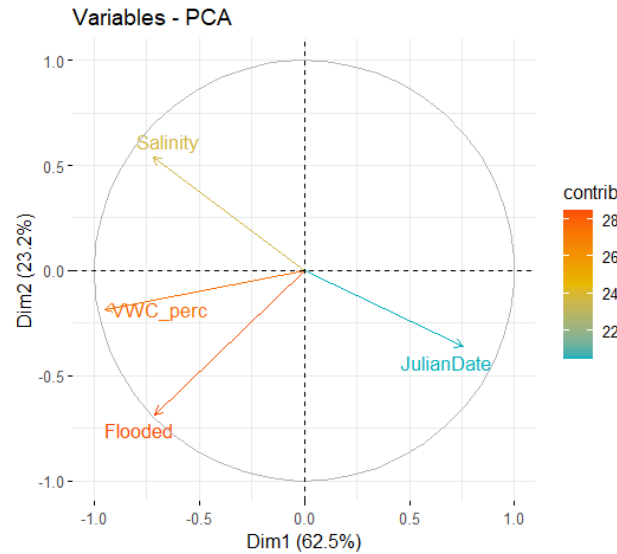


Figure 38. PCA visualization of correlated predictors for transect analysis.

Table 14. Principle components for transect PCA 2022 including salinity, VWC, flooding presence, and date.

	PC1	PC2	PC3	PC4
Standard Dev	1.581	0.9624	0.6979	0.29429
Proportion of Variance	0.625	0.2315	0.1218	0.02165
Cumulative Variance	0.625	0.8566	0.9784	1

Table 15. Single binomial predictor models for transect 2022 predictors.

Predictors	K	Estimate	Std. Error	Pr (> z)	AIC	Delta AIC
Depth	5	-0.5589	0.2580	0.0303	327.7	0.00
Flooding	5	0.0103	1.0329	0.992	345.14	17.23
Temp	5	-0.0736	0.0377	0.0507	349.14	21.84
I-VWC	5	0.0158	0.0180	0.38	349.76	24.04
Salinity	5	0.1943	0.3615	0.5910	352.12	24.20

Table 16. Multi-predictor models for transect 2022 predictors. Hardstem bulrush presence (binomial) is the response variable.

Model	K	Estimate	Std. Error	Pr (> z)	AIC	Delta AIC
PC1		-0.4141	0.2426	0.0879		
Temp	7	-0.6492	0.1941	0.0003	319.18	0
Depth		-1.5326	0.3482	1.08e-5		
PC 1		-0.3531	0.2673	0.1865		
PC 2	8	0.0846	0.2139	0.6924	321.14	1.96
Depth		-1.472	0.3703	7.07e-5		
Temp		-0.6425	0.1939	0.00092		
Depth	5	-1.9516	0.9009	0.0303	327.92	8.74
PC1		-0.5031	0.2329	0.0308		
Depth	6	-1.1881	0.2977	6.59e-5	328.61	9.43
PC2		0.3421	0.2621	0.19185		
Temp	7	-0.5579	0.1703	0.001056	329.14	9.96
Depth		-1.2800	0.3165	5.27e-5		
PC1		0.04183	0.2530	0.0983		
PC2	7	0.1152	0.2048	0.5738	330.42	11.24
Depth		-1.1213	0.3126	0.0004		
PC2		0.4202	0.2388	0.0785		
Depth	6	-0.9338	0.2826	0.00095	338.21	19.03
PC1		-0.0492	0.1632	0.7631		
PC2	7	0.4881	0.1978	0.0136	344.9	25.72
Temp		-0.3875	0.1765	0.0282		
PC1		-0.0569	0.1598	0.7216		
PC2	6	0.4382	0.1907	0.0216	347.64	28.46
PC1		-0.1068	0.1735	0.5384		
Temp	6	-0.3564	0.1769	0.0440	348.18	29.00
PC2		0.1657	0.3325	0.61829		
Temp	6	-0.2939	0.1583	0.06342	349.62	30.44
Temp	5	-0.3312	0.1695	0.0507	349.76	30.58
PC1	5	-0.1854	0.1772	0.2956	350.09	30.91
PC2	5	0.2722	0.3029	0.3687	351.01	31.83

Additionally, we evaluated factors affecting new germinant emergence. The best performing multi-predictor model included the first two principal components, soil temperature, and water depth (Table 17). Individual predictor models revealed that increasing soil temperature (mean difference = $-0.339 + 0.084$; $p = 5.38e-5$) and water depths (mean difference = -1.03 ± 0.462 ; $p = 0.025$) decreased the number of new germinant counts, while increasing I-VWC (mean difference = $0.05 + 0.021$; $p = 0.018$) increased the number of new germinants. Salinity and flooding had no effect on new growth observations (Table 18).

Table 17. Multi-predictor models for new hardstem bulrush germinants for PCA 2022 transect data.

Model Names	K	Estimate	Std. Error	Pr (> z)	AIC	Delta AIC
PC1	8	-2.0725	0.7692	0.0071	2543.21	0
PC 2		-0.3569	0.1493	0.0168		
Temp		-2.4711	0.1294	<2e-16		
Depth		-3.2258	0.1904	<2e-16		
PC1	7	-1.7919	0.7277	0.01381	2546.73	3.52
Temp		-2.4364	0.1266	<2e-16		
Depth		-3.1841	0.1868	<2e-16		
PC2	7	-0.1004	3.2992	0.976	2652.59	109.38
Temp		-3.1032	0.1451	<2e-16		
Depth		-1.7255	0.1269	<2e-16		
PC2	6	-1.6586	1.5056	0.271	2893.3	350.09
Temp		-2.1481	0.0982	<2e-16		
Temp	5	-0.3386	0.0838	5.38e-5	2907.7	364.49
PC1	7	-0.2663	0.1293	0.0394	3025.65	482.43
PC 2		-0.5647	0.1475	0.00013		
Temp		-1.2563	0.0663	<2e-16		
PC1	6	-0.1184	0.1084	0.275	3039.15	495.94
Temp		-1.2522	0.0656	<2e-16		
PC1	7	-1.0531	0.2172	1.24e-6	3330.99	787.78
PC2		-0.5966	0.1604	0.0002		
Depth		-0.8391	0.0704	<2e-16		
PC1	6	-0.7253	0.1875	0.00011	3343.14	799.93
Depth		-0.8379	0.0681	<2e-16		
PC1	6	-0.5660	0.1587	0.000361	3495.85	952.64
PC2		-0.7505	0.1485	4.35e-7		
PC1	5	-0.3346	0.1284	0.00918	3521.87	978.66
PC2	5	-0.5344	0.7600	0.482	3730.49	1187.28
PC2	6	-0.5432	0.7618	0.476	3732.53	1189.32
Depth		0.0116	0.0583	0.843		
Depth	5	-1.0335	0.4624	0.0254	4105.01	1561.79

Table 18. Single predictor models for new hardstem bulrush germinants for transect 2022 predictors.

Model	K	Estimate	Std. Error	Pr (> z)	AIC	Delta AIC
Temp	5	-0.3386	0.0838	5.38e-5	2907.7	0
I-VWC	5	0.0498	0.0211	0.0181	3370.99	463.29
Salinity	5	0.4788	0.5393	0.375	3495.28	587.58
Flooding	5	1.1928	1.9281	0.536	3849.36	941.66
Depth	5	-1.0335	0.4624	0.0254	4105.01	1197.3

Lastly, we evaluated predictors' effects on apparent germinant mortality. The best performing multi-predictor model included the second principal component, soil temperature, and depth (Table 19). Individual predictor models revealed increasing soil temperature increased mortality (mean difference = 1.101 ± 0.448 ; $p = 0.014$). Conversely, the presence of water in the previous week decreased mortality (mean difference = -1.28 ± 0.55 ; $p = 0.02$). Salinity, water depth, and I-VWC had no effect on mortality (Table 20).

Table 19. Multi-predictor models for hardstem bulrush mortality for the PCA 2022 transect data.

Model Names	K	Estimate	Std. Error	Pr (z)	AIC	Delta AIC
PC2	7	1.4010	0.8887	0.1149	1835.26	0
Temp		0.3719	0.0585	2.04e-10		
Depth		-2.1364	0.3237	4.12e-11		
PC1	8	0.3519	0.3308	0.2875	1858.68	23.42
PC2		2.1068	0.2640	1.45e-15		
Temp		0.5236	0.0704	1.01e-13		
Depth	6	-2.5488	0.3409	7.59e-14	1874.77	39.51
PC2		1.4579	0.8286	0.0785		
Depth		-2.3128	0.2939	3.56e-15		
PC1	7	0.5082	0.3341	0.1283	1915.16	79.9
PC2		2.5032	0.2651	<2e-16		
Depth		-2.9032	0.3295	<2e-16		
Temp	5	4.958	2.044	0.0153	1917.44	82.18
PC1	7	-0.0061	0.1271	0.962	1938.95	103.69
Temp		0.6140	0.06264	<2e-16		
Depth		-1.7065	0.2684	2.04e-10		
PC2	6	1.1459	0.6794	0.0917	1958.84	123.58
Temp		0.6074	0.0559	<2e-16		
PC1	7	0.4132	0.1925	0.0318	1986.01	150.75
PC2		1.1155	0.2022	3.47e-8		
Temp		0.6294	0.0617	<2e-16		
PC1	6	0.1366	0.1321	0.301	2022.43	187.17
Temp		0.6844	0.0589	<2e-16		
PC1	6	0.0425	0.1188	0.721	2047.44	212.18
Depth		-1.9750	0.2640	7.37e-14		
PC2	5	1.1878	0.6375	0.0624	2080.91	245.65
Depth	5	-4.593	2.520	0.0684	2092.81	257.55
PC1	6	0.6884	0.1958	0.00044	2097.38	262.12
PC2		1.6071	0.2064	6.88e-15		
PC1	5	0.2646	0.1077	0.014	2175.22	339.96

Table 20. Single predictor models for transect 2022 data. The response variable is hardstem bulrush mortality.

Predictor	K	Estimate	Std. Error	Pr ($> z $)	AIC	Delta AIC
Temp	5	1.1012	0.4483	0.0140	1917.44	0
I-VWC	5	-0.2952	0.2135	0.167	2006.91	89.47
Salinity	5	-0.0106	0.5026	0.983	2058.33	140.89
Depth	5	-1.3159	0.7246	0.0693	2092.81	175.37
Flooding	5	-1.2843	0.5541	0.0205	2183.18	265.74

3.4. Hardstem Bulrush Expansion

In both years, exclosure type had no effect on hardstem bulrush expansion for the entire growing season (Figure 39). Exclosure type also had no effect on expansion compared to controls within designated periods of the growing season: May-July or July– Sept (Table 21). In 2021, hardstem bulrush expansion was greater between May-July compared to July-September ($R^2 = 0.584$, $df = 52$, $F = 75.26$; $p = 1.108e-11$) (Figure 40). This trend was also present in 2022 ($R^2 = 0.104$, $df = 52$, $F = 7.176$; $p = 0.0099$) (Figure 41).

Although there was no significant difference between controls and exclosure type in either year, there were some differences detected between treatment exclosures. In 2021, Hardware cloth exclosures experienced more growth compared to hog wire exclosures between May-July (average difference: 1.6288; $p_{adj} = 0.043$). In 2022, sheet panel exclosures experienced more growth compared to hardware cloth between July - Sept (average difference: 5.183; $p_{adj} = 0.048$).

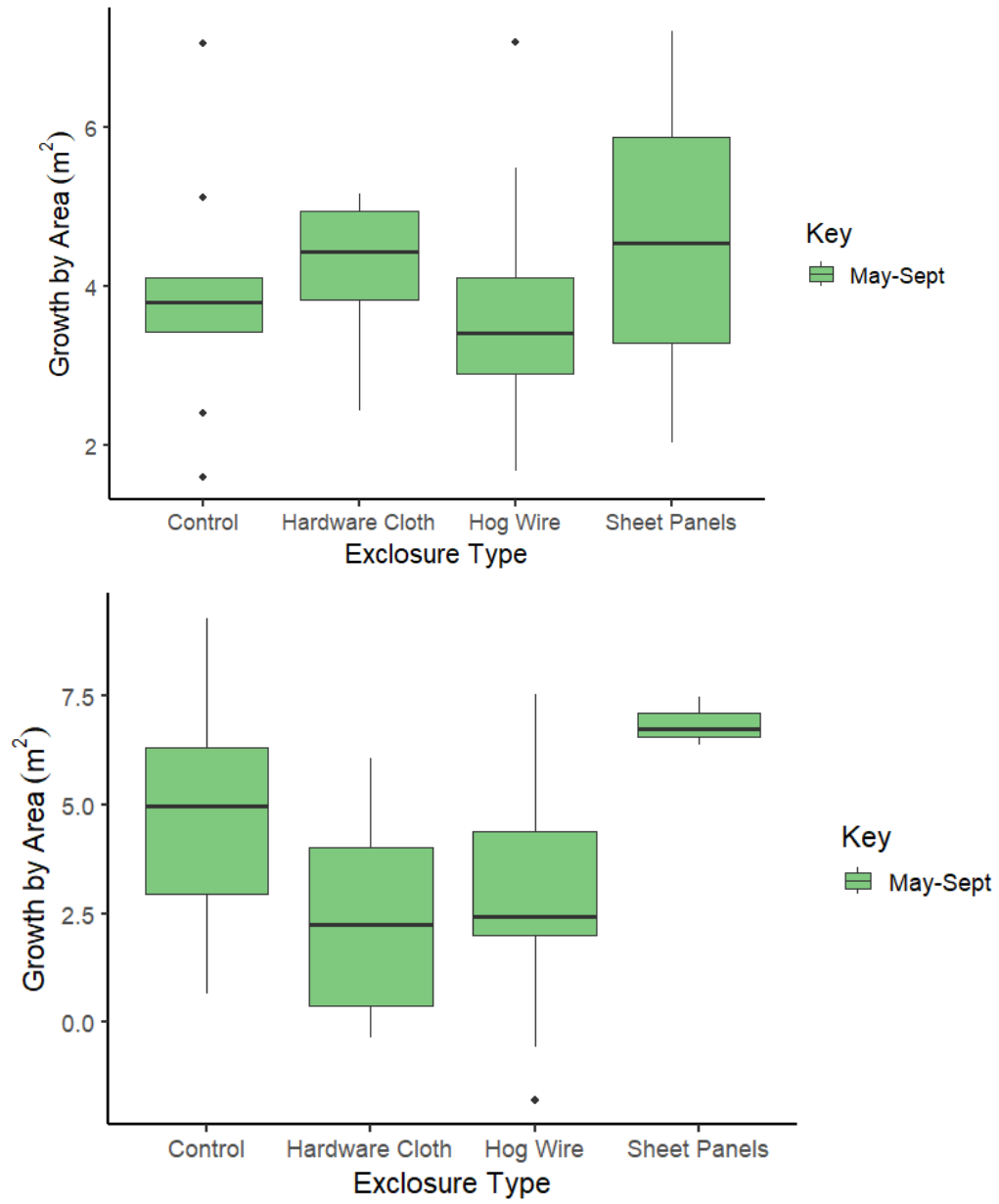


Figure 39. Hardstem bulrush expansion total in 2021 (top) and 2022 (bottom).

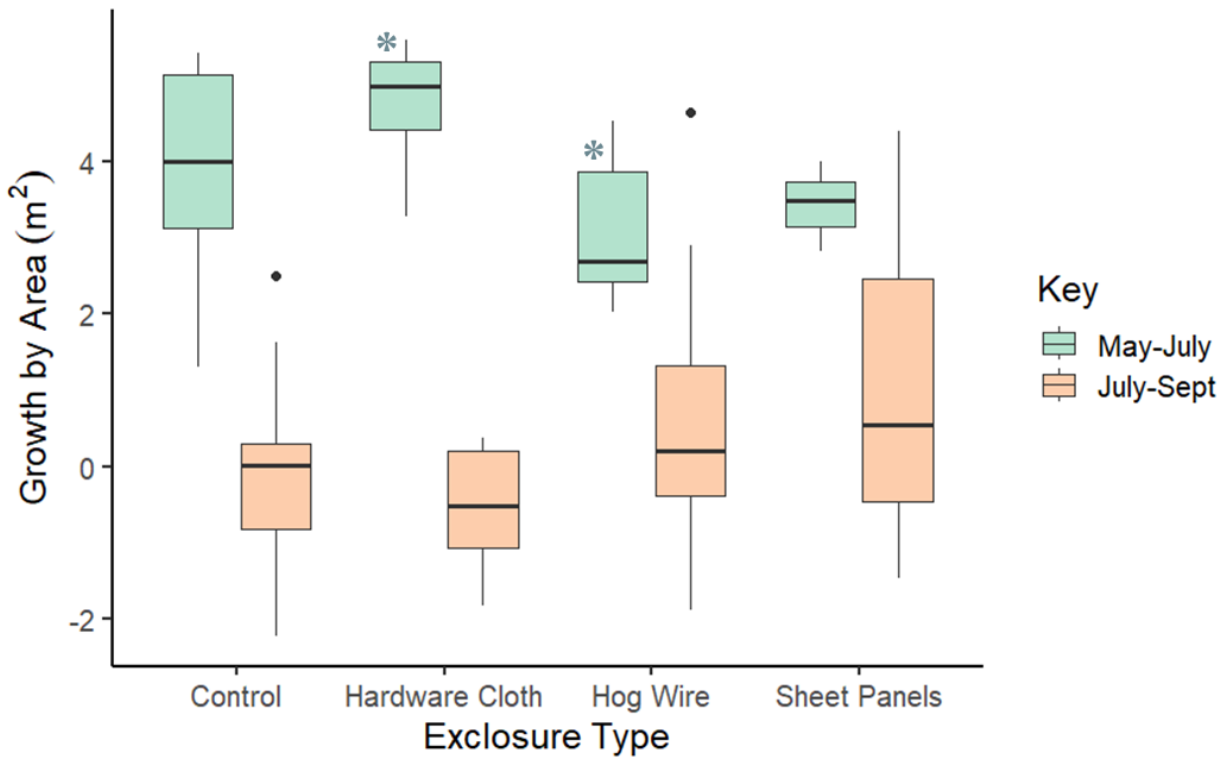


Figure 40. Hardstem bulrush expansion in enclosure experiment 2021 designated by early and late growing season expansion. (* indicates statistical significance)

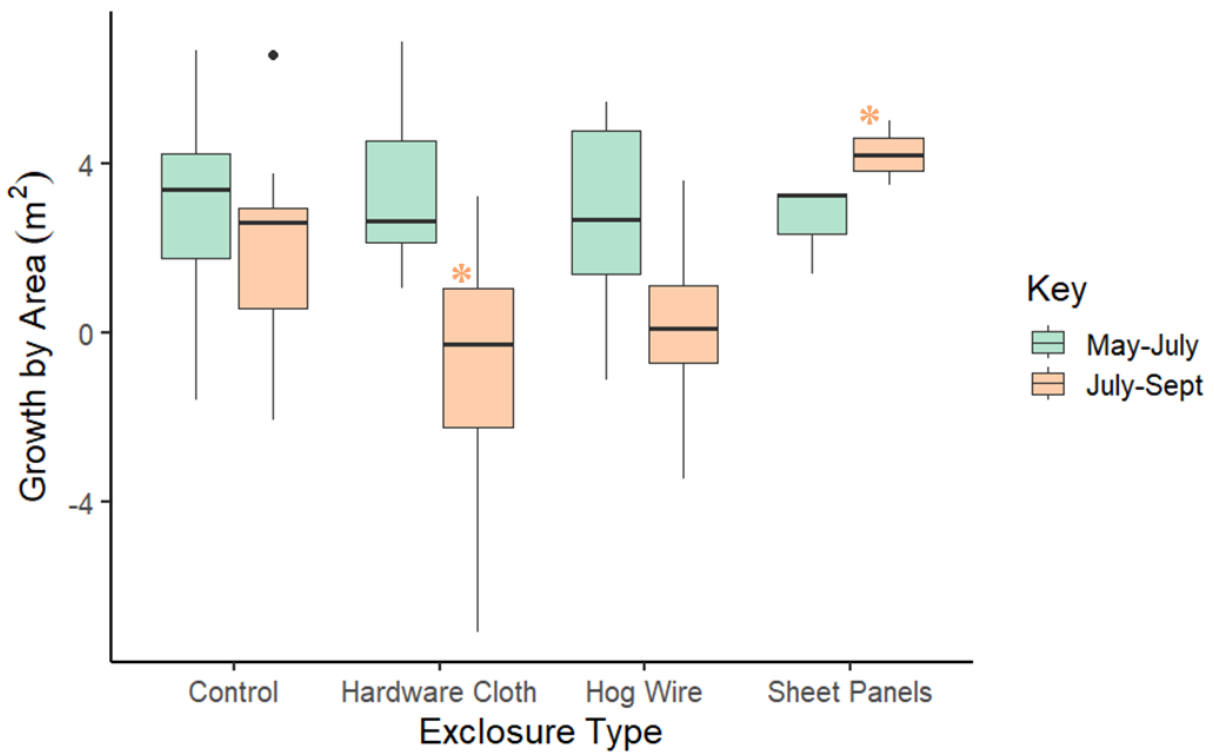


Figure 41. Hardstem bulrush expansion in enclosure experiment 2022 for early and late growing season comparisons. (* indicates statistical significance)

Table 21. Exclosure type confidence intervals (95%) for 2021 and 2022 by growing season. Adjusted p-values are bold to indicate significance.

	May-July 2021				May-July 2022			
	diff	lwr	upr	padj	diff	lwr	upr	padj
HWCloth-Control	0.8400	-0.7496	2.4296	0.4753	0.6044	-2.7711	3.9799	0.9593
HogWire-Control	-0.7888	-2.2106	0.6330	0.4338	-0.1222	-3.1414	2.8969	0.9995
SheetPanels-Control	-0.4696	-2.4805	1.5409	0.9156	-0.1456	-4.4153	4.1242	0.9997
HogWire-HWCloth	-1.6288	-3.2184	-0.0392	0.0432	-0.7267	-4.1022	2.6488	0.9323
SheetPanels-HWCloth	-1.3090	-3.4425	0.8228	0.3467	-0.7500	-5.2787	3.7787	0.9673
SheetPanels-HogWire	0.3190	-1.6918	2.3296	0.9711	-0.0233	-4.2930	4.2464	1.0000
	July-Sept 2021				July-Sept 2022			
	diff	lwr	upr	padj	diff	lwr	upr	padj
HWCloth-Control	-0.5045	-3.0644	2.0554	0.9469	-2.9611	-6.7920	0.8697	0.1708
HogWire-Control	0.7638	-1.5258	3.0535	0.7928	-1.8800	-5.3064	1.5464	0.4433
SheetPanels-Control	1.2010	-2.0370	4.4391	0.7359	2.2222	-2.6235	7.0679	0.5910
HogWire-HWCloth	1.2683	-1.2916	3.8282	0.5293	1.0811	-2.7497	4.9120	0.8623
SheetPanels-HWCloth	1.7055	-1.7289	5.1400	0.5274	5.1833	0.0437	10.323	0.0476
SheetPanels-HogWire	0.4372	-2.8008	3.6752	0.9818	4.1022	-0.7435	8.9479	0.1175
	May-Sept 2022				May-Sept 2022			
	diff	lwr	upr	padj	diff	lwr	upr	padj
HWCloth-Control	0.2237	-1.6381	2.0855	0.9890	-1.5715	-3.8313	0.6883	0.2691
HogWire-Control	-0.0166	-1.6819	1.6486	1.0000	-1.3359	-3.3575	0.6853	0.3126
SheetPanels-Control	0.4875	-1.8675	2.8425	0.9480	1.3852	-1.4733	4.2436	0.5830
HogWire-HWCloth	-0.2403	-2.1021	1.6215	0.9865	0.2356	-2.0243	2.4954	0.9928
SheetPanels-HWCloth	0.2638	-2.2341	2.7616	0.9925	2.9567	-0.0752	5.9885	0.0586
SheetPanels-HogWire	0.5041	-1.8509	2.8591	0.9429	2.7211	-0.1373	5.5796	0.0679

DISCUSSION

My process-based approach provided important insights into the potential limiting factors affecting plant establishment at Malheur Lake. The presence of robust perennial emergents within the greenhouse experiment effectively eliminated seedbank paucity and viability as limiting factors for vegetation establishment. The widespread distribution of broadleaf cattail and hardstem bulrush seeds are consistent with the long-term dominance of these species in the lake, the high level of wind and wave action that can aid seed dispersal, and the presence of these plants along certain lake margins (Soons 2006, Soomers et al. 2013). Hardstem bulrush and broadleaf cattail were present at almost all sites sampled, although their densities varied (Figure 42). Hardstem bulrush had greater germination along the southwest side of the lake, in Unit 4. Broadleaf cattail proliferated in the southern portion of Unit 5, although it was still detected in Unit 4. I expected to see alkali bulrush as that species is present in some areas of Unit 4 and was historically abundant in the past (Duebbert 1969), but it was not observed in the greenhouse experiment. This may have been because the water-bed was maintained with municipal freshwater, which may have not provided suitable germination conditions for this alkaline species. Alkali bulrush is also not present on the lake in as high densities as other perennial emergent species, so their seedbank distributions may be more limited. Nevertheless, the response of hardstem bulrush and broadleaf cattail within the greenhouse experiment confirms that the seedbank of robust emergent vegetation is intact and seed dispersal mechanisms are not limiting establishment.

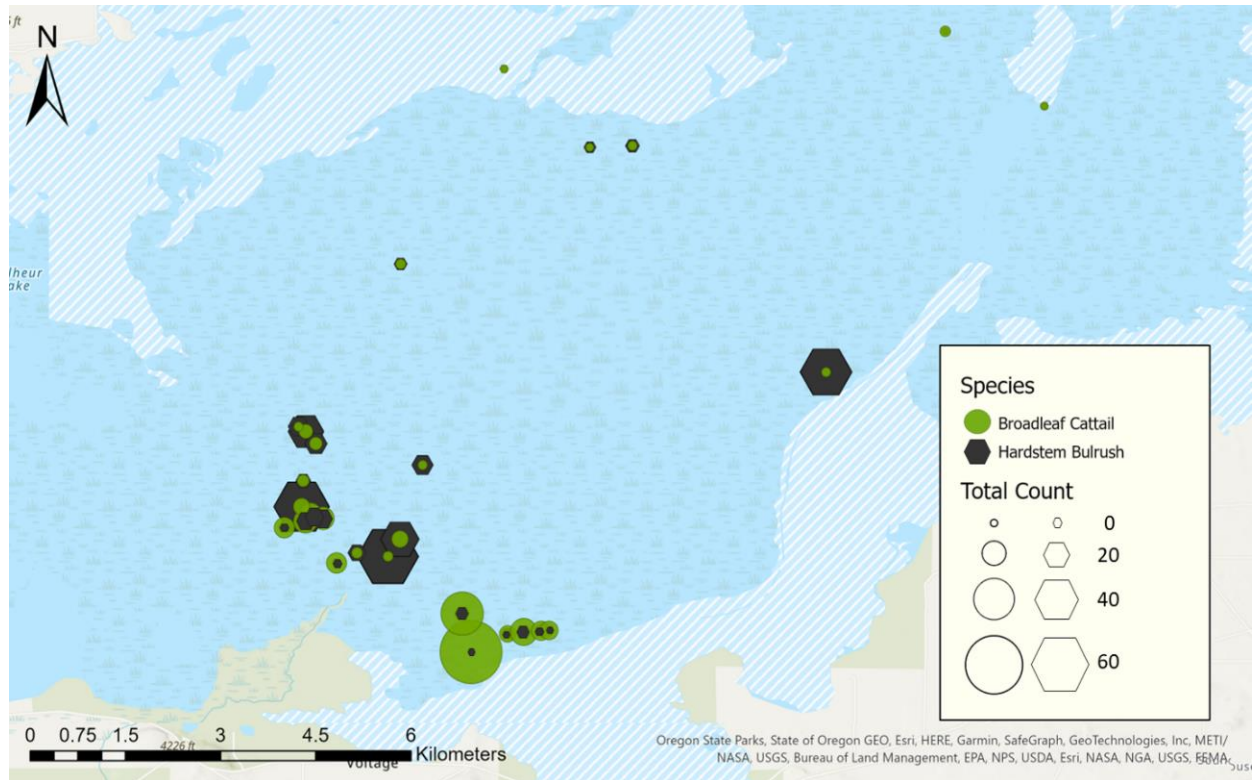


Figure 42. Greenhouse germination counts by site for 2021 and 2022 for hardstem bulrush and broadleaf cattail.

Overall, however, the seedbank was species depauperate when compared to Duebbert's (1969) description of lake vegetation. The comparatively poor seedbank was not necessarily surprising as I initially predicted that the seedbank may be buried by sediments potentially generated during the 1980s floods. However, I collected several soil cores prior to the study and all cores had a thin (< 2 cm thick), fine mineral sediment layer overtopping about 25 cm of fine, loosely consolidated organic material, overlaying a dense clay layer of unknown thickness. Thus, seedbank burial did not appear to be an issue and this idea was abandoned. Seed longevity may have played a role, however. Little vegetation has been established since the mid-1980s floods, and seeds have been exposed to flooding, drying under high temperatures, and ice scouring. Temperature and water stress are influential to seedling emergence and survival, with increasing temperatures encouraging germination but increasing seedling mortality (Lewandrowski et al.

2021). Seed longevity and dormancy breakage can also limit seedbank resilience, and dormancy breaks are not well understood for many wetland plants (Baskin and Baskin 1998). Thus, it is possible that drought and increasing temperatures combined with variability in dormancy has led to the decline in species diversity.

My germination plots also indicated a low number of species compared to historic diversity (Duebbert 1969). The lack of historic species in germination plots are likely due to their poor representation in the seedbank, but it is possible that germination requirements for many of these species were not met. I found only eight facultative wetland species in my germination plots (A.10), and many species such as *Juncus balticus*, *Carex spp.*, and *Eleocharis palustris* were noticeably absent. Hardstem bulrush was the most prolific perennial emergent vegetation species detected in both years. Although broadleaf cattail and alkali bulrush were recorded at germination exclosures in 2021, their numbers declined in 2022, with alkali bulrush going undetected. Based on the greenhouse seedbank experiment, broadleaf cattail was expected to be present in high abundances, but I could not identify what factor limited their establishment. Exclosure type had a varying effect on germination depending on species, but I do not believe this result is biologically significant. Sediment became trapped in exclosures and may have actually inhibited vegetation establishment (Figure 43). In 2022, there was an emergence of coyote willow (*Salix exigua*) in Unit 5, which has historically been observed bordering streams and perennial ponds (Figure 44) (Piper et al. 1939). Additionally, there was an emergence of broadleaf cattail in 2022 in previously unvegetated areas within the lake. Broadleaf cattail is known to be highly responsive to hydrologic conditions and often creates a monoculture in disturbed systems, but this has not occurred at Malheur Lake. Although robust perennial emergent germinants were observed at all exclosure sites, the mortality rate suggests the impetus

to vegetation establishment may be related to abiotic factors affecting seedling survival, such as soil chemistry, soil temperature, soil moisture, soil structure, and flooding patterns.



Figure 43. Sediment deposition inside germination exclosures in May 2022.



Figure 44. Comparison of Briggs Bay vegetation in September of 2021 and September 2022. In 2021 (left), annual plants such as nettleleaf goosefoot and red sorrel dominated. In 2022 (right), willows began to dominate this region.

Salt accumulations in arid wetlands can limit plant establishment (Jolly et al. 2008) but our soil and water chemistry analysis did not reveal any soil chemistry conditions that may be inhibiting vegetation. Lab results indicate that alkalinity and pH are not a concern for the perennial emergent species (e.g., broadleaf cattail, hardstem bulrush) at Malheur as these species are known to tolerate a pH of 5-9 (Anderson 1977), and sulfate concentrations are low enough to indicate that reduction to hydrogen sulfide gas is occurring. Our water analysis confirmed the assumption that ions are accumulating in the lake until a flushing event occurs (Piper et al. 1939). Historically, this has likely occurred during high water levels as it outflows to Harney Lake, although in dry years it is likely that wind is an important mechanism of salt dispersal

(Abuduwaili et al. 2008). It is currently unknown where potential accumulation is occurring as result of this system. This process may be interrupted if lake levels continue to decline, and hydrologic connectivity is lost. Sodium salts are highly water soluble, but our results show that something is capturing sodium ions in Unit 5, and this process remains unknown. NCSS data showed high concentrations of calcium carbonate that may explain the high calcium ion concentrations in the Extractable Salts Test (Table 1). This calcium level also suggests that the salt rimming the lake during low water years may be gypsum ($\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$). It is unlikely that soil or water chemistry has contributed to the failure of vegetation re-establishment.

Soil temperature and salinity can strongly affect vegetation establishment (Freeland et al. 2020, Lewandrowski et al. 2021), and although I identified effects of these two processes on plant establishment, collinearity of our abiotic predictors limited my ability to identify specific limiting processes. The effect of temperature varied by species and between years, which suggests that the cumulative nature of the experiment was not conducive to monitoring this variable, and I do not believe that there was biological significance based on estimated coefficients. However, there were isolated periods in 2022 where temperatures reached 35°C, and these high temperatures can limit germination and survival. Lewandrowski (2020) found that increases in temperature from 25 °C to 35-40 °C encouraged germination but decreased seedling survival. Similarly, Garssen (2014) concluded that increased temperature combined with reduced precipitation, especially related to increasing frequency and intensity of drought, may lead to strong declines in seedling survival. Salinity did not influence hardstem bulrush germination in 2021, and although a positive relationship was detected in 2022, I do not think that the result is biologically significant. Increasing salinity was also found to decrease broadleaf cattail emergence in 2021. Salinity levels were relatively low throughout the experiment (ranging 1-3

ppt), and those levels are unlikely to influence germination and survival of these salinity-tolerant species. Additionally, salinity was not found to significantly affect hardstem bulrush germination at transect sites, which experienced greater variation in these conditions. The results of our PCAs show that the models with the most predictors typically explained the most variation, which allows us to conclude that these abiotic factors all have some effect on germination. Although any abiotic condition can limit plant establishment (Bornette and Puijalon 2011), soil moisture and soil structural changes are more likely the driving factors, particularly in arid environments.

The dynamic nature of this system, especially drawdowns and reflooding events, created a range of soil moisture conditions across the lake. Increasing depth and duration of flooding was not conducive to germination and establishment due most likely to restricted light (i.e., high turbidity) and oxygen availability. Conversely, some areas lacked flooding events and only received moisture through direct precipitation, and although germination occurred in these conditions, seedlings were not able to survive. Floodwaters began to initially recede from germination plots in July in 2021 and most continued to be dry through 2022, although transect plots experienced more variability in flooding through September in 2022. Some plots (i.e., transects 8-12; Figure 15) experienced an initial drawdown, but wind seiche resulted in multiple flooding and drawdown events, sometimes even on the same day (Figure 3). Wind and seiche effects contribute to water availability, and the temporal and spatial variability of these effects may provide essential moisture to seedlings (Figure 45). The sites that were further into the perceived center of the lake (13-15) retained water throughout almost the entirety of the growing season, which was a condition we were unable to observe the previous year. These sites did not support germination, and I can conclude it is unlikely that emergent vegetation will germinate when water depths exceed 2 cm.

I observed high levels of germination following the first drawdowns in June 2021. As drought persisted and water levels decreased, germinant counts began to decline in mid-July at germination exclosures (Figure 26; Figure 30). At transect sites with more varied moisture (6-10), germination events were followed by immediate sharp declines with soil moisture. The transect points further inland (1-5) also experienced steep declines of germinants in mid to late July as soil moisture likely became too dry for seedling tolerances. The timing and quantity of precipitation in summer months may provide essential moisture for seedlings in some cases (A.11). Unfortunately, I cannot identify the soil moisture threshold for germination because both extremes of conditions were observed within the experiment, and there are additional factors that may have affected seedling survival.

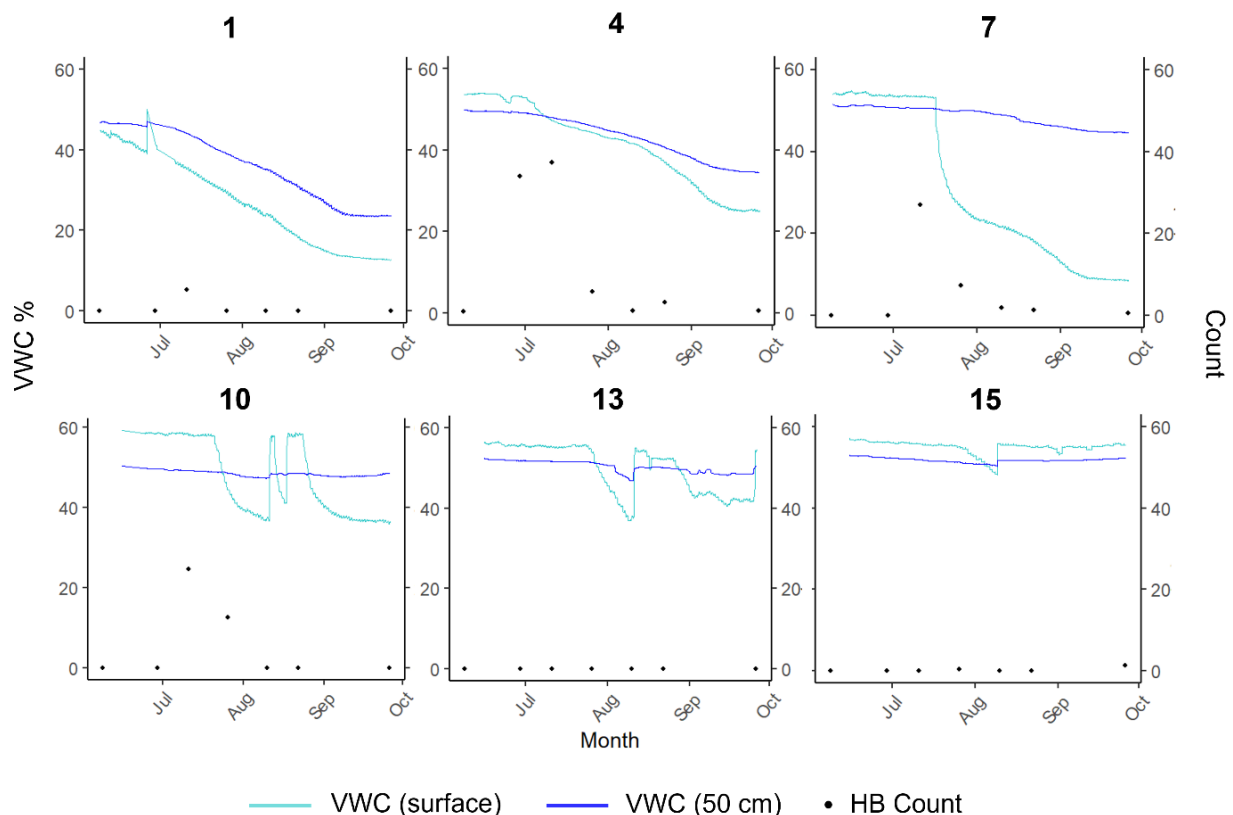


Figure 45. Continuous data logger measurements at transect sites in 2022 plotted with biweekly hardstem bulrush counts.

Long term changes to soil structure, deposition, and sediment distribution may also affect seedbank density and seedling survival (Jurik et al. 1994, Stirling et al. 2020). Jessup observed a peat layer of up to 60 cm by the Blitzen River and 30-75 cm in the northern portion of the lake which he believed was at least partially derived from emergent vegetation (The United States vs. The State of Oregon 1932). This peat layer indicates prolonged wet conditions were present to allow for organic matter production and preservation as peat development requires water on the landscape for most of the year (Boelter and Verry 1977). According to Jessup, the peat layer was underlain by fine organic detrital sediments (The United States vs. The State of Oregon 1932). I did not observe a soil organic layer throughout any portion of the lake, but upper layers consisted of a fine silt about 1 cm thick and then a 0.25 m layer of fine organics (A.11). Both the loss of the organic mat and the characteristics of the silt layer as it dries could affect germination and establishment through combined effects on soil moisture dynamics and potential physical restriction of plant rooting.

The lack of an organic mat may be related to both the frequency and intensity of drought, high temperatures, and ice scour on the lake. Peat forms under anaerobic conditions created by soil saturation from groundwater or surface water. Peat rapidly decomposes, however, when exposed to aerobic conditions such as during drawdowns without groundwater saturation. Interestingly, however, Malheur Lake has always had wildly fluctuating lake levels (Piper et al. 1939), but during the early 1900s it maintained the peat layer despite climatic fluctuations and the extreme drought in the 1930s, suggesting that more recent hydrologic modifications may have played a role in the loss, or reduction, of this organic layer. Furthermore, following the 1980s floods, vegetation has occupied only a small fraction of its historic extent. Perennial emergent vegetation would have historically limited ice movements on the lake, and the loss of

this vegetative coverage may have facilitated ice scouring of the organic mat. The effects of ice scouring were not evaluated in this study, although in our study years the water levels and following ice cover did not reach our study sites. This variable should be examined more thoroughly as scouring can sever above-ground growth, especially in regions where water level fluctuations occur (Hill and Johansson 1992).

Perennial emergent vegetation, including broadleaf cattail and hardstem bulrush, are known to expand rapidly in wetland systems through rhizomes, but the rate of expansion during my study was extremely low compared to historic expansion rates. In fact, coarse calculations indicate that it would take 6000-10000 years for full coverage to occur based on current expansion rates. The immediate recovery of vegetation was noted in historical reports (Piper et al. 1939) in the Silvies River basin following drought conditions. In 1917, estimated ‘tule’ coverage was only 800 ha (1000 acres); in the following year, that estimate jumped to 3200 ha (8000 acres) (Piper et al. 1939). It is also known, however, that some of the historic tule coverage in and around the lake has been removed for over a century due to hydrologic alterations, fire, and deliberate removal (The United States vs the State of Oregon 1932). The lake has been able to support vast numbers of migratory waterfowl and breeding populations historically (Duebbert 1969) even with vegetative losses noted, but this role may vary depending on vegetation availability. I was able to determine that significantly more expansion occurs in the first portion of the growing season, between May-July, compared to the later growing season, between July-September. This aligns with plant physiology and energy demands, especially in arid environments where water availability is limited (Warwick and Brock 2003). The exact reasons for the overall slow expansion are unknown, but similar to seedling establishment, it is likely not related to soil chemistry but more related to soil moisture and soil structure.

Fluctuations in water levels have been observed throughout the last century at Malheur, and strong historic vegetation responses indicate that there are additional factors currently limiting vegetation establishment.

Initially, herbivory was the primary concern for vegetation establishment and expansion, especially herbivory by waterfowl. Current waterfowl populations are unlikely limiting vegetation expansion, although there is concern that decreased flyway connectivity will limit available habitat for these species and may increase herbivory pressure. The exclosure results support this conclusion as exclosure type had no effect on growth, but herbivory by waterfowl may be more important in high water years. We observed more herbivory of germinants in areas with water connectivity, suggesting that lake size and seiche effects may affect herbivore presence. During dry years, terrestrial herbivores including mule deer (*Odocoileus hermionus*) and pronghorns (*Antilocapra americana*) contribute to herbivory, and accidental cattle incursion can also occur (Figure 47). The effects of herbivores are dependent on water distribution, and although they may vary based on lake coverage and depth, the history of waterfowl presence combined with my observations do not suggest that herbivory is a main threat to vegetation establishment and expansion.

Carp were also expected to be a limiting factor for vegetation expansion through disturbance of sediments and potential uprooting of vegetation. Due to low water levels, there was a limited time (about 1 month in 2021) where any carp could access our sites, so we cannot conclude what effect these exclosure would have on carp presence. However, it is unlikely that carp could generate enough disturbance to uproot established emergent vegetation, especially in low water years. There is some evidence that exclusion of carp may create more suitable foraging habitat for waterfowl and allow for macroinvertebrate population responses within one

year (Schrage and Downing 2004, Bonneau and Scarnecchia 2015). However, the results of my enclosure experiment combined with carp modeling completed by Pearson (2020) concludes that management actions facilitating the removal of carp will not restore the system to its previous condition, and a broad systems approach is necessary to restore vegetation.



Figure 47. Potential sources of herbivory observed by trail cameras and in the field including Greater sandhill crane (*Grus canadensis tabida*) (top left), cattle (top right), Canada goose (*Branta canadensis*) (bottom left), and mule deer (bottom right).

Although the effects of wind-wave action are important to soil moisture dynamics (Petrov et al. 2007) and vegetation survival, we were not able to sufficiently test the effects of wind reduction on vegetation expansion. I could not quantify the reduction in wind provided by barriers and the identified prominent wind direction was not as dominant as anticipated.

Additionally, we experienced such low water levels that our sites were rarely in greater than 3 cm of water in 2021, and sites were continuously dry starting in July of 2022 with a maximum water level of 3 cm. Wind-wave action is limited by water availability, so it may be of greater importance during high water years. Wind barriers did have observable effects on sediment deposition and recruitment. Sediment deposition increased directly behind the barriers and in the exclosures, varying between 2-4 cm (Figure 46) which affected water distribution within and around the exclosure. We noted earlier germination of facultative upland and facultative annuals in areas directly protected by barriers where deposition was present (Figure 31). In this study, wind-wave action was not limiting plant establishment, but future research should address the potential effects of sedimentation and elevation on vegetation responses (Figure 47).



Figure 46. Sediment deposition in wind barrier exclosures in 2021 (left), and annual plant emergence behind the barrier in 2022 including *Rumex acetosella*, *Lactuca serriola*, and *Hordeum jubatum* (right).



Figure 47. New cattail growth following sediment deposition near the Blitzen River mouth in 2022.

4.1. Synthesis

The results of this study, along with a review of historic and current literature, suggest that large-scale hydrologic alterations within the Harney Basin have initiated changes that have affected soil structure, soil moisture, plant community composition, and reduced expansion rates of wetland vegetation within Malheur Lake. Historically, Malheur Lake supported an inland deepwater marsh that promoted a diverse wetland plant community (Duebbert 1969), with a dense organic layer that varied in depth across the lake (The United States vs. The State of Oregon 1932). Although water levels fluctuated dramatically among years, groundwater springs and surface and groundwater connections throughout the lake allowed sufficient soil moisture to support a diverse wetland plant community throughout large regions of the lake (Piper et al. 1939, Duebbert 1969). However, modifications of the Blitzen and Silvies Rivers, including surface water diversions, river channelization and entrenchment, and increased groundwater

pumping in the Harney Basin, has likely “modified groundwater recharge patterns and reduced groundwater storage and discharge in many parts of the lowland groundwater system” (Hubbard 1975, Garcia et al. 2022, Gingerich et al. 2022). The Silvies River often fails to connect to Malheur Lake altogether, and the drying of springs within the watershed and the loss, or reduction, of the organic mat on Malheur Lake combined with the anthropogenic modifications to the river systems has undoubtedly impacted the ability of the lake to support wetland vegetation.

It is difficult to synthesize all the hydrologic changes in the Harney Basin and quantify their individual impacts to hydrologic and soil moisture conditions in Malheur Lake, although the shift in characterizations of this habitat provides some context for these conditions. In the late 1800s to early 1900s, Malheur Lake was described as a playa or alkaline lake, populated by saline vegetation such as *Salicornia*, whereas Duebbert (1969) and Hubbard (1975) described it as an inland deep fresh marsh in the late 1900s. It is now typically described as a shallow lake system (Pearson 2020). The General Land Office (GLO) records indicate that water diversions were present on the Blitzen River as early as the 1800s. Park and Piper (1939) note that diversions were already extensive on the Silvies in the 1930s (Be Rights to Waters of Silvies River 1925; Russell 1905) and that during dry years, the Silvies did not connect to Malheur Lake. Although some variation is natural in arid systems (cite), it is clear from early investigations and descriptions that Harney Basin was much wetter historically. Piper and Park (1939) noted that Blitzen River Valley was “under natural conditions...sluggish and meandered through a swampy plain from the very head of its alluvial basin...this condition has been rectified by canalizing the stream for about 20 miles.” They also noted that the Blitzen floodplain remained very wet and consisted of several channels that flowed toward Malheur Lake. Furthermore, they noted that in autumn there was often a groundwater pulse through the system that entered into the lake.

Evidence of a much wetter hydrology is evident from the peat mat that now sits high above the entrenched Blitzen River. Presumably, this mat would have been much thicker prior to drying of the system and would have stored copious amounts of water. According to historic records, the Silvies may have been an even greater source of water to Malheur Lake than the Blitzen, but irrigation and extraction significantly reduced flows that reached Malheur Lake (Hubbard 1975). Russell (1903) states that the Silvies River is “much the larger” compared to the Blitzen and even recommends power generation as a potential use. By the late 20th century, the Silvies River was considered the second largest runoff source for Malheur Lake (Hubbard 1975). The Blitzen River has not shown a clear change in mean annual discharge over time, but interannual variability has increased (Schultz et al. 2017, Snyder et al. 2019)) which has implications for water availability and groundwater recharge within the basin.

Endorheic basins are a product of their watershed, and globally these systems are threatened by climate change and anthropogenic alterations (Wang and Ma 2016). Activities in the watershed that alter the volume and temporal and spatial distribution of groundwater and surface water resources affect the terminal receiving basin. The first comprehensive groundwater study in the basin was completed by Gingerich (2022) and concluded that annual groundwater discharge exceeds recharge by 370,000 m³/day (110,000 acre-ft/yr.). Additionally, 95% of groundwater pumped was attributed to irrigation (Garcia et al. 2022, Gingerich et al. 2022), and total pumpage has increased about 300% since 1990 (Gingerich et al. 2022). Springs in the lake have ceased flowing (do we have a citation), and although currently make up a small component of the water budget, they could have had important soil moisture benefits within their surrounding area. Despite the emphasis placed on irrigation over the last century, a specific hydrologic budget considering diversions and groundwater pumpage was not constructed until

2022 (Garcia et al. 2022). Not only do these modifications affect the total volume of water, but they also affect the volume of sediment entering the lake and timing of flows. The channelization and entrenchment of the Blitzen would have increased sediment loads into the lake, and possibly more importantly, increased the rate at which water moved through the system. This single, disconnected channel would have reduced the spatial distribution and temporal variation of water entry into the lake. These ideas, albeit conceptual based upon literature, if true, would significantly affect the temporal and spatial patterns of soil moisture in the lake which could have significant effects on plant germination and establishment.

The Harney Basin has also experienced increasing frequency and intensity of drought in the last several years (Snyder et al. 2019) that exacerbate water availability and affect soil structure properties. Soil physical responses to drought are varied, but often include accelerated decomposition as organic matter is exposed to oxygen and increased temperatures (Stirling et al. 2020). When soils dry, aerobic respiration allows for rapid decomposition and volatilization of organic materials, as well as facilitating eolian transport from the wetland. Although acidification and reduced inorganic sulfate deposits have not been detected, the soil structure has been degraded (cracking, ecological degradation, decreased erosion resilience) and may be impossible to recover (Stirling et al. 2020). Peat development requires soil saturation for extended periods of time, and declining water supplies are not conducive to this accumulation (Williams et al. 2000, Cusell et al. 2015, Stirling et al. 2020). The climate projections for the High Desert region demonstrate increased susceptibility to drought and loss of hydrologic connectivity in the future (Snyder et al. 2019), and increasing annual temperatures (Kunkel et al. 2013) may affect seed dormancy and germination opportunities for wetland vegetation.

MANAGEMENT IMPLICATIONS

As stopover sites along the Pacific Flyway are becoming increasingly isolated, maintaining connectivity is a crucial issue in endorheic watersheds in the Great Basin (Donnelly et al. 2020), and habitat types are an important consideration to wetland restoration. While some shorebirds and wading birds can utilize a shallow lake or seasonal wetland system, there has been a loss in deepwater habitat and hydroperiod duration within the region (Haig et al. 2019, Donnelly et al. 2022). It may be useful to evaluate distributions of habitat types available within the region and adapt restoration plans to make an informed decision towards restoration efforts. Wildlife refuges, including Malheur NWR, often irrigate hay meadows and divert water to ponds to provide important habitat (Patton and Judd 1970, Straubinger et al. 2022). These diversions prioritize certain habitat types and may limit opportunities for restoration of wetland habitats in Malheur Lake. A quantitative understanding of how much water is being diverted for irrigation to help inform decisions about water availability for lake restoration.

Malheur Lake is a product of its watershed and its restoration, if a goal, will require an understanding of temporal and spatial hydrologic and sedimentation processes occurring outside the lake. Addressing channel incision and erosion in the Blitzen River would help reduce sediment inputs and restore connection to the floodplain (Hohensinner et al. 2018). Much of the Blitzen River is on the refuge, and restoring the multi-channel form and addressing channel entrenchment could facilitate a broader spatial distribution of water resources and prolong flow later into the season which could have positive benefits to newly germinating plants. The Malheur Lake system was historically wetter; if deepwater marsh is the goal then it will require sufficient groundwater and surface water flows—including timing, spatial distribution, and volume—to facilitate plant germination and establishment.

The restoration of the Malheur Lake system may not be possible as the current alternative stable state may be unrecoverable (Scheffer and Jeppesen 1998, Scheffer and van Nes 2007). Based on historic lake descriptions, the reduction in organic material and presumed increase in mineral sediments may have shifted key biogeochemical processes. Furthermore, the thin mineral layer on the surface of the organic mat may inhibit seed germination and establishment because of its rapid drying and hardening. Large shallow lakes experience increased wind fetch, especially in the absence of macrophytes, that increase turbidity and inhibit restoration (Janssen et al. 2014). It is possible that due to the number of modifications in the Malheur system and Harney Basin in .conditions. Hydrologic restoration does not always lead to successful wetland restoration (Nilsson et al. 2015), especially when other factors are inhibiting community composition (Richards et al. 2020). Despite this risk, successful wetland restoration cannot occur without appropriate hydrologic conditions.

Hydrologic alterations are clearly a major issue affecting Malheur Lake, but there are many other processes that may also be influencing lake conditions. Furthermore, this study does not provide a complete picture of Malheur Lake. Relative to the size of the lake, our sampling intensity was small, and it is known that there is spatial variability in soil and hydrologic processes in the lake. Additional research is needed to investigate the chemistry of the upper mineral crust in the lake and to determine its potential impact, if any, on limiting seedling establishment through chemical or physical constraints. More detailed information on soil moisture dynamics, including their temporal and spatial drivers, would benefit understanding of the lake.

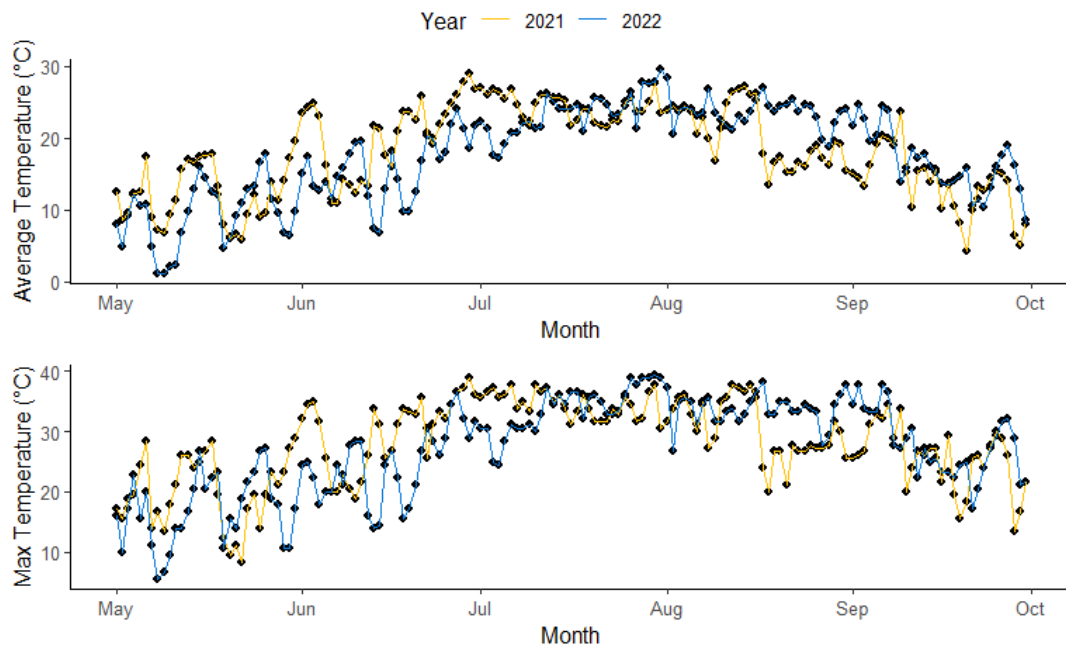
APPENDIX A. SUPPLEMENTARY TABLES AND FIGURES

A.1. Soil analysis packages for Mehlich 3 and Flood Testing

Mehlich 3 Elements	Flood Test Elements
pH	Calcium, ppm
Phosphorus, ppm	Chloride, ppm
Potassium, ppm	Conductivity, dS/m
Calcium, ppm	Magnesium, ppm
Magnesium, ppm	Salts, ppm
Sodium, ppm	Sodium Adsorption Ratio (SAR)
Sulfur, ppm	Sodium, ppm
Copper, ppm	Sulfur, ppm
Zinc, ppm	

A.2. Water chemistry analysis packages for nutrients and metals.

Nutrient Testing	Metals Testing	Metals Continued
Fluoride	Aluminum	Potassium
Chloride	Boron	Magnesium
Sulfate	Barium	Manganese
Nitrate	Calcium	Sodium
Phosphate	Cadmium	Nickel
TN as N (persulfate)	Cobalt	Lead
TP as P (persulfate)	Chromium	Silicon
TN as N (ppm)	Copper	Vanadium
	Iron	Zinc



A.3. Average daily and maximum daily temperatures in 2021 and 2022 in Burns, Oregon.

A.4. Greenhouse Counts for all species 2021.

Tray	Location	<i>Schoenoplectus acutus</i> Hardstem Bulrush	<i>Typha latifolia</i> Broadleaf Cattail	<i>Chenopodium murale</i> Nettleleaf Goosefoot	<i>Lindernia dubia</i> False Pimpernel	<i>Gnaphalium uliginosum</i> Marsh Cudweed	<i>Poa spp.</i> Bluegrass	<i>Rumex fuginus</i> Golden Dock	<i>Ranunculus sceleratus</i> Cursed Buttercup	<i>Brassicaceae Rorippa spp.</i> Yellowcress	<i>Sinapis arvensis</i> Wild Mustard	<i>Rumex acetosella</i> Red Sorrel	<i>Crypsis schoenoides</i> Swamp Timothy	<i>Ranunculus spp.</i> Buttercup	<i>Brassicaceae juncea</i> Brown Mustard
1	Inner Briggs Bay	0	9	7	2	0	2	0	0	3	0	0	0	0	0
2	Inner Briggs Bay	0	33	7	4	0	0	0	0	4	0	0	0	0	0
3	Inner Briggs Bay	0	16	17	4	0	0	0	0	1	0	0	0	0	0
4	Outer Briggs Bay	3	10	13	1	0	7	1	0	2	0	0	0	0	0
5	Outer Briggs Bay	4	6	11	6	0	8	1	0	4	1	0	0	0	0
6	Outer Briggs Bay	1	21	8	1	0	9	0	0	4	0	0	0	0	0
7	Briggs Bay East	0	5	21	2	0	1	6	0	5	1	0	0	0	0
8	Briggs Bay East	1	4	30	6	0	0	8	0	0	3	0	0	0	0
9	Briggs Bay East	4	0	18	0	0	0	0	0	0	1	4	0	0	0
10	South Shore West	3	2	23	4	0	0	0	0	5	1	0	0	0	0
11	South Shore West	1	7	9	0	0	0	0	0	8	0	0	0	0	0
12	South Shore West	3	11	19	1	0	0	3	0	7	0	0	0	0	0
13	South Shore Central	1	1	27	1	0	1	1	0	2	1	0	0	0	0
14	South Shore Central	4	8	13	0	0	4	0	0	4	1	0	0	0	0
15	South Shore Central	1	3	43	3	0	1	0	0	4	0	0	0	0	0
16	South Shore East	2	3	11	1	0	2	0	0	2	0	0	0	0	0
17	South Shore East	1	6	13	3	0	4	0	0	2	0	0	0	0	0
18	South Shore East	1	2	11	1	0	0	0	0	5	0	0	0	0	0
19	Germination Set 1	3	13	47	0	0	0	0	0	3	0	0	0	0	0
20	Germination Set 1	7	3	58	0	0	2	0	0	7	0	0	0	0	0
21	Germination Set 1	5	1	52	0	0	5	2	0	1	0	0	0	0	0
22	Germination Set 2	2	5	19	0	0	0	0	0	2	0	0	0	0	0
23	Germination Set 2	2	6	36	0	0	0	0	0	7	0	0	0	0	0
24	Germination Set 2	17	2	35	0	0	2	1	0	1	0	0	0	0	0
25	Germination Set 3	0	0	29	0	0	0	0	0	12	0	0	0	0	0
26	Germination Set 3	5	2	27	0	0	3	0	0	4	0	0	0	0	0
27	Germination Set 3	25	4	10	0	0	3	1	0	7	0	0	0	0	0

(Figure cont'd.)

		<i>Schoenoplectus acutus</i>	<i>Typha latifolia</i>	<i>Chenopodium murale</i>	<i>Lindernia dubia</i>	<i>Gnaphalium uliginosum</i>	<i>Poa spp.</i>	<i>Rumex fueginus</i>	<i>Ranunculus sceleratus</i> Celery Leaved Buttercup	<i>Brassicaceae Rorippa spp.</i>	<i>Sinapis arvensis</i>	<i>Rumex acetosella</i>	<i>Crypsis schoenoides</i>	<i>Ranunculus spp.</i>	<i>Brassicaceae juncea</i>
Tray	Location	Hardstem Bulrush	Broadleaf Cattail	Nettleleaf Goosefoot	False Pimpernel	Marsh Cudweed	Bluegrass	Golden Dock		Yellowcress	Wild Mustard	Red Sorrel	Swamp Timothy	Buttercup	Brown Mustard
28	West South	9	7	49	0	0	2	0	0	8	0	0	0	0	0
29	West South	15	0	35	0	0	3	0	0	9	0	0	0	0	0
30	West South	27	2	49	0	0	1	0	0	7	0	0	0	0	0
31	West Central	8	0	45	0	0	0	1	0	1	0	0	0	0	0
32	West Central	0	2	55	0	0	0	0	0	7	0	0	0	0	0
33	West Central	0	2	109	0	1	0	0	0	3	0	0	1	0	0
34	West North	3	0	53	0	0	4	0	0	14	0	0	0	0	0
35	West North	2	0	62	0	0	10	0	0	13	0	0	0	0	0
36	West North	9	1	120	0	0	8	0	0	24	0	0	0	0	0
37	Transplant	7	2	32	0	0	2	0	0	2	0	0	0	0	0
38	Transplant	9	3	39	0	0	6	0	0	9	0	0	0	0	0
39	Transplant	0	0	35	0	0	9	0	0	12	0	0	0	0	0
40	Last Year Point	2	1	22	0	0	4	0	0	5	0	0	0	0	0
41	Last Year Point	3	6	11	0	0	2	0	0	3	0	0	0	0	0
42	Last Year Point	7	8	7	0	0	0	1	0	3	0	0	0	1	0
43	Last Year West	1	6	10	0	0	0	0	0	6	0	0	0	0	0
44	Last Year West	0	5	14	0	0	0	0	0	14	0	0	0	0	0
45	Last Year West	3	2	16	0	0	0	0	0	7	0	0	0	0	0
46	North Island	1	0	79	0	0	0	0	0	7	0	0	0	0	0
47	North Island	0	0	8	0	0	0	0	0	10	0	0	0	0	0
48	North Island	0	0	33	0	0	0	0	0	8	0	0	0	0	0
49	Blitzen Inlet	2	5	0	98	4	10	0	21	3	0	27	0	0	2
50	Blitzen Inlet	0	4	3	213	8	19	0	15	11	0	64	0	0	0
51	Blitzen Inlet	0	4	2	94	5	20	2	36	6	0	31	0	0	0
Totals:		204	243	1502	445	18	154	28	72	298	9	126	1	1	2

A.5. Average Shannon Diversity Index, Simpson's Diversity Index and average richness by sampling location in 2021.

Location	Region	Shannon	Simpson	Richness
Outer Briggs Bay	South	1.61	0.777	4.33
South Shore East	South	1.38	0.703	7.00
Last Year Point	West	1.35	0.657	5.67
South Shore West	West	1.31	0.687	5.33
Briggs Bay East	South	1.24	0.620	6.67
Inner Briggs Bay	South	1.14	0.627	5.67
Blitzen Inlet	West	1.14	0.573	5.00
South Shore Central	South	1.13	0.510	4.67
Last Year West	West	1.10	0.653	4.33
West South	West	1.07	0.580	4.67
Germination North	West	1.03	0.553	4.00
Transplant	West	1.03	0.543	4.33
Germination Central	West	0.96	0.520	4.33
West North	West	0.85	0.447	5.33
Germination South	West	0.84	0.417	3.67
North Island	North	0.51	0.337	2.33
West Central	West	0.46	0.227	8.33

A.6. Greenhouse experiment average and total counts by sampling location for target vegetation species detected during 2021 and 2022.

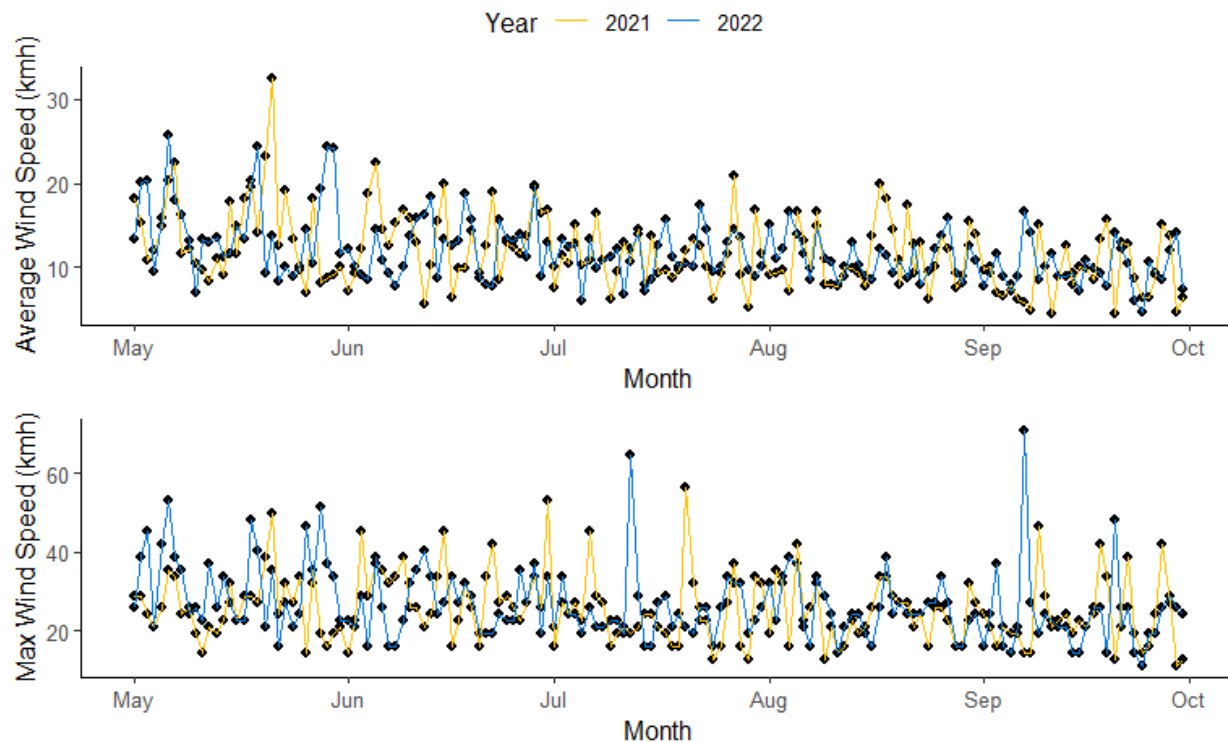
Year	Location	Latitude	Longitude	Species	Average by Location	Total Count
2021	Blitzen Inlet	43.290511	-118.823642	Bulrush	0.67	2
2021	Blitzen Inlet	43.290511	-118.823642	Cattail	4.33	13
2021	Briggs Bay East	43.280657	-118.799479	Bulrush	1.67	5
2021	Briggs Bay East	43.280657	-118.799479	Cattail	3.00	9
2021	Germination Central	43.297392	-118.827298	Bulrush	7.00	21
2021	Germination North	43.308743	-118.827997	Bulrush	10.00	30
2021	Germination Set 1	43.296298	-118.828053	Cattail	5.67	17
2021	Germination Set 2	43.297392	-118.827298	Cattail	4.33	13
2021	Germination Set 3	43.308743	-118.827997	Cattail	2.00	6
2021	Germination South	43.296298	-118.828053	Bulrush	5.00	15
2021	Inner Briggs Bay	43.278157	-118.804652	Bulrush	0.00	0
2021	Inner Briggs Bay	43.278157	-118.804652	Cattail	19.33	58
2021	Last Year Point	43.296701	-118.825554	Bulrush	4.00	12
2021	Last Year Point	43.296701	-118.825554	Cattail	5.00	15
2021	Last Year West	43.295413	-118.831071	Bulrush	1.33	4
2021	Last Year West	43.295413	-118.831071	Cattail	4.33	13
2021	North Island	43.359073	-118.799965	Bulrush	0.33	1
2021	North Island	43.359073	-118.799965	Cattail	0.00	0
2021	Outer Briggs Bay	43.283461	-118.805897	Bulrush	2.67	8
2021	Outer Briggs Bay	43.283461	-118.805897	Cattail	12.33	37
2021	South Shore Central	43.281084	-118.794714	Bulrush	2.00	6
2021	South Shore Central	43.281084	-118.794714	Cattail	4.00	12
2021	South Shore East	43.281152	-118.793594	Bulrush	1.33	4
2021	South Shore East	43.281152	-118.793594	Cattail	3.67	11
2021	South Shore West	43.280912	-118.797171	Bulrush	2.33	7
2021	South Shore West	43.280912	-118.797171	Cattail	6.67	20
2021	Transplant	43.307060	-118.826583	Bulrush	5.33	16
2021	Transplant	43.307060	-118.826583	Cattail	1.67	5
2021	West Central	43.301895	-118.828374	Bulrush	2.67	8
2021	West Central	43.301895	-118.828374	Cattail	1.33	4
2021	West North	43.309442	-118.829061	Bulrush	4.67	14
2021	West North	43.309442	-118.829061	Cattail	0.33	1
2021	West South	43.298313	-118.828606	Bulrush	17.00	51
2021	West South	43.298313	-118.828606	Cattail	3.00	9
2022	Cole North	43.353900	-118.723500	Bulrush	0.00	0
2022	Cole North	43.353900	-118.723500	Cattail	0.00	0
2022	Cole South	43.317000	-118.754400	Bulrush	15.67	47
2022	Cole South	43.317000	-118.754400	Cattail	0.33	1
2022	North Central 1	43.348200	-118.787800	Bulrush	1.67	5
2022	North Central 1	43.348200	-118.787800	Cattail	0.00	0
2022	North Central 2	43.348400	-118.781800	Bulrush	2.33	7
2022	North Central 2	43.348400	-118.781800	Cattail	0.33	1
2022	Northeast	43.364300	-118.737500	Bulrush	0.00	0
2022	Northeast	43.364300	-118.737500	Cattail	1.00	3
2022	Northwest Edge	43.332000	-118.814600	Bulrush	2.00	6
2022	Northwest Edge	43.332000	-118.814600	Cattail	0.67	2
2022	Southwest Central	43.304100	-118.811500	Bulrush	5.00	15
2022	Southwest Central	43.304100	-118.811500	Cattail	0.33	1
2022	Southwest Edge	43.291900	-118.820800	Bulrush	3.67	11
2022	Southwest Edge	43.291900	-118.820800	Cattail	1.00	3
2022	Tern Island North	43.293800	-118.814700	Bulrush	11.00	33
2022	Tern Island North	43.293800	-118.814700	Cattail	3.00	9
2022	Tern Island South	43.291400	-118.816400	Bulrush	19.00	57
2022	Tern Island South	43.291400	-118.816400	Cattail	0.67	2

A.7. Greenhouse Counts for all species in 2022.

Tray	Location	<i>Schoeneplectus acutus</i>	<i>Typha latifolia</i>	<i>Chenopodium murale</i>	<i>Lindernia dubia</i>	<i>Poa spp.</i>	<i>Rumex fueginus</i>	<i>Rumex acetosella</i>	<i>Hordeum jubatum</i>	<i>Ranunculus spp.</i>	<i>Brassicaceae Rorippa spp</i>	<i>Crypsis schoenoides</i>	<i>Eragrostis hypnoides</i>
		Hardstem Bulrush	Broadleaf Cattail	Nettleleaf Goosefoot	False Pimpernel	Bluegrass	Golden Dock	Red Sorrel	Foxtail Barley	Buttercup	Yellowcress	Swamp Timothy	Teal Lovegrass
1	Tern South	30	0	0	2	4	0	3	0	0	0	1	0
2	Tern South	12	2	6	0	3	0	3	0	0	0	1	0
3	Tern South	15	0	2	0	0	0	1	0	0	0	0	0
4	Tern North	5	3	14	0	1	0	15	0	0	0	0	0
5	Tern North	13	4	34	1	0	0	24	1	0	0	0	0
6	Tern North	15	2	4	0	0	0	17	2	0	0	0	1
7	Southwest Edge	8	0	14	2	3	1	0	0	0	0	0	1
8	Southwest Edge	3	3	8	4	5	0	4	0	0	0	0	0
9	Southwest Edge	0	0	0	0	0	0	0	0	0	0	0	0
10	Southwest Central	2	1	30	0	1	1	5	0	0	0	0	0
11	Southwest Central	10	0	4	0	2	5	3	0	0	0	0	0
12	Southwest Central	3	0	13	0	0	5	3	0	0	0	0	0
13	Northwest Edge	5	1	16	0	0	0	4	0	0	0	0	0
14	Northwest Edge	0	1	6	0	0	0	0	0	0	0	0	0
15	Northwest Edge	1	0	5	0	0	0	1	0	0	0	0	0
16	North Central 1	3	0	39	0	0	0	2	0	0	0	0	0
17	North Central 1	1	0	52	0	0	1	5	0	0	0	0	0
18	North Central 1	1	0	23	0	0	0	0	0	0	0	0	0
19	North Central 2	2	0	20	0	0	0	6	0	0	0	0	0
20	North Central 2	5	1	15	0	0	0	2	0	0	1	0	0
21	North Central 2	0	0	36	0	0	0	4	0	1	0	0	0
22	Northeast	0	0	49	0	1	1	4	0	0	0	0	0
23	Northeast	0	1	12	0	0	0	7	0	0	0	0	0
24	Northeast	0	2	40	0	1	0	5	0	0	0	0	0
25	Cole North	0	0	3	0	0	1	12	0	0	0	0	0
26	Cole North	0	0	5	0	0	0	9	0	0	0	0	0
27	Cole North	0	0	2	0	0	0	11	0	0	0	0	0
28	Cole South	16	0	3	0	0	0	5	0	0	0	0	0
29	Cole South	6	1	0	0	0	0	1	0	0	0	0	0
30	Cole South	25	0	1	0	0	0	0	0	0	0	0	0

A.8. Average Shannon-Weiner Diversity Index, Simpson Diversity Index, and average richness by sampling location in 2022.

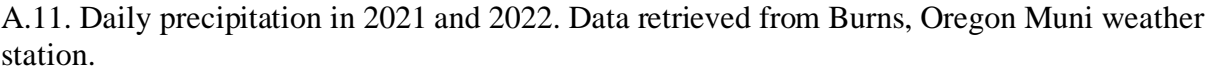
Location	Region	Shannon	Simpson	Richness
Tern North	West	1.311	0.697	5.67
Southwest Central	West	1.179	0.617	5.00
Southwest	West	1.028	0.513	4.00
Tern South	West	0.979	0.497	4.00
North Central 2	North	0.761	0.42	3.67
Northwest	North	0.745	0.463	3.00
Northeast2	East	0.621	0.347	3.00
Cole North	East	0.595	0.4	2.33
Cole South	East	0.585	0.353	2.67
North Central 1	North	0.354	0.17	3.00

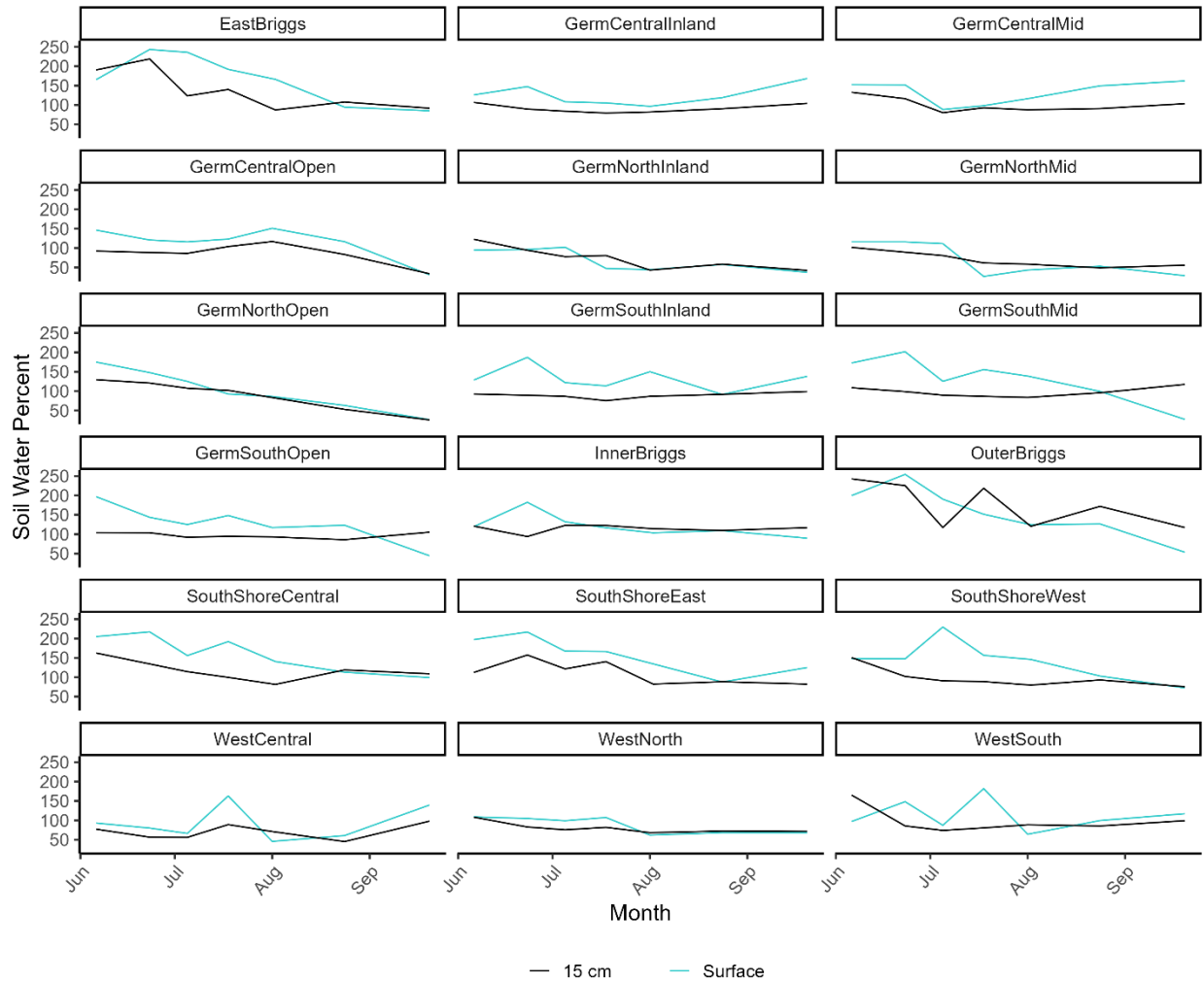


A.9. Daily average wind speeds and maximum daily wind speeds in 2021 and 2022. Data retrieved from Burns, Oregon Muni weather station.

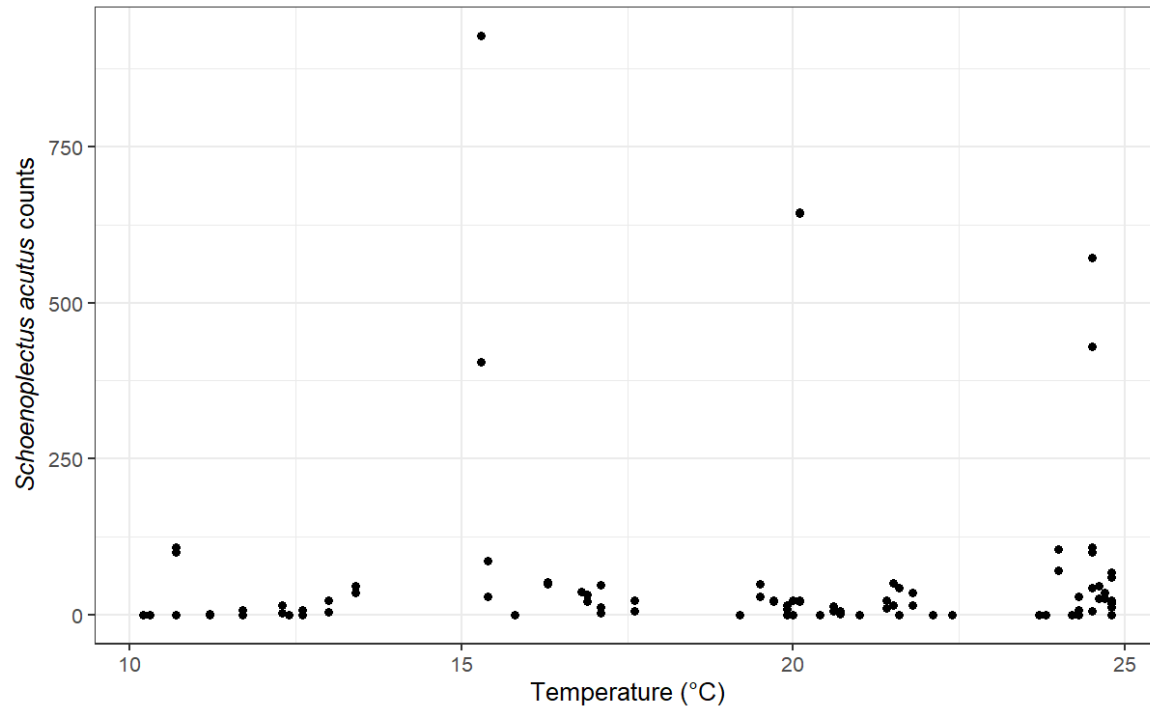
A.10. Germination Enclosure species detected by year and wetland status. Status (-) indicate either no status available for species or identification was not specific enough to identify wetland status.

2021			2022		
Common Name	Latin Name	Wetland Status	Common Name	Latin Name	Wetland Status
Alkali Bulrush	<i>Bolboschoenus maritimus</i>	OBL	Alkali Aster	<i>Symphyotrichum frondosum</i>	FACW
Broadleaf Cattail	<i>Typha latifolia</i>	OBL	Bluegrass	<i>Poa spp.</i>	-
False Pimpernel	<i>Lindernia dubia</i>	OBL	Broadleaf Cattail	<i>Typha latifolia</i>	OBL
Foxtail Barley	<i>Hordeum jubatum</i>	FAC	Buttercup	<i>Ranunculus spp.</i>	-
Hardstem Bulrush	<i>Schoenoplectus acutus</i>	OBL	Canada Thistle	<i>Cirsium arvense</i>	FACU
Nettleleaf Goosefoot	<i>Chenopodium murale</i>	FACU	Common Dandelion	<i>Taraxacum officinale</i>	FACU
Red Sorrel	<i>Rumex acetosella</i>	FACU	Curly Dock	<i>Rumex crispus</i>	FAC
			Dock	<i>Rumex spp.</i>	-
			Foxtail Barley	<i>Hordeum jubatum</i>	FAC
			Hardstem Bulrush	<i>Schoenoplectus acutus</i>	OBL
			Nettleleaf Goosefoot	<i>Chenopodium murale</i>	FACU
			Prickly Lettuce	<i>Lactuca serriola</i>	FACU
			Red Sorrel	<i>Rumex acetosella</i>	FACU
			Swamp Timothy	<i>Crypsis schoenoides</i>	FACW
			Wild Mustard	<i>Sinapis arvensis</i>	-

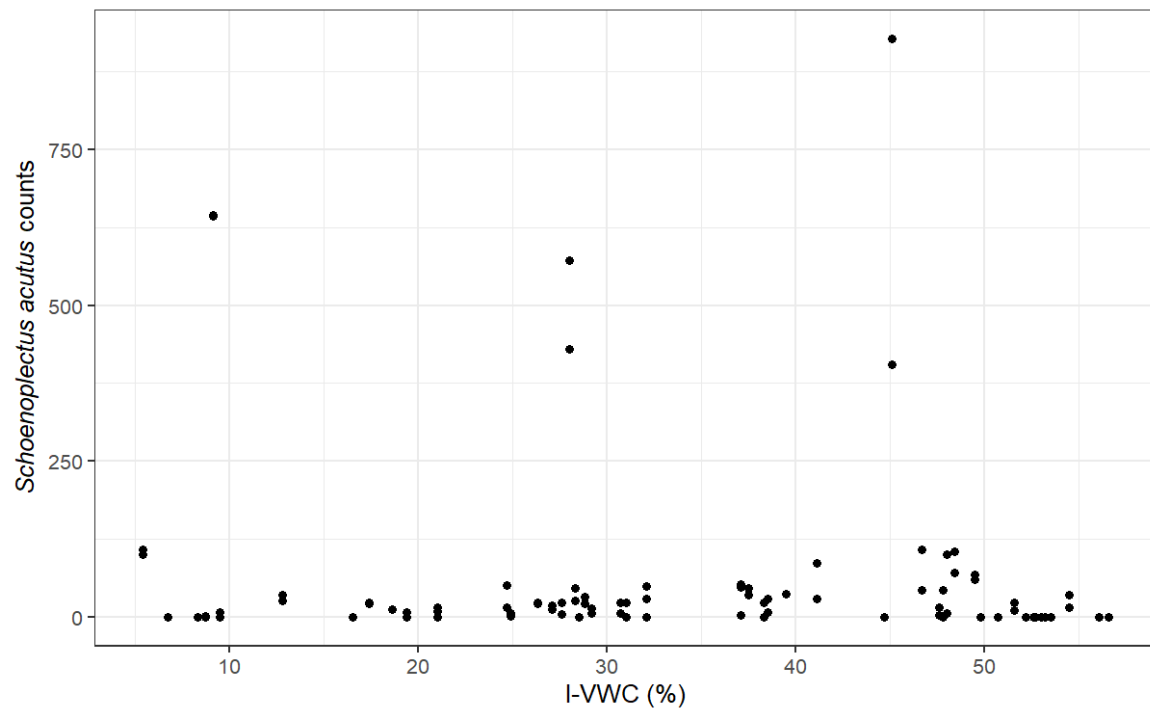




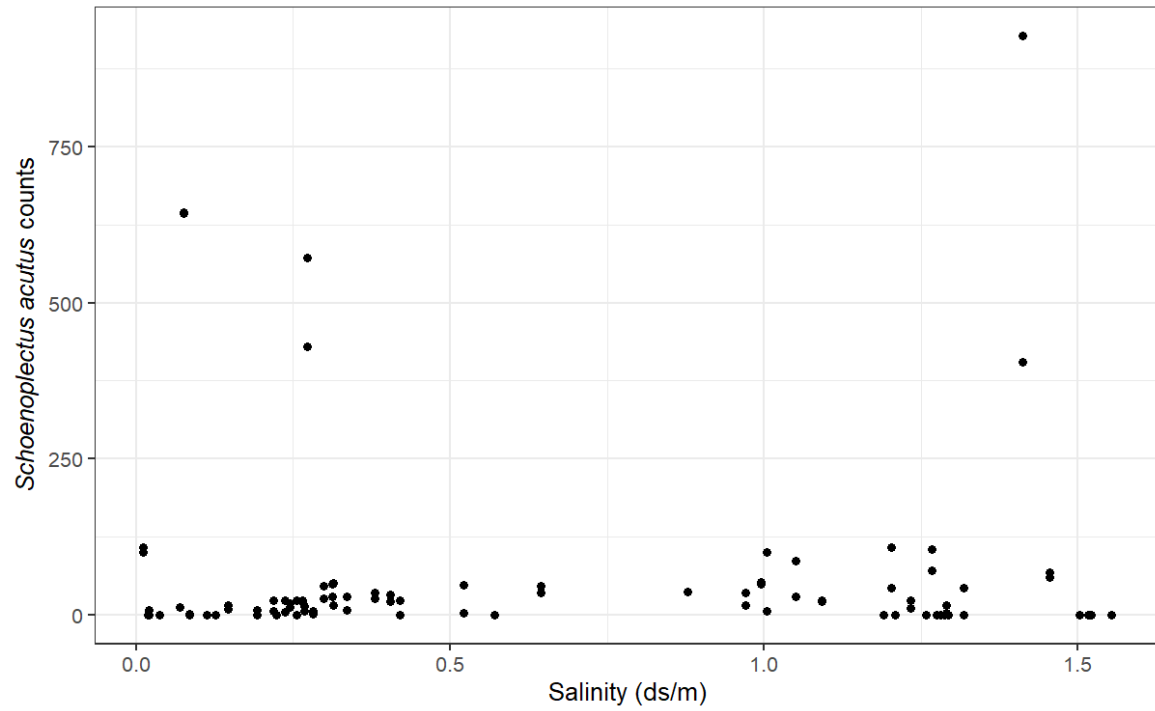
A.12. Ratio of soil water content (gravimetric water content) in 2022 at all sites sampled for objectives 2 and 3.



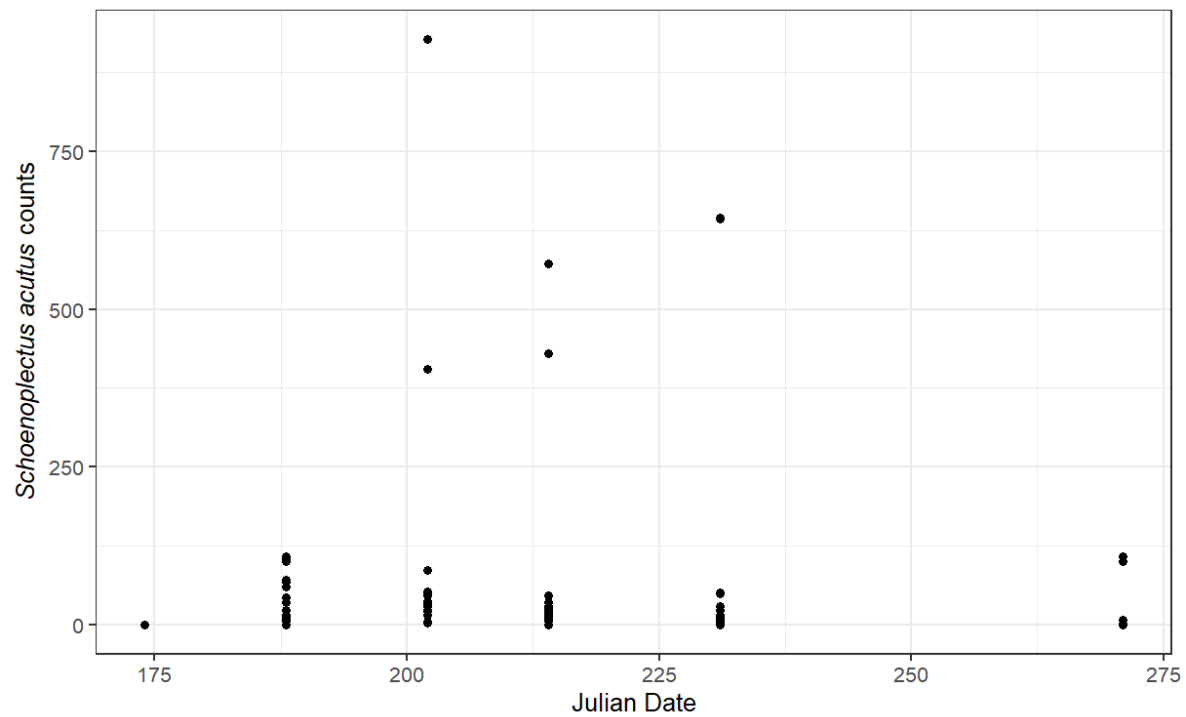
A.13. Scatterplot of temperature and hardstem bulrush counts in 2021 at G-exclosures.



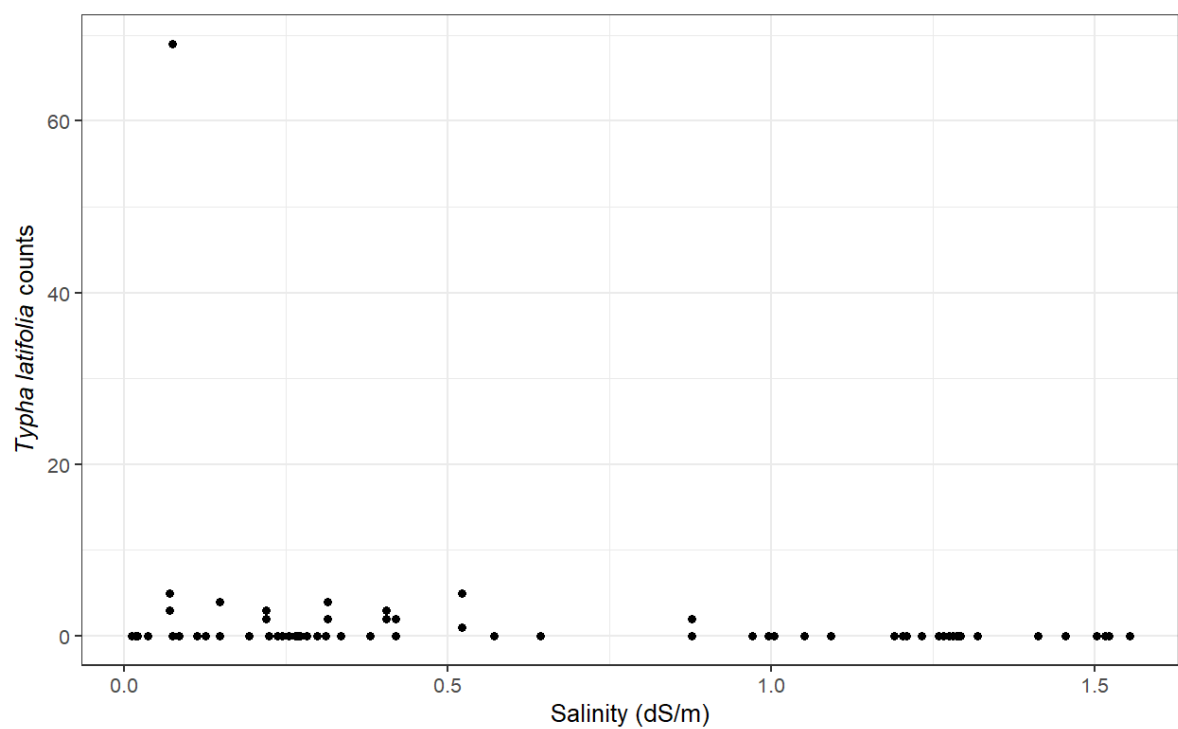
A.14. Scatterplot of I-VWC and hardstem bulrush counts in 2021 at G-exclosures.



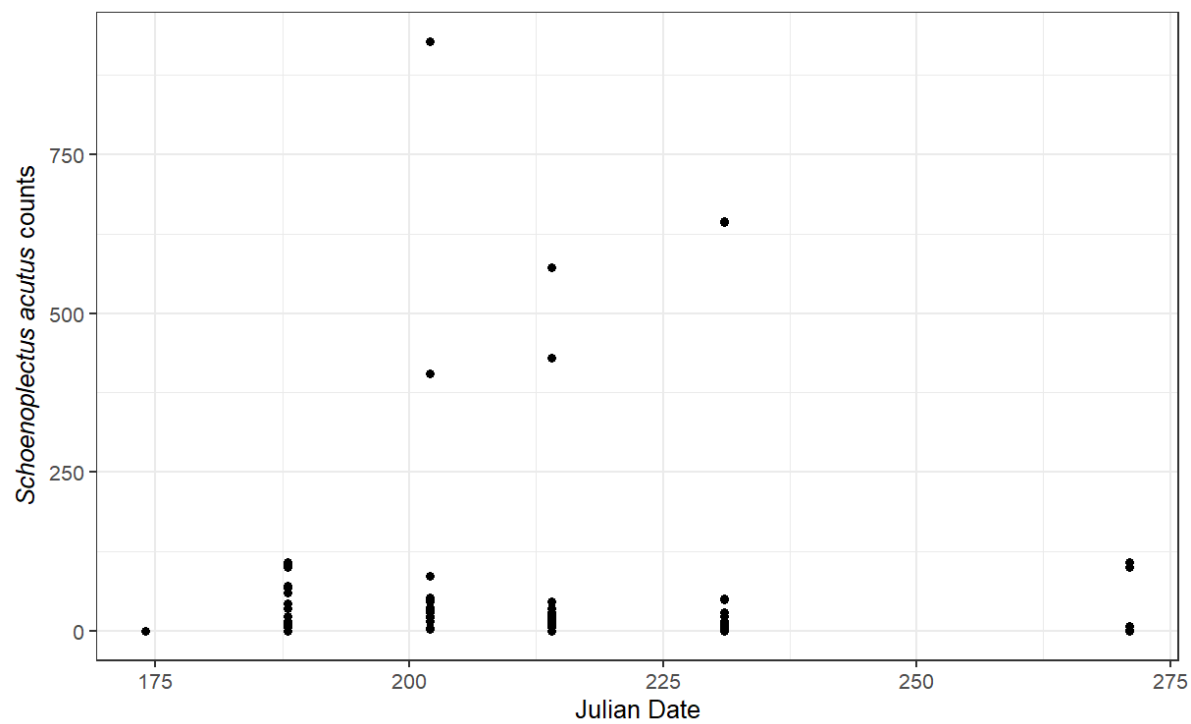
A.15. Scatterplot of salinity and hardstem bulrush counts in 2021 at G-exlosures.



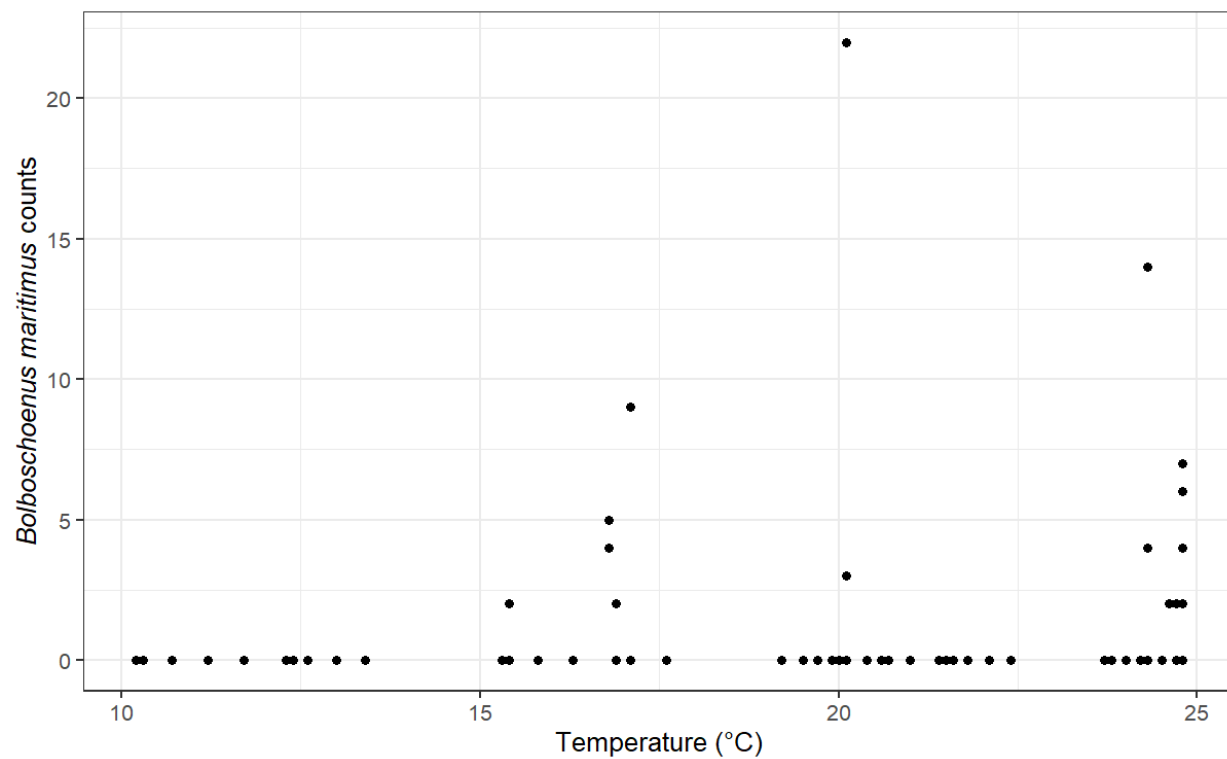
A.16. Scatterplot of Julian date and hardstem bulrush counts in 2021 at G-exlosures.

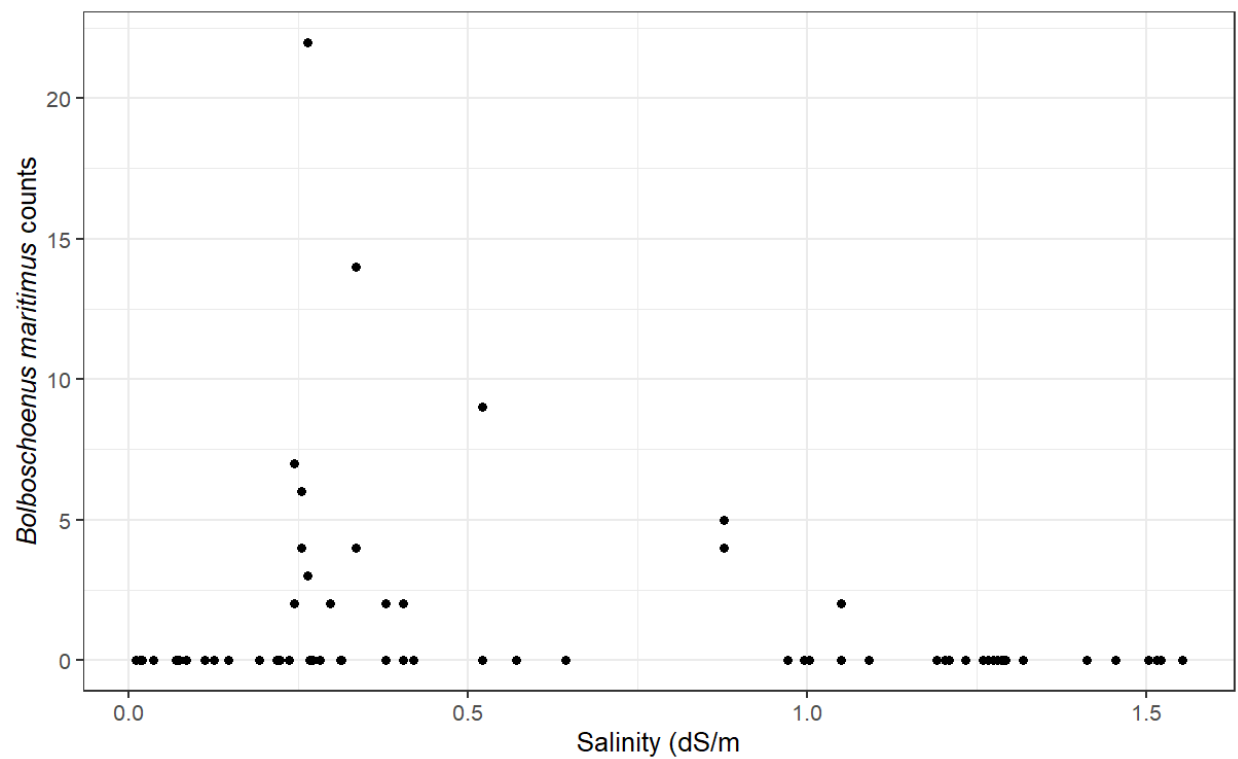


A.19. Scatterplot of salinity and broadleaf cattail counts in 2021 at G-exclosures.

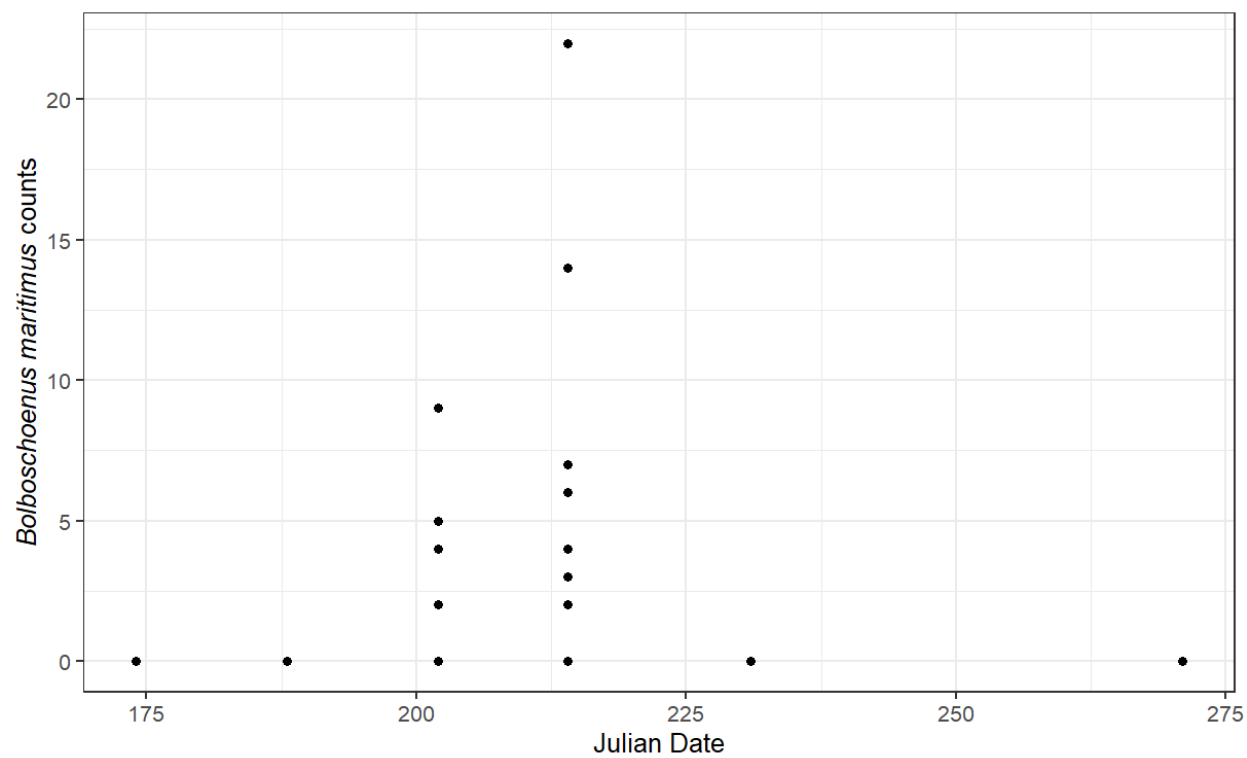


A.20. Scatterplot of Julian date and broadleaf cattail counts in 2021 at G-exclosures.

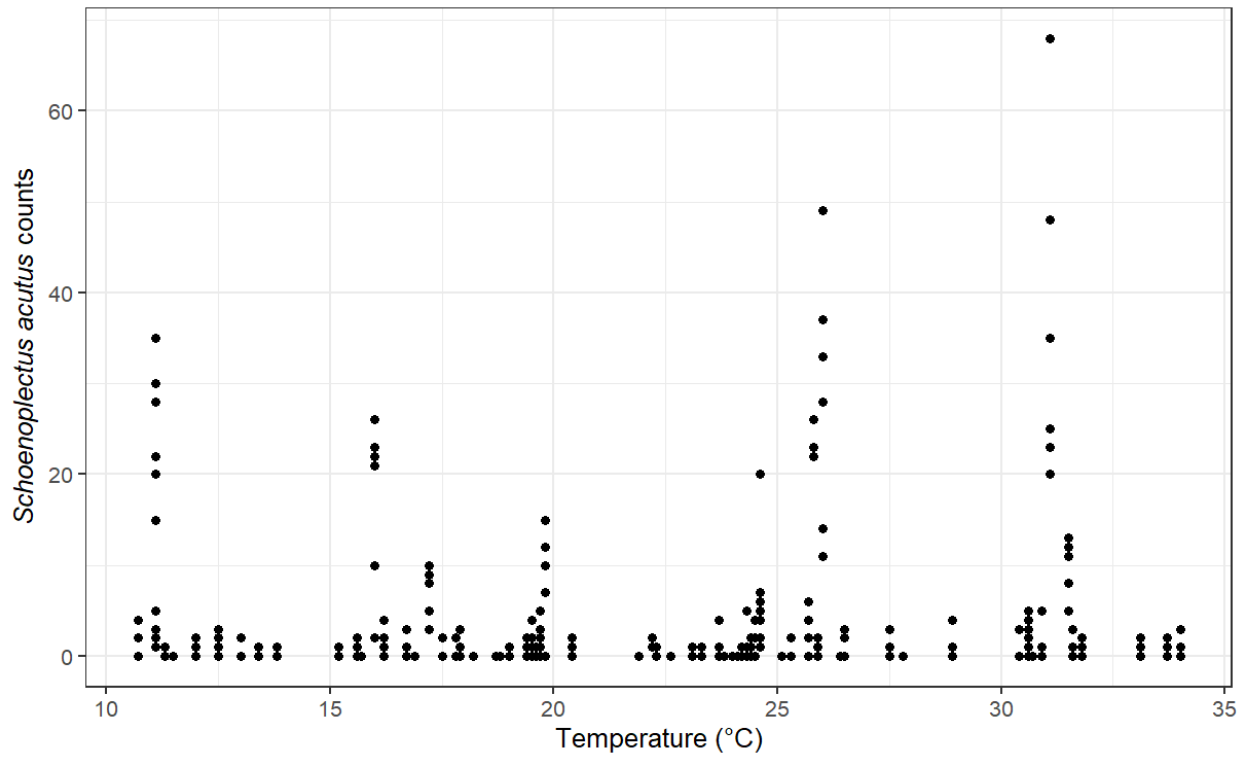




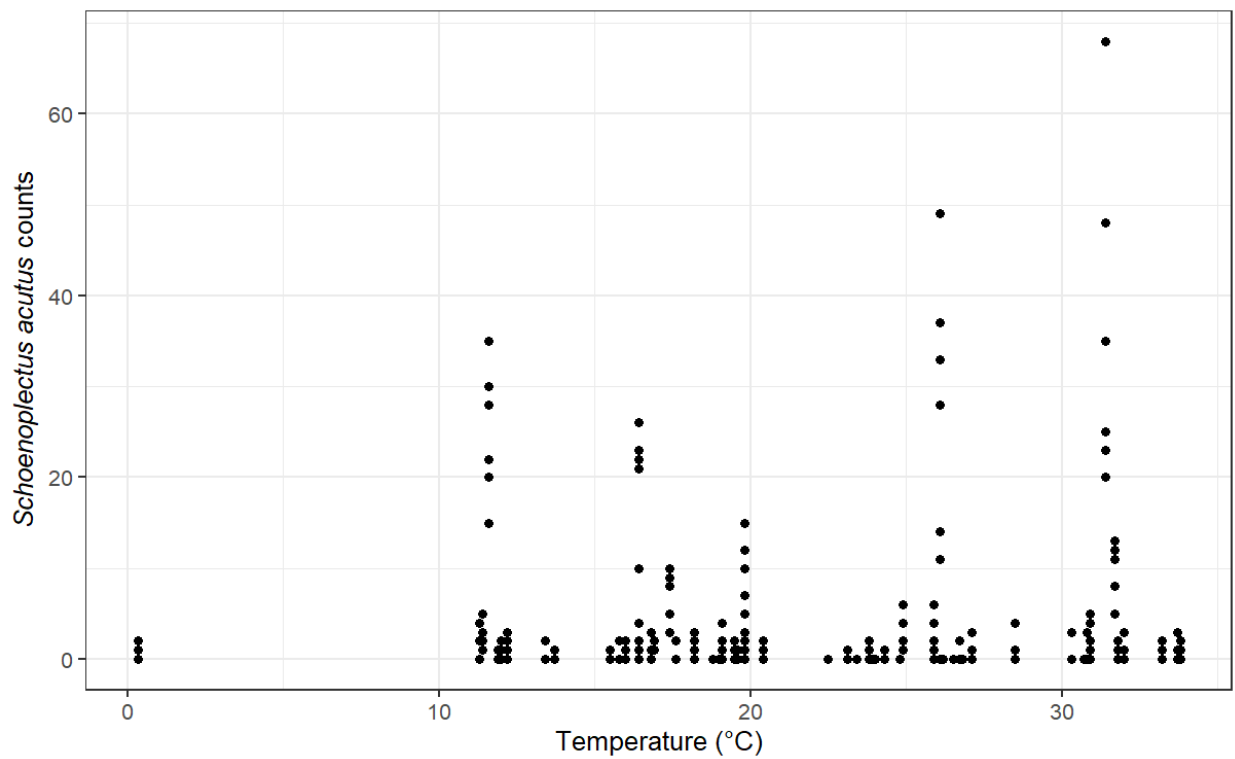
A.23. Scatterplot of salinity and alkali bulrush counts in 2021 at G-exclosures.



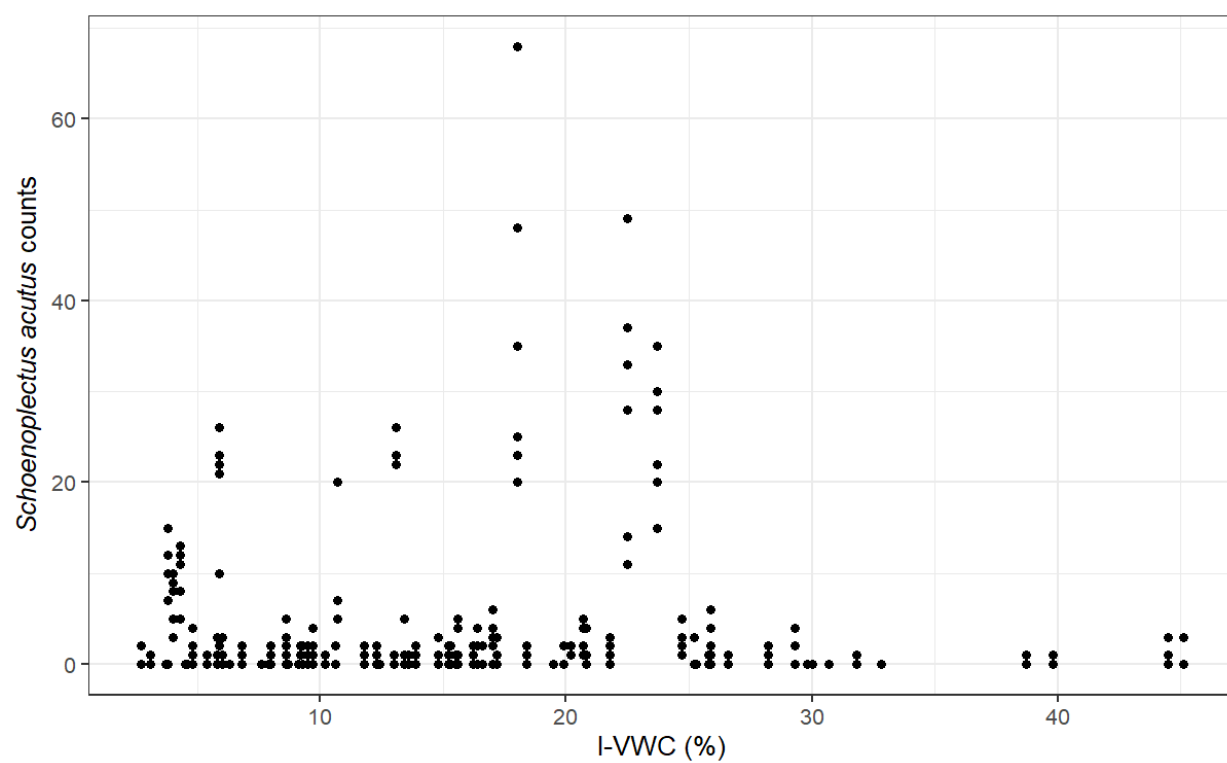
A.24. Scatterplot of Julian date and alkali bulrush counts in 2021 at G-exclosures.



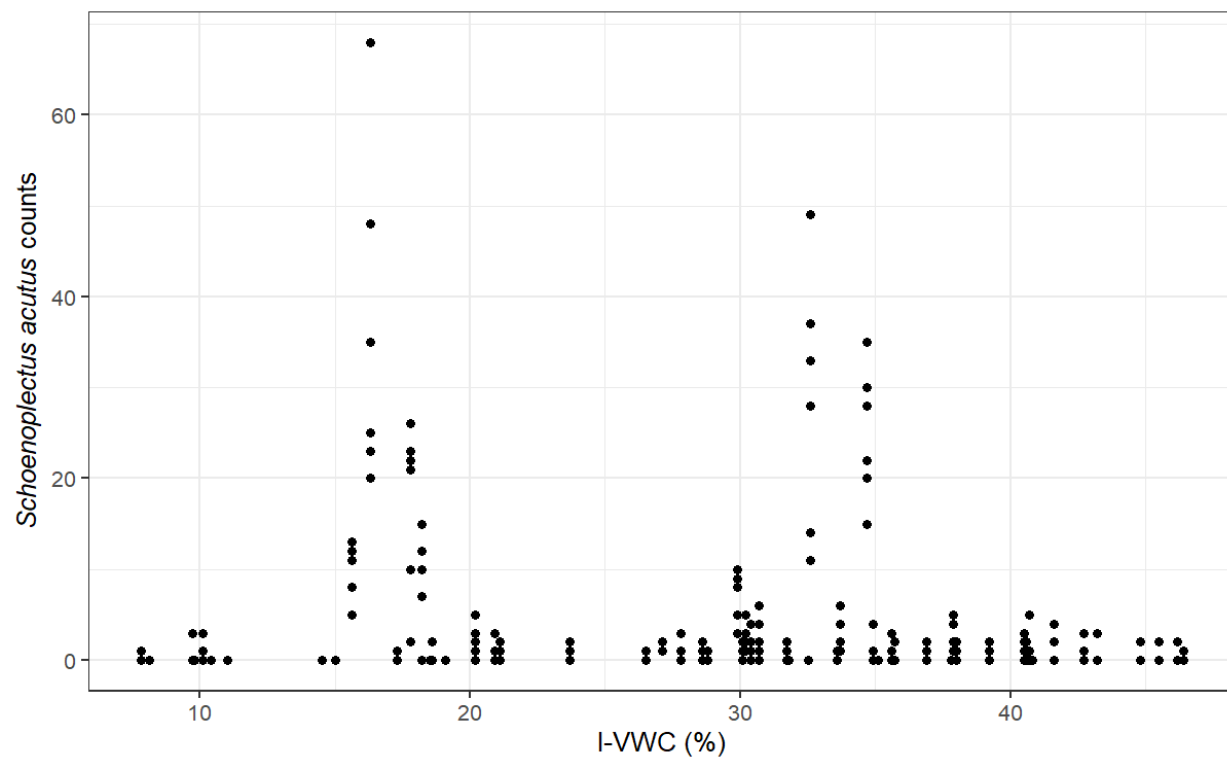
A.25. Scatterplot of temperature at the surface and hardstem bulrush counts in 2022 at G-exlosures.



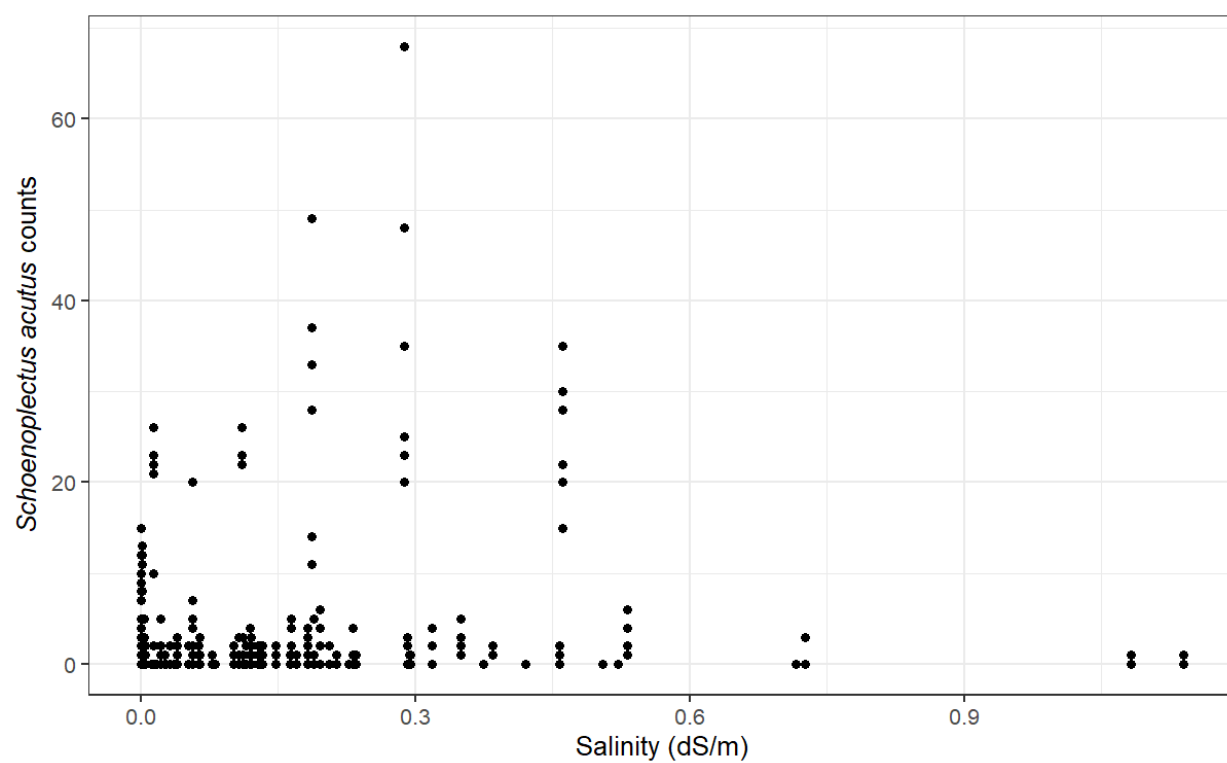
A.26. Scatterplot of temperature at 10-15 cm and hardstem bulrush counts in 2022 at G-exlosures.



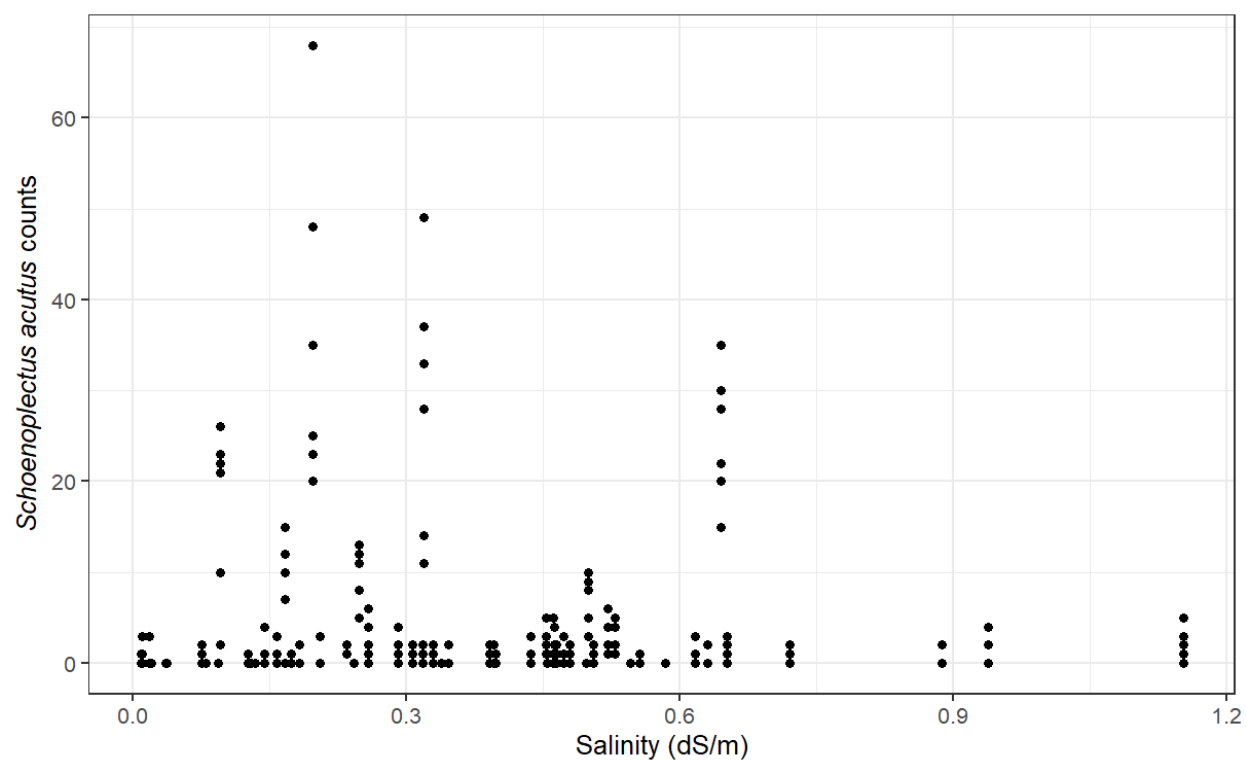
A.27. Scatterplot of I-VWC at the surface and hardstem bulrush counts in 2022 at G-exlosures.



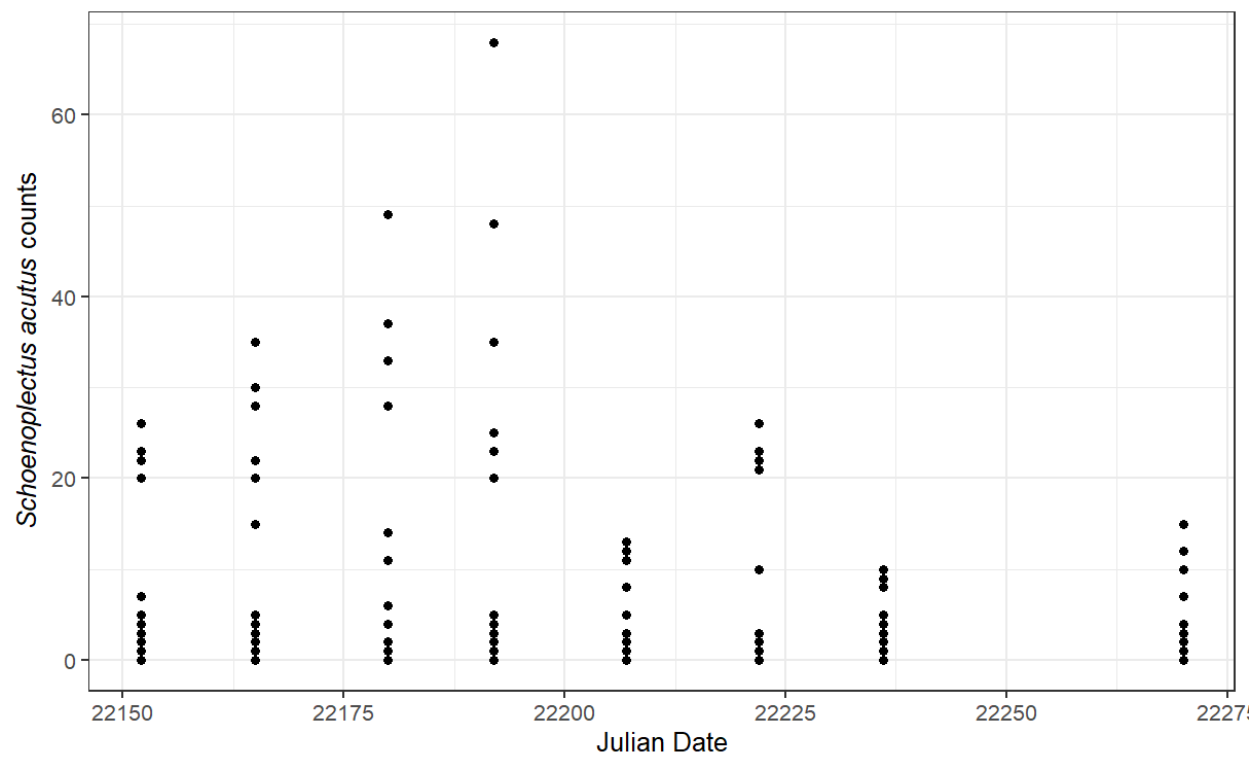
A.28. Scatterplot of I-VWC at 10-15 cm and hardstem bulrush counts in 2022 at G-exlosures.



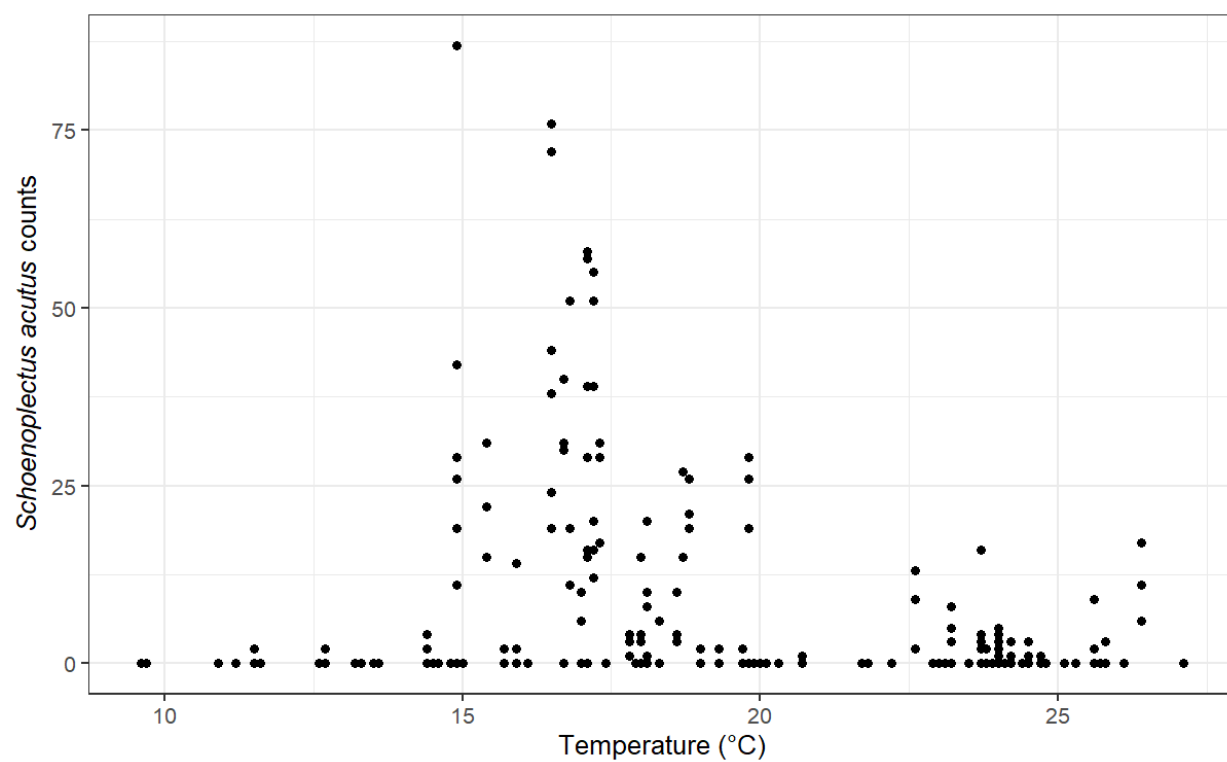
A.29. Scatterplot of salinity at the surface and hardstem bulrush counts in 2022 at G-exclosures.



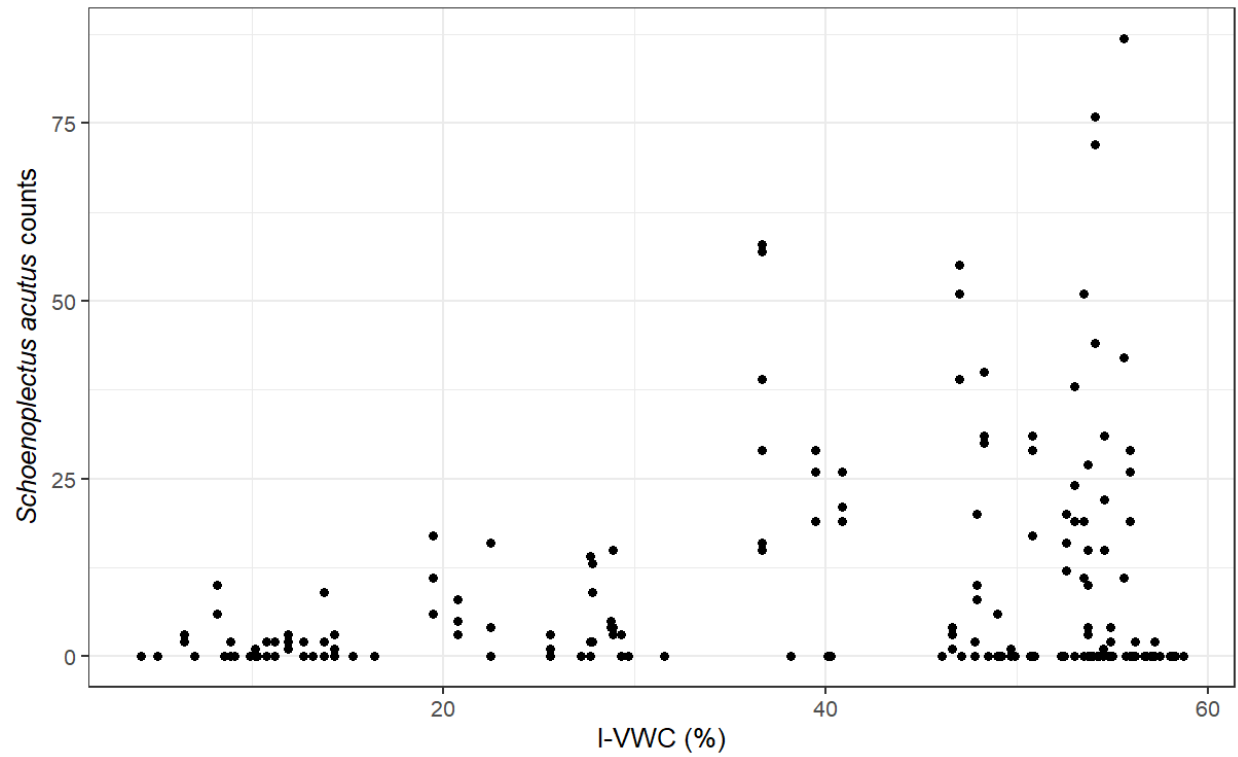
A.30. Scatterplot of salinity at 10-15 cm and hardstem bulrush counts in 2022 at G-exclosures.



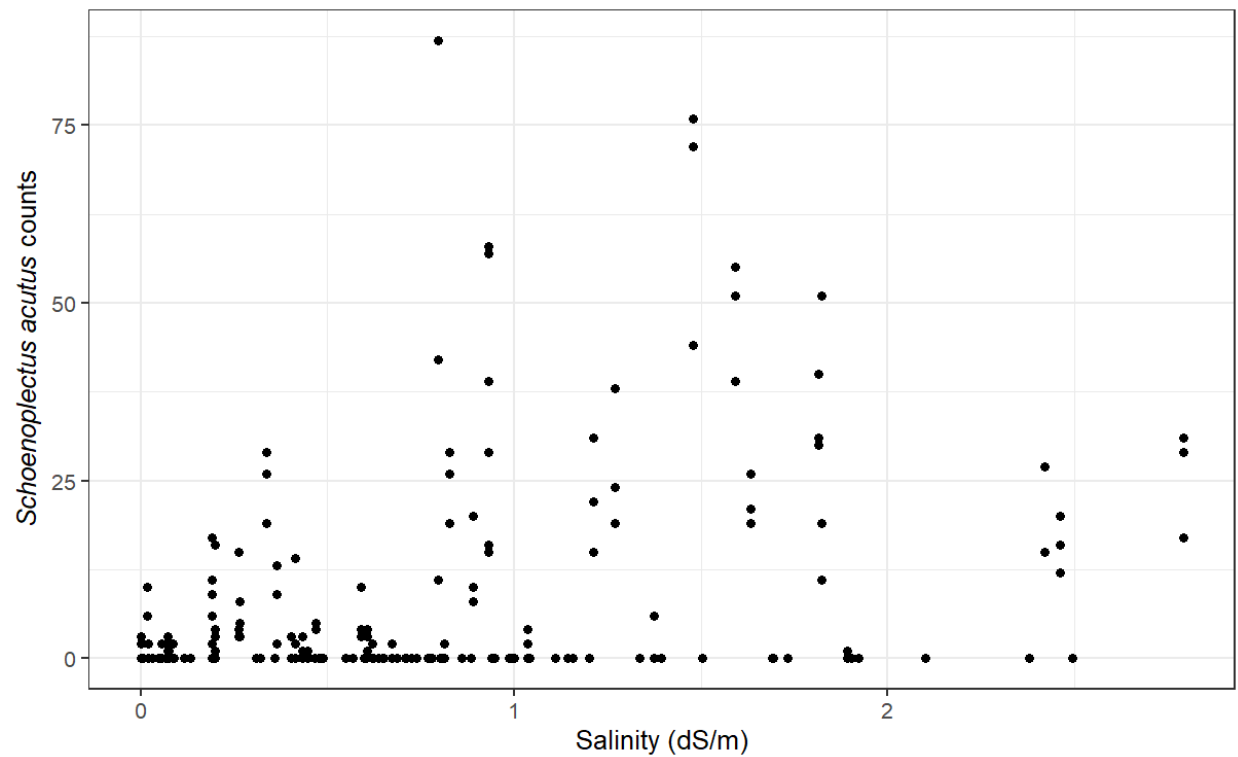
A.31. Scatterplot of Julian date and hardstem bulrush counts in 2022 at G-exclosures.



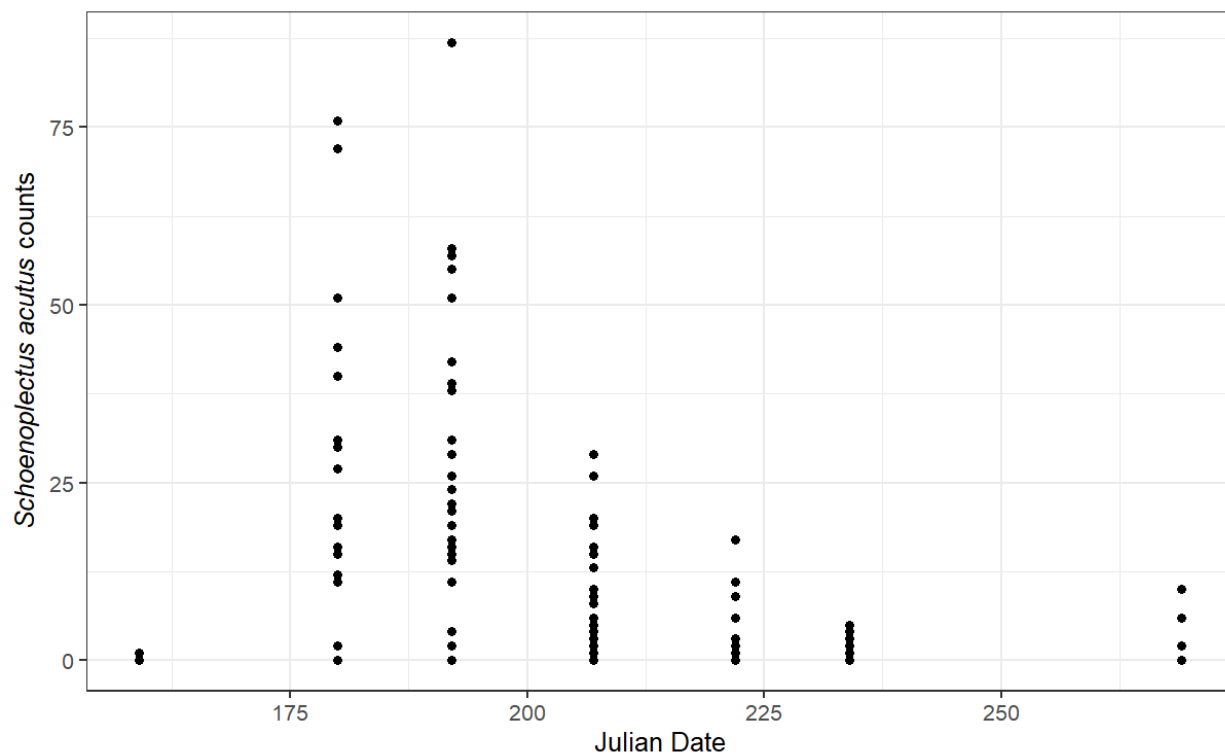
A.32. Scatterplot of temperature and hardstem bulrush counts in 2022 at germination transect.



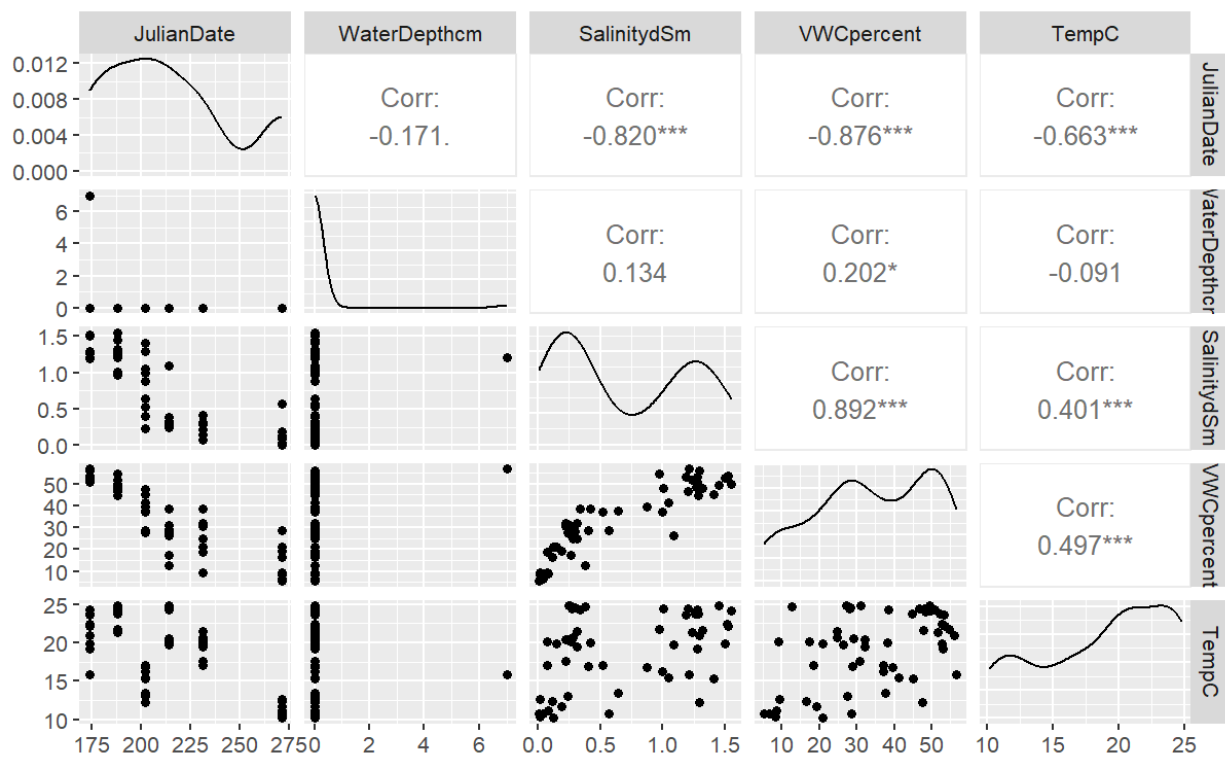
A.33. Scatterplot of I-VWC (%) and hardstem bulrush counts in 2022 at germination transect.



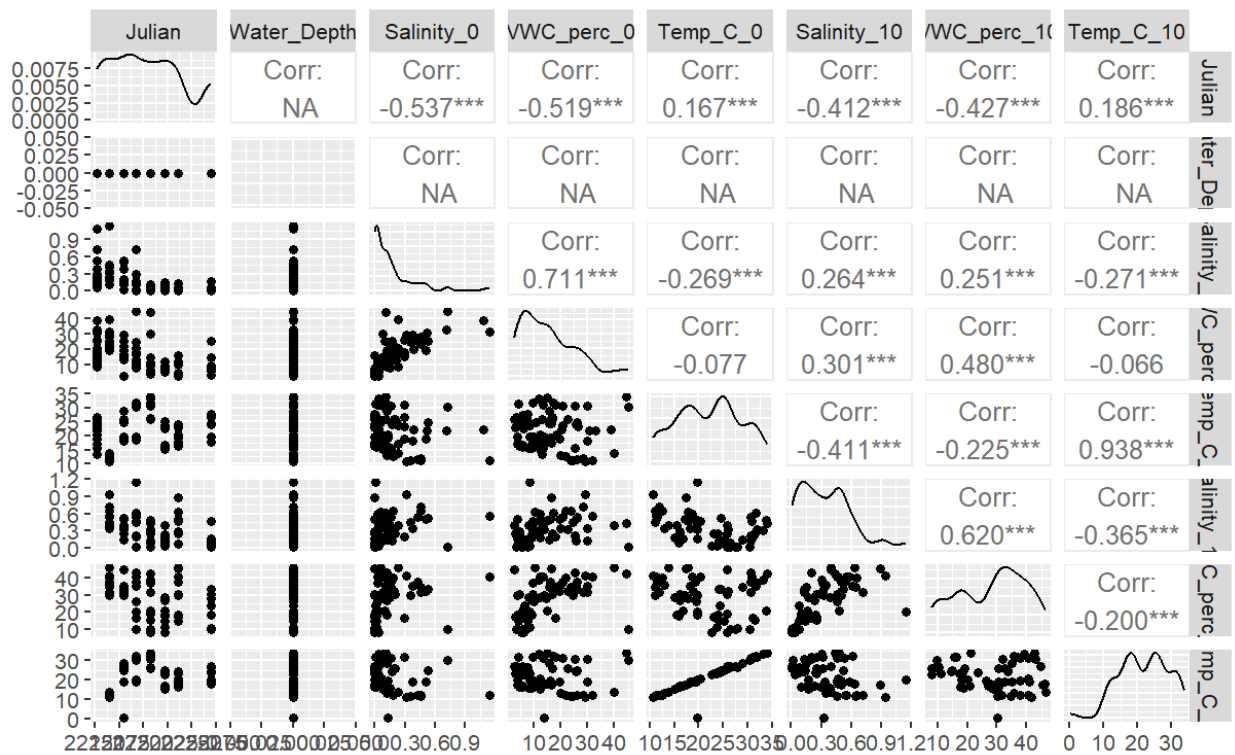
A.34. Scatterplot of salinity and hardstem bulrush counts in 2022 at germination transect.



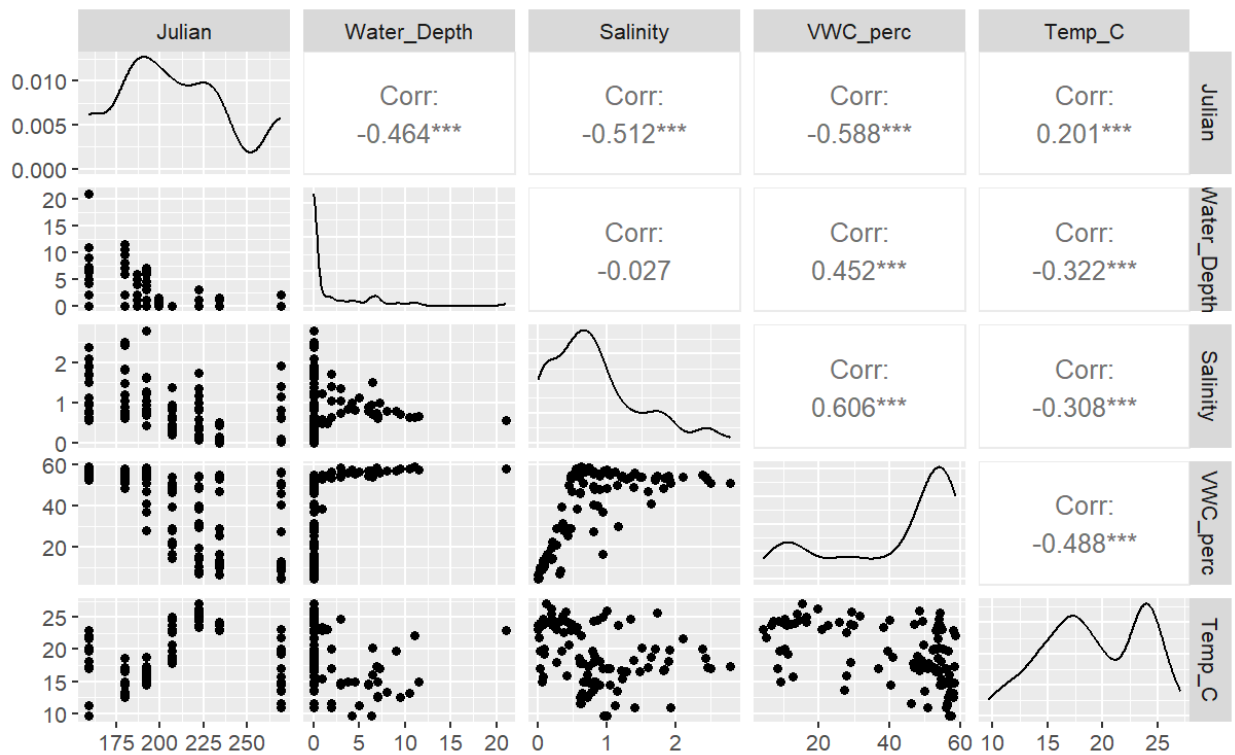
A.35. Scatterplot of Julian date and hardstem bulrush counts in 2022 at germination transect.



A.36. Correlation plot for 2021 G-exclosure independent variables.



A.37. Correlation plot for 2022 G-exclosure independent variables.



A.37. Correlation plot for 2022 germination transect independent variables.

APPENDIX B. SUPPLEMENTARY IMAGES



B.1. Cole Island Dike organic layer and bulrush.



B.2. Soil cracking following hardstem bulrush germination.



B.3. Fine silt layer overlaying fine organic detrital sediments.



B.4. Entrenchment of Blitzen River near Frenchglen, OR.



B.5. Entrenchment of the Blitzen River at Malheur NWR refuge headquarters.



B.6. Entrenchment of Blitzen River near Page Springs, OR.

APPENDIX C. TRANSPLANTS

In addition to testing exclosures as restoration techniques, the refuge pilot experiment included hardstem bulrush transplants. Transplantation was supplementary tested during my study to assess if this technique would be viable for restoration practices. There were three controls and three hog wire panel sites constructed in the north end of Unit 4. Transplants 0.5 m x 0.5 m were transported from Briggs Bay (Unit 5) by airboat and dug into new sites at water depths of 1-2 cm in June 2021. These were monitored throughout the study, and only 3 new shoots were detected during that timeframe. Most of the transplants died within the first year, and no growth was observed in either season. The sample size is minimal, but based on my observations, transplantation is not a viable technique for large scale restoration projects. The survival of transplants is likely related to timing of transplantation, soil type and structure, and water availability.



C.1 Transplantation process including transportation, placement, and survival.

APPENDIX D. SATELLITE IMAGERY



D.1. Most recent connection of Malheur to Harney Lake in June 2012 (53,000 ha). Landsat-8 image courtesy of the U.S. Geological Survey.



D.2. Drawdown in October 2014 (9500 ha). Landsat-8 image courtesy of the U.S. Geological Survey.



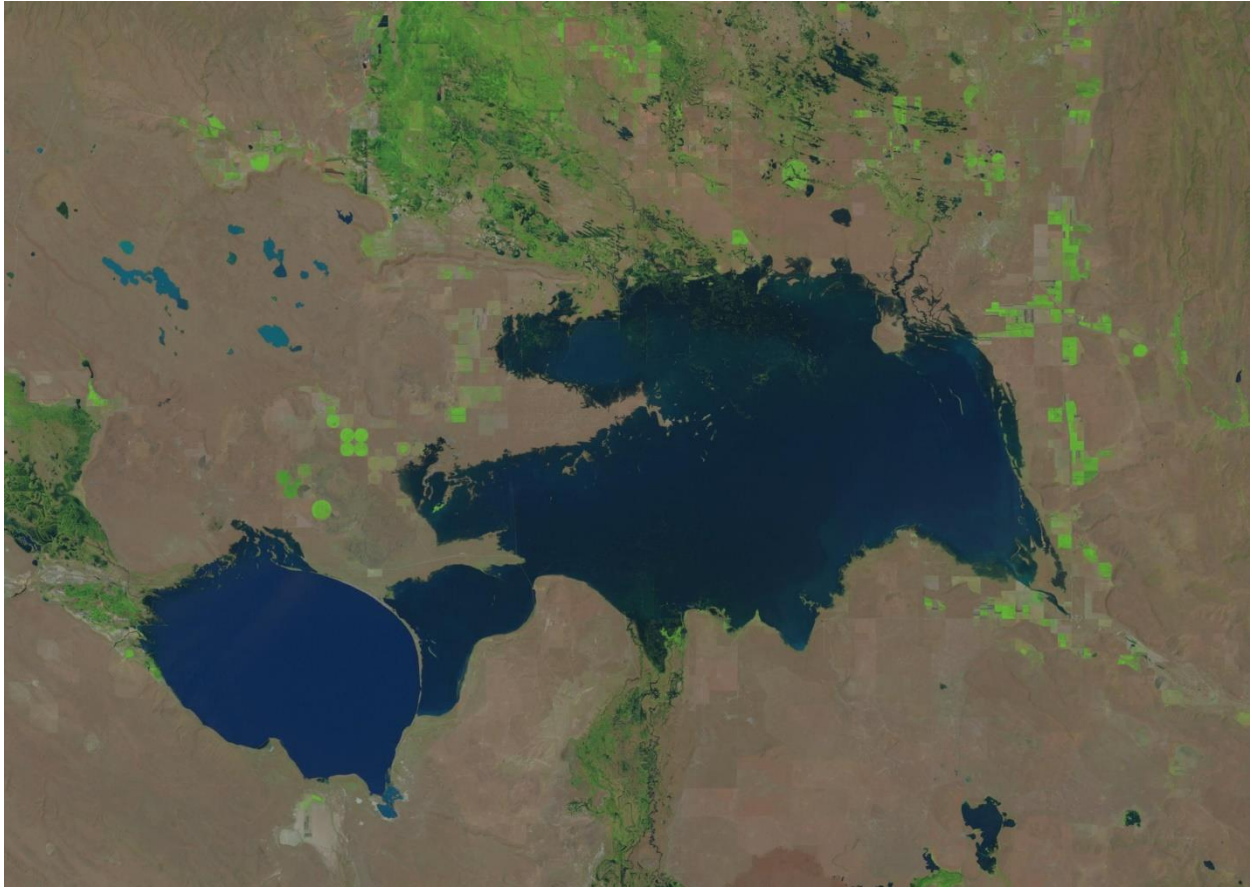
D.3. June 2015 drawdown conditions (11000 ha). Landsat-8 image courtesy of the U.S. Geological Survey.



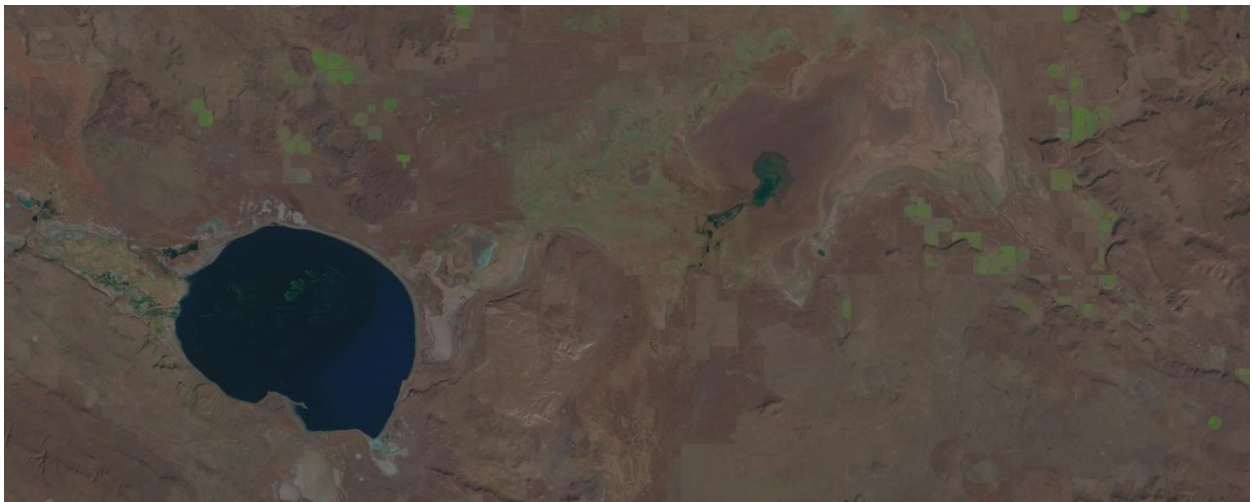
D.4. July 2015 drawdown conditions (5000 ha). Landsat-8 image courtesy of the U.S. Geological Survey.



D.5. August 2015 drawdown conditions (1300 ha). Landsat-8 image courtesy of the U.S. Geological Survey.



D.6. Peak flood conditions in June 1984 (90,000 ha). Landsat-5 image courtesy of the U.S. Geological Survey.



D.7. October 1992 significant drawdown in Malheur Lake (630 ha). Landsat-5 image courtesy of the U.S. Geological Survey.

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VITA

Beth Boos was born in Dayton, Ohio. She received her B.S. in Fisheries and Water Resources from the University of Wisconsin Stevens Point. As an undergraduate, she was active with the American Water Resource Association and Environmental Educators and Naturalists Association. Throughout her career, she has worked in various sectors of the natural resource field including recreation, conservation, and education positions. She has worked with several wildlife nonprofits as an educator, and she has collaborated with several nonprofits and organizations throughout her research. After graduating from UWSP, Beth served with Squam Lakes Association in New Hampshire completing various conservation and education programs throughout her tenure. In January 2021, she began working towards her master's degree in Renewable Natural Resources at Louisiana State University where she plans to graduate in August 2023. Her graduate research focused on restoration ecology and plant succession processes in a shallow lake wetland system of Eastern Oregon. After graduation, Beth plans to continue working in science communication and aquatic ecology.