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The Abundance, Production, and Depletion of Food Resources for Wintering Waterfowl in the Suisun Marsh, California

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The Abundance, Production, and Depletion of Food Resources for Wintering Waterfowl in the Suisun Marsh, California

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ABSTRACT

Wetland conservation in California faces a multitude of challenges, this is especially true in the Suisun Marsh, one of the largest tidal marshes on the west coast of North America. The marsh has historically supported large numbers of non-breeding waterfowl but the capacity of the marsh to continue to do so remains uncertain, due to drought, habitat loss, future sea level rise, and conflicting conservation needs for many species of fish and wildlife.

A guiding principle for the conservation of non-breeding waterfowl is to manage for food resources, under the working hypothesis that food resources may be limiting in winter, and the decline in the abundance of waterfowl within Suisun Marsh may be due to reduced food production or availability. Non-breeding waterfowl depend on plant seeds as a primary source of food throughout winter. However, we lack information concerning what food resources may be in limited supply because there has never been a direct assessment of total seed abundance in Suisun Marsh. Efforts to recover threatened and endangered species within the marsh – through the conversion of managed wetlands to tidal marsh – could further impact the carrying capacity of the marsh for waterfowl by reducing the abundance or availability of waterfowl food resources.

To evaluate these concerns, I undertook a multifaceted study to evaluate the abundance, production, and depletion of food resources for wintering waterfowl in both tidal and managed wetlands. I found that seed abundance in both wetland types was much lower than previously predicted. Seed abundance in Fall was similar in tidal (172.9 kg/ha) and managed (163.8 kg/ha) wetlands, but there was considerable spatial variation. The species composition of seeds differed substantially according to wetland type; over 75% of aggregate seed mass in managed wetlands was comprised of food species that waterfowl prefer, while a non-preferred food, *Schoenoplecutus* sp., was the dominant seed in tidal marshes. The occurrence of several plant species within managed wetlands that produce waterfowl-preferred seeds was correlated with salinity, wetland management intensity, and disking. The best predictor of total seed abundance in managed wetlands was habitat zone, which is defined by shared physical factors known to impact vegetation growth and production in different regions in the marsh. These regional differences in seed abundance have important implications for tidal restoration efforts, as the loss of seasonal wetland acreage within more productive regions could have a disproportionate impact on total food availability.

To evaluate seed dynamics at a finer scale, I used small-scale sampling sites and foraging exclosures in a managed wetland within the marsh and stratified these sampling locations according to high and low waterfowl use areas. Contrary to expectations of a “table-is-set” hypothesis, I found seed that abundance increased over three weeks post-flooding, and over seven to ten weeks in foraging exclosures. Observed declines in the abundance of seeds were substantially greater than rates of decomposition, suggesting seed removal by waterfowl was a major source of seed depletion. However, the amount of seed consumption that could be attributed to waterfowl was spatially variable and correlated with waterfowl locations – high use areas exhibited significantly higher rates of seed loss. Hydrochory (movement of seed due to water flow) was likely responsible for the changes in seed abundance observed for several weeks after the wetlands were flooded, as abundances within foraging exclosures nearly tripled over ten weeks in high waterfowl use areas. These results suggest that seed removal by waterfowl and hydrochory can impact our ability to accurately estimate peak seed abundance. Without accounting for seed removal by waterfowl, and hydrochory, bioenergetic models may produce inaccurate estimates of habitat carrying capacity. My results provide new insight and greater

refinement of estimates of seed abundance to more accurately determine the carrying capacity of the Suisun Marsh for wintering waterfowl, and to assess the potential impacts of future changes.

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CHAPTER 1– Food Abundance for Wintering Waterfowl in Tidal Marsh and Managed Wetlands in the Suisun Marsh, California

ABSTRACT

Waterfowl abundances are declining within Suisun Marsh and one hypothesis is that limited food resources could be contributing to this decline. Non-breeding waterfowl depend on plant seeds as a primary source of food throughout winter. However, there has never been a direct assessment of total seed abundance in Suisun Marsh. Efforts to recover threatened and endangered species within the marsh – through the conversion of managed wetlands to tidal marsh – could potentially exacerbate the decline of waterfowl by inadvertently reducing the abundance or availability of waterfowl food resources. To evaluate these concerns, we estimated the abundance of food seeds available to waterfowl using both a site-specific and a marsh-wide assessment. We collected soil core samples in three paired tidal and managed sites (site-specific) in addition to an extensive marsh-wide assessment during late fall and early winter. In both assessments, we found seed abundance in both wetland types was much lower than previously predicted. Fall seed abundance was similar in tidal (172.9 kg/ha) and managed (163.8 kg/ha) wetlands, but spatial variation was considerable. We detected declines in seed abundance between fall and winter sampling (the start and end of the waterfowl wintering period) in our site-specific assessment of managed wetlands (-1.31 ± 0.50, $p < 0.001$), but not at the marsh-wide level, suggesting depletion of food resources is spatially variable. The species composition of seeds differed substantially according to wetland type; over 75% of aggregate seed mass in managed wetlands was comprised of food species that waterfowl favor, while a non-preferred food, *Schoenoplecutus* sp., was the dominant seed in tidal marshes. Our results suggest that tidal marshes do not currently provide food to wintering waterfowl, and low seed abundance in managed wetlands is likely limiting waterfowl abundance.

INTRODUCTION

California has lost nearly 90% percent of its original wetlands to agricultural development and flood control features, resulting in loss of ecological function and the decline of waterfowl and native fish species throughout the state (Mount 1995, Mitsch and Gosselink 2007, Sommer et al. 2007, Sheaves 2009). The Suisun Marsh, situated between the San Francisco Bay and the Sacramento–San Joaquin River Delta, historically consisted of diverse, tidally influenced, brackish wetland habitats which supported large populations of native wildlife and fishes (Moyle et al. 2014). Following a series of landscape conversions from natural tidal marsh to agricultural diked lands, and then to diked managed wetlands, only 15% of historical tidal marsh remains (Mall 1969, Moyle et al. 2014). Despite these changes, the current managed seasonal wetlands and tidal marshes within Suisun Marsh provide habitat to endangered and threatened native fish, bird, plant, and mammal species (SMP 2013, Moyle et al. 2016, Smith and Kelt 2019).

In 2011, The U.S. Bureau of Reclamation (USBR), Suisun Resource Conservation District (SRCD), California Department of Fish and Wildlife (CDFW), and California Department of Water Resources (CDWR) jointly developed the Suisun Marsh Habitat Management, Preservation, and Restoration Plan (SMP) in recognition of the need to protect and strategically manage Suisun Marsh at a landscape scale. The SMP includes goals to nearly double the current acreage of tidal marsh by converting 2,000-2,800 ha of seasonal wetlands over a thirty-year timeframe to aid in the recovery of native species, such as salt marsh harvest mouse (*Reithrodontomys raviventris*), salmonids, and delta smelt (*Hypomesus transpacificus*) (SMP 2013). Tidal wetlands are thought to support these species by enhancing nutrient cycling, supporting more diverse food webs, and providing nursery habitat via complex and connected aquatic habitat features that are typically absent in managed wetlands (Boesch and Turner 1984, Zedler and Callaway 2001, Sheaves et al. 2015). Concerns have been expressed that conversion from managed wetlands to tidal marsh habitat could have adverse effects on waterfowl populations, and while the SMP aims to offset these impacts by enhancing managed wetlands, we lack quantitative information to evaluate how the conversion of managed wetlands might impact waterfowl food resources (SMP 2013).

Suisun Marsh supported approximately 300,000 wintering waterfowl as recently as the 1960s; however, numbers have declined by over 50% in the past decade (George et al. 1965, Mall 1969, CDFW 2020). Most species of dabbling ducks, as well as some geese, depend on annual plant seeds as a primary source of energy and nutrients throughout winter (Fredrickson and Taylor 1982). Early studies in Suisun Marsh confirmed that wintering waterfowl utilized a variety of annual wetland plant seeds grown in managed seasonal wetlands (George et al. 1965, Mall 1969, Burns 2003). The management of seasonal wetlands within Suisun Marsh has focused on promoting seed-producing annual plants that waterfowl prefer to meet the energetic demands of wintering populations (Rollins 1981, Fredrickson and Taylor 1982, Euliss and Harris 1987, Baldassarre and Bolen 2006).

The Central Valley Joint Venture (CVJV) sets regional waterfowl population goals, derived from continental population objectives (NAWMP 2012) using bioenergetic models (CVJV 2020). These models evaluate the food abundance (energy supply) available on a landscape to determine if the energetic needs of a population are being met (Goss-Custard et al. 2002, Williams et al. 2014, Petrie et al. 2016). When informed by data, these models allow conservation planners to anticipate and assess habitat conservation and management needs (Miller et al. 2014, Williams et al. 2014). However, we lack any quantitative information on food availability for waterfowl in Suisun Marsh. Currently, management plans have been based on an approximation that seed abundance in the marsh will be 50% lower than the typical managed wetland in the Central Valley (CVJV 2020). The 50% reduction was an approximation, based on the assumption that food plant productivity would be lower within Suisun Marsh due to the high salinity of applied water, invasive species, frequent droughts, aging water management infrastructure, poor levee maintenance, subsidence, and unique plant communities; all of which pose challenges to wetland managers (Mall 1969, Rollins 1973, 1981; SMP 2013, Chappell et al. 2018). However, the impact of these factors on seed production cannot be estimated easily across regions in the marsh that have different water regimes, wetland types, and plant communities. A thorough assessment of the availability and variation in food seed abundance among tidal marsh, managed wetlands and in different regions of the marsh is a critical need to plan for the sustainability of waterfowl, fish and a diversity of wetland dependent species.

To address this need, we conducted a two-fold sampling approach to provide the first quantitative estimate of seed abundance in managed wetlands and tidal marshes in Suisun Marsh. First, we conducted site-specific studies at three sites with paired managed and tidal wetlands, staggered across the north-south and east-west salinity gradients present in Suisun Marsh (Barthman-Thompson et al. 2005). This provided a comparison of seed abundance between adjacent managed and tidal wetlands while simultaneously providing insight as to how salinity gradients across the marsh influence seed production. Second, to assess the range of seed production, species composition, yearly variation, and the average seed abundance available to waterfowl, we sampled managed wetlands and tidal marshes throughout the entire Suisun Marsh over two consecutive wintering periods. To determine waterfowl foraging pressure we collected samples in fall, as waterfowl numbers increase, and again in late winter, near the end of the wintering period. By combining sampling schemes — site-specific and marsh-wide — with early (fall) and late (winter) sampling periods, we were able to evaluate how the abundance and composition of seeds available in managed wetlands and tidal marshes vary temporarily and spatially.

METHODS

Study system: Suisun Marsh

Suisun Marsh is located between the Sacramento-San Joaquin Delta and San Francisco Bay (Fig. 1.1) It comprises 11,635 ha of seasonally managed wetlands, 75% of which are privately managed by 150 duck clubs, while the remainder are managed by the California Department of Fish and Wildlife (CDFW) (Gill and Buckman 1974, CVJV 2006, SMP 2013, CVJV 2020). Water control structures and levees isolate managed wetlands from tidal inundation and allow managers to determine flood periods (typically October to February); tidal marshes, in contrast, are exposed to tidal inundation (Barthman-Thompson et al. 2005). Approximately 2,550 ha of tidal marshes are distributed across Suisun Marsh as complete islands, or attached to adjacent managed wetlands, often occurring on the slough side of managed wetland levees (Fig. 1.1). Water salinities vary (0 – 22 mS) spatially and temporally due to tidal cycles, rain fall, and freshwater outflows from the Sacramento-San Joaquin Delta (Barthman-Thompson et al. 2005, Sommer et al. 2020). Salinity levels are lowest in February (< 5 mS) and increase throughout spring into summer, often peaking (> 15 mS) in late August (Barthman-Thompson et al. 2005, Sommer et al. 2020, California Department of Water Resources: California Data Exchange Center). Drought can lead to increased saltwater intrusion from the San Francisco Bay, impacting water quality (Kimmerer et al. 2009, Feyrer et al. 2010). Spatial variability in salinity results in different plant communities and management needs for different regions of Suisun Marsh (Chappell et al. 2018). Wetland managers attempt to moderate the impact of salinity on vegetation by flooding managed wetlands during periods of freshened water to promote the germination and production of favored plants (Mall 1969, Rollins 1981, Chappell et al. 2018).

Methods

We used two sampling protocols to assess seed abundance in tidal marsh and managed wetland units within Suisun Marsh. Our first sampling protocol, led by C. Roddy, was a site-specific study, conducted from fall of 2015 through the winter of 2016, focused on three study locations, Denverton Duck Club, Joice Island Unit, and Goodyear Slough Unit (Roddy 2017). At each of these locations we sampled a seasonal managed wetland and an immediately adjacent tidal wetland, providing a paired comparison. These sites were chosen due to differences in management and environmental conditions that would be likely to result in variation in productivity (Fig. 1.1). Our second sampling protocol, led by D. Smith, was a large-scale evaluation of wetland food availability between the fall and winter of 2017-2018 and 2018-2019, in which we sampled managed and tidal wetlands throughout Suisun Marsh. Fall and winter sampling (conducted for each sampling protocol) allowed us to assess how seed abundance changed over the waterfowl wintering period and infer seed depletion as a result of waterfowl foraging.

Site-Specific

We selected three areas distributed across the north-south and east-west salinity gradients for our site-specific investigation (Fig. 1.1) The most northern site, Denverton Club, was located near Denverton Slough and Luco Slough. This site typically experiences lower than average salinities due to the input of freshwater from the north and being located near Montezuma Slough which benefits from the Suisun Marsh salinity control gates. The Joice Island Unit was located in central Suisun Marsh, and typically exposed to average salinities. The Goodyear Slough Unit was located between Interstate 680 and Goodyear Slough in the southeastern portion of Suisun Marsh. Of the three sampling sites, Goodyear Slough is exposed to the highest salinities due to its proximity to Suisun Bay.

At each of six study sites (one tidal and managed site at each of the three locations) we marked a 0.5 ha (1.2 acre) sampling grid comprised of 60 sampling points spaced 15 meters apart. We collected samples from 20 grid points selected at random (using a random number generator) in fall (Nov. 19 to Dec. 7, 2015) and winter (Feb. 2 to Mar. 1, 2016). Samples were collected 1 meter north of the grid point to avoid sampling on walking paths.

Marsh-Wide

To determine sampling locations in our marsh-wide assessment we generated a map of the managed and tidal wetland units within Suisun Marsh in ArcGIS (10.8.1) using manual observation and visual interpretation of remotely sensed LiDAR data layers which helped identify levee features acting as wetland unit boundaries. We then used this map in conjunction with the *spsurvey* package in the program R (Dumelle et al. 2021). We used a generalized random tessellation stratification (GRTS) method to randomly select 75 managed wetland units and 20 tidal wetland units for each sampling year (Kincaid et al. 2016). We chose the GRTS method as it produces a spatially balanced selection of sites and avoids clumping and potential over-sampling that can occur with traditional random sampling approaches (Stevens and Olson 2003, 2004). We collaborated with the Suisun Marsh Resource Conservation District to obtain permission for access and participation by landowners who owned and managed the selected wetland units. We were granted access to approximately half of our initially selected sites in both sampling years, allowing us to sample a total of 80 unique managed wetlands units (37 in 2017, 32 in 2018, and 11 were sampled in both years). All but one (owned by CDFW) of our tidal wetland sampling locations were publicly accessible. We sampled 19 tidal units (12 in 2017, 13 in 2018; 6 were sampled in both years). We used the same GRTS approach within each wetland unit to randomly select 10 sampling locations.

Sample collection and processing

Samples were collected for both protocols using a soil coring device (5 cm deep, 6 cm dia.) in Fall (Nov.1-14th) and Winter (Feb.1-14th) (Naylor 2002). Samples were then frozen to prevent seed deterioration until they were thawed, washed, and stored in ethanol prior to processing. Additional details are provided in Roddy (2017). Seeds contained within each soil core were identified using stereo dissecting microscopes and separated by species, when possible, dried at 80°C for 48 hours, and weighed to the nearest 0.0001 gram. Occasionally the dried mass of species with small seeds weighed less than 0.0001 gram, we enumerated seeds in these instances to record them, but we did not include them in our analyses due to the negligible impact that their presence has at the landscape level (roughly 0.36 kg/ha).

In our site-specific assessment we collected and processed 177 soil cores, including 78 from managed wetland sampling locations (44 in fall, 34 in winter) and 99 from tidal wetland sampling locations (43 in fall, 56 in winter). In our marsh-wide assessment, we collected and processed a total of 1429 soil cores across two years, including 1176 from managed wetlands (731 in fall, 445 in winter), and 253 from tidal wetlands (163 in fall, 90 in winter). We prioritized fall sampling in our marsh-wide assessment to gain a better understanding of the total possible food present in Suisun Marsh at the start of the waterfowl wintering period. In the second year of sampling (2018) we reduced sample collections to 5 samples for each tidal wetland unit. We grouped species to genera when differentiation between species was unreliable. We grouped all *Schoenoplecutus* sp.*, Bolboschoenus* sp.*, Rumex* sp., *Lotus* sp., and *Typha* sp. to genus. We also grouped *Atriplex* species with *Chenopodium* species, as distinguishing features such as bracts and seed coats were not always present following the washing process, and a wide variety of sizes were encountered. We also found seeds that were 'rare', with only a few seeds occurring across all samples. We classified these rare seeds as unknown and gave them unique identifiers but grouped them in our analyses.

Waterfowl diet

We examined three previous waterfowl diet studies conducted in Suisun Marsh to determine what seed waterfowl prefer. We used these data to adjust our seed abundance estimates to accurately reflect seeds consumed by waterfowl, improving the accuracy of bioenergetic models using these data to assess waterfowl carrying capacity (Goss-Custard et al. 2002, Hagy and Kaminski 2012, Williams et al. 2014). We used preliminary results from a concurrent diet study which examined the esophageal contents from 549 dabbling ducks, consisting of 6 species (*Anas platyrhynchos, Spatula clypeata*, *Anas crecca*, *Anas acuta*, *Mareca americana*, *Mareca strepera*) collected in the fall and winter of 2017 to 2019 in Suisun Marsh (J. Satter, UC Davis, in prep). These data confirmed that 10 seed genera/species comprised over 90% of the aggregate dry mass of seed found in esophageal samples: *Atriplex/Chenopodium*, *Bolboschoenus* spp.*, Echinochloa crus-galli*, *Lolium multiflorum*, *Polygonum* spp.*, Polypogon monspeliensis, Salicornia virginica*, *Sesuvium verrucosum*, and *Crypsis schoenoides*. In addition to these genera, we include d*Cotula coronopifolia* as it was an important food item in previous studies (George et al. 1965, Burns et al. 2003).

Analysis

We used R and the *lme4* package (Bates et al. 2012) to conduct linear analyses of the relationship between total seed abundance and wetland type (managed and tidal). We created two linear models, one for the site-specific data and a second for the marsh-wide data. We log normalized (ln(x+1)) total seed abundance (kg/ha) as our response variable for both models to meet assumptions of normality. The linear model for the site-specific data included study location, wetland type, and sampling season as fixed effects, and the linear model was constructed using the core linear model function in R. For our marsh-wide data, we included wetland type, collection season, and collection year as fixed effects, and wetland unit as a random effect (random intercept) to account for the possibility of spatial autocorrelation. We also tested two additional models to determine if there was a significant interaction between season and wetland type, and if the random effect of wetland unit improved model fit. We determined the best model by comparing AIC values and selected the model with the lowest value. We visually assessed all models for normality of residuals, normality of random effects, linear relationship, homogeneity of variance, and multicollinearity using the R package *performance* (Gotelli and Ellison 2004, Lüdecke et al. 2021). We used the package *multcomp* to conduct Tukey post-hoc contrasts to determine if the different levels within each fixed effect were significantly different from one another (Hothorn et al. 2008).

RESULTS

Seed abundance

In our site-specific assessment we found mean fall seed abundance in tidal wetlands was greater than in managed wetlands (tidal = 115.7 ± 20.6 kg/ha, managed = 96.2 ± 16.4, $p = 0.010$)

(Table 1, Fig. 1.2). In our marsh-wide, there was no significant difference in mean seed abundance between tidal and managed wetlands in fall (tidal = 172.9 ± 20.4 kg/ha, managed = 163.8 ± 10.0, *p* = 0.928) (Table 1) in our marsh-wide linear mixed model (adjusted $r^2 = 0.225$, AIC = 5161) (Table 1). Our marsh-wide model including an interaction between season and wetland type (adjusted $r^2 = 0.225$, AIC = 5164) indicated that the interaction was not significant (estimate = 0.09 ± 0.41, p = 0.670). Additionally, we found no difference in seed abundance due to collection year in our marsh-wide assessment (0.110 ± .124, *p* = 0.375).

Seed abundance was highly skewed with most samples containing few seeds. The highest skew value (5.38) was within our marsh-wide assessment (fall managed wetlands), while skew values for tidal wetlands were typically smaller (between 2.3-3.3). This trend was still present when averaging seed abundance values at the wetland unit level for our marsh-wide assessment (Fig. 1.3). Only two wetland units (managed) had a mean seed abundance in fall that was greater than the Central Valley average (556 kg/ha) (Fig. 1.3), and the geometric mean seed abundance of wetlands units was less than 1/5th of the central valley average (geometric mean = 106 kg/ha). The addition of wetland unit (n = 72) as a random effect in our marsh-wide model greatly improved model fit (r^2 increased from 0.002 to 0.225, ΔAIC = -186), yet the intraclass correlation coefficient of 0.24 indicates that seed abundance varied significantly within wetland unit.

Sampling location also influenced seed abundance in our site-specific assessment (Fig. 1.4, Table 1.1). Denverton, the site with the freshest water, had the highest log normalized seed abundance in fall for in both managed and tidal sites (4.13 ± 0.50). Goodyear (exposed to the highest salinity) had the lowest seed abundance in the site-specific abundance (3.18 ± 0.55).

Species composition

We encountered more seed species in our marsh-wide assessment (47 species in managed, 42 species in tidal) compared to our site-specific assessment (11 species in managed, 16 species in tidal). The species that comprised the largest proportion of total seed mass was the same in both site-specific and marsh-wide assessments but differed substantially between tidal and managed wetlands. Seeds of *Sesuvium verrucosum* were the most abundant species in managed wetlands, whereas seeds of *Schoenoplectus* spp. were the most abundant in tidal wetlands (Fig 1.5). In our marsh-wide assessment, four species (*Sesuvium verrucosum*, *Schoenoplectus* sp., *Bolboschoenus* sp., and *Crypsis schoenoides*) comprised the majority of total seed mass in managed wetlands (78% in fall, 75.9% in winter), while a single species (*Schoenoplectus* sp.) comprised a similar proportion (77.6% in fall,71.6% in winter) in tidal wetlands. *Schoenoplectus* sp. was also common in managed wetlands for both the marsh wide assessment, (17.7% in fall, 16.3% in winter) and the site-specific assessment (13.8% in fall, 34.9% in winter). The food plant species consumed by waterfowl – based on existing and contemporary diet data – comprised a much larger proportion of fall seed abundance in managed wetlands (66.7% in 2017, 73.1% in 2018), than tidal wetlands (13.9% in 2017, 10.12% in 2018) (Fig. 1.6).

Seed depletion

There was a significant decline in seed abundance between fall and winter in our site-specific assessment (estimate = -1.31 ± 0.50, p < 0.001), but not at the marsh-wide level (0.043 ± 0.083, *p* = 0.602) (Table 1.1) (Fig. 1.2). All managed wetland sites in the site-specific assessment experienced declines in seed abundance between fall and winter sampling, yet the Denverton site had the largest decline (-104 kg/ha).

DISCUSSION

Variation in seed abundance

Our study provides some of the first quantitative estimates of seed abundance and species composition in the Suisun Marsh. We found substantial variability in total seed abundance in tidal and managed wetlands, with most areas exhibiting low (< 125 kg/ha) abundance (Fig. 1.2 & 1.3). Managed and tidal wetlands had similar seed abundances when compared at the marsh-wide level, but tidal wetlands did occasionally contain higher abundances when compared at smaller site-specific spatial scales. The largest difference in seed abundance between managed and tidal wetlands occurred at the Goodyear sampling location (Fig. 1.4). We also found that spatial scale (site-specific vs. marsh-wide) influenced our ability to detect seasonal changes in seed abundance. Declines in seed abundance between fall and winter occurred in managed wetlands at the local, site-specific scale (Fig. 1.4), but we did not find significant differences between sampling periods in our marsh-wide assessment (Fig. 1.2). Perhaps one of the most striking results of the marsh-wide assessment was the marked difference in species composition in managed and tidal wetlands (Fig. 1.5); over 70% of seeds in managed wetlands were species commonly consumed by waterfowl, while these species comprised only 12% of the total seed mass encountered in tidal wetlands (Fig. 1.6)

Our quantitative estimates of seed abundance are considerably lower than those assumed and used in previous Central Valley Joint Venture (CVJV) Implementation Plans (CVJV 2006, 2020). In the absence of data, the CVJV developed qualitative approximations assuming that managed wetland seed production within Suisun would be roughly half (295 kg/ha) of the Central Valley average (588 kg/ha). This was assumed to be a conservative estimate given the higher salinity levels which impact plant growth, production, and species composition within both tidal and managed wetlands within Suisun Marsh (Callaway et al. 1990, Mushet et al. 1992, Janousek and Folger 2013, CVJV 2020). In contrast, our marsh-wide assessment indicated an average seed abundance of approximately 168 kg/ha, while our site-specific assessment average was 106 kg/ha (Fig. 1.2). Although the CVJV and other planners conservatively expected Suisun Marsh seed production to be half of what commonly occurs in the interior Central Valley, our data indicate that actual values are closer to a quarter (25%). This has important implications for estimates of waterfowl carrying capacity and wetland management and conservation planning. In short, our food production targets are too low and carrying capacity in the Suisun Marsh may be half of what it was thought to be, even compared to conservative estimates.

Why is food production so low in the marsh? The high degree variability in seed abundance, driven by applied water salinities, management practices, and management history (Chappell et al. 2018) likely explains why past qualitative estimates of seed abundance have been inaccurate. These factors impact plants differently across the extent of Suisun Marsh, resulting in the substantial amount of spatial variation in seed abundance, as we observed in both local scale and marsh-wide assessments (Fig. 1.3, Fig. 1.4). This extreme variability highlights the challenges for managers in treating the Suisun Marsh as a single entity within a single management plan.

We found correlative support in our site-specific estimates for the predicted trend that seed abundance would decline with increasing salinity gradients; the highest seed abundance occurred in a region with low salinity (Denverton), and the lowest seed abundance in a region with high salinity (Goodyear) (Fig. 1.4). Additionally, drought likely impacted the lower overall estimates of seed abundance in our site-specific assessment, compared to our marsh-wide investigation. Site-specific sampling took place during the fourth year of a prolonged drought, while our marsh-wide sampling occurred following the wettest year in nearly a century (since 1923) (CDWR 2020). Nevertheless, we believe that our combination of small and large-scale seed assessments, conducted across three wintering periods, provides an accurate representation of seed abundance, species composition, and seasonal changes within Suisun Marsh's tidal and managed wetlands.

Managed versus tidal wetlands

Our results indicate that total seed abundance was similar in managed and tidal wetlands at the marsh-wide scale, but seed abundance in tidal wetlands was occasionally higher than managed wetlands when compared at smaller, site-specific spatial scales. This is considering all seed plants species. The results are markedly different when we restrict estimates of seed abundance to only those foods that waterfowl prefer – preferred food plants comprised 66.7-73.1% of the seeds in managed wetlands, but only 10.12 to 13.9% of seeds in tidal marshes (Fig. 1.6). These results indicate that while the total seed abundance of all plants does not differ strongly between tidal and managed wetlands, the food items that support waterfowl are substantially different and, ultimately, that tidal marshes provide little food energy value to sustain waterfowl populations.

These results are driven by considerable differences in the species composition of seeds in managed wetlands and tidal marshes (Fig. 1.5). *Schoenoplectus* sp. comprised over 70% of the total seed mass found in our marsh-wide estimate for tidal wetlands. Conversely, total seed mass in managed wetlands was primarily comprised of four different species (*Sesuvium verrucosum, Schoenoplectus* sp., *Bolboschoenus* sp., and *Crypsis schoenoides*) (Fig. 1.5). This pattern at the marsh-wide level was comparable to what we found in our site-specific study, although some differences in species composition occurred. Our site-specific assessment encountered far fewer species (11 in managed, 16 in tidal) compared to our marsh wide assessment (47 in managed, 42 in tidal), and we observed some differences in the most abundant species. These differences between assessments are most likely the result of sampling intensity and number of sites sampled. Regardless of assessment method, *Sesuvium verrucosum* was the dominant species in managed wetlands while *Schoenoplectus* spp. was the most abundant seed in tidal marshes (Fig 5).

The differences in species compositions by wetland type are likely driven by the modified hydrological cycles and management actions taken by wetland managers. Extensive effort is undertaken to produce favorable flooding cycles, salinity levels, and germination conditions by controlling inundation timing and frequency, paired with methods of vegetation control to encourage the growth of plants which waterfowl favor (Barthman-Thompson 2005, Chappell et al. 2018). Specifically, vegetation control efforts by managers to maintain open pond areas that waterfowl favor (Smith et al. 2004, Casazza 2021) through the mechanical removal of *Schoenoplectus* sp. prevent it from dominating wetlands, as it tends to do in tidal areas. Ultimately, water salinity plays a large role in determining plant species presence in managed wetlands, and is primarily dependent on rain fall, tidal cycles, and freshwater outflows from nearby creeks and rivers (Kimmerer et al. 2009, Feyrer et al. 2010, Chappell et al. 2018). As such, the most abundant seeds in managed wetlands, *Sesuvium verrucosum*, *Schoenoplectus* spp., *Bolboschoenus* spp. are from species typically considered to be saline tolerant, occurring naturally in brackish marshes (Ferren 2012, Smith 2012a, b). The pervasive presence of these species within managed wetlands, even with efforts to control salinities, suggests that the effectiveness of management actions are limited by the salinities of available water.

Seed depletion during fall and winter

If food availability is impacting waterfowl carrying capacity in the Suisun Marsh, we expected to find evidence that seed abundance would decline in managed wetlands between fall and winter, as seeds would be lost due to consumption by animals (depletion), and decomposition (Neely 1956, Greer et al. 2009, Hagy and Kaminski 2012). Diet studies in Suisun Marsh confirmed that annual wetland plant seeds compose the majority of wintering waterfowl diets (George et al. 1965, Mall 1969, Burns 2003), and recent work found the endangered salt marsh harvest mouse consumed some of the same species (Smith and Kelt 2019, Aylward et al. 2022). Although we did not directly assess waterfowl presence at our sampling sites, a concurrent study examining dabbling duck movements found that daily use was overwhelmingly constrained to managed wetlands (> 90%) (Casazza et al. 2021). Seed decomposition rates are highly species-dependent, yet studies conducted on species similar to those found in Suisun Marsh found roughly 30% of initial seed mass is lost over the wintering period (Neely 1956, Nelms and Twedt 1996, Hagy and Kaminski 2012). We observed a decline in seed abundance (approximately 60% between late Nov. to early Mar.) in our site-specific assessment, but no significant decline in our assessment at the marsh-wide level. These results indicate that foraging is occurring and was more apparent at smaller spatial scales. Low average seed abundance combined with multiple factors which influence foraging rate – density of waterfowl, density and distribution of seeds, predation risk, and forager condition – and obscure the signal at the larger scale (Nolet et al. 2006, Arzel et al. 2007, Greer et al. 2009, Hagy and Kaminski 2015).

Implications for waterfowl management and wetland conservation

The different plant species assemblages found in tidal and managed wetlands have important implications for waterfowl, as only the seeds of some plant species are preferred or favored in waterfowl diets. Three diet studies have been conducted in Suisun Marsh; in the 1960's, George et al. (1965) and Mall et al. (1969) examined waterfowl gizzards and found *Bolboschoenus* spp. was the most common diet item, accounting for 88% of foods consumed by waterfowl despite covering only 6% of the marsh. There were some seasonal shifts in diet, with *Cotula coronopifolia* being the most important food in early season (Aug-Oct), while *Atriplex/Chenopodium* was consumed, albeit to a lesser extent, between November to January (George et al. 1965, Mall et al. 1969). Burns et al. (2003) followed up in the early 2000s and examined esophageal contents to better capture softer seeds and invertebrates, and found waterfowl consumed more than 30 species of plant seeds. Three species (*Sesuvium verrucosum* (37%), *Bolboschoenus* spp. (24%), and *Echinochloa crus-galli* (21%) comprised over 80 percent of the aggregate dry mass of duck diets (Burns et al. 2003). A contemporary diet study (Satter et al. in prep) examining esophageal contents concurrently to our marsh-wide sampling effort found diets of six dabbling duck species (n = 549) were primarily comprised of *Crypsis schoenoides* (33%), S. *verrucosum* (15%), *Polygonum* spp. (13%), and *Atriplex/Chenopodium* (10%).

While there have been shifts in waterfowl diets over the last six decades, plant seeds consistently comprise the majority of diet items. Moreover, the species of seeds consumed occur more frequently in managed wetlands (Fig 1.6). Some important waterfowl foods were never found in tidal wetlands, or occurred at extremely low densities (i.e., total dried mass of < 0.003 g total for each sampling season for *Cotula coronopifolia*, *Sesuvium verrucosum, Crypsis* *schoenoides,* and some *Polygonum* spp.). Overall, our data indicate managed wetlands provide more species that waterfowl consume. If we adjust our seed abundance estimates to only include seeds commonly consumed by waterfowl (Fig 1.6, averaged across years), our estimate for tidal wetlands is reduced by 88% (e.g., 172.9 kg/ha to 20.7 kg/ha) while that for managed wetlands is reduced by 30% (e.g., 163.8 kg/ha to 114.7 kg/ha). This adjustment to only include waterfowl foods agrees with the recommendation of Hagy and Kaminski (2012) who found that estimates of seed abundances in the lower Mississippi Valley should also be reduced by 30% to accurately represent seeds ducks consume. The addition of these adjustments increases the accuracy of bioenergetic models used to assess waterfowl carrying capacity (Goss-Custard et al. 2002, Hagy and Kaminski 2012, Williams et al. 2014).

To further evaluate the potential impact of the current abundances of food resources in Suisun Marsh, we used a simple daily ration model (DRM) to estimate the size of the waterfowl population that could be supported energetically based on our marsh-wide estimates. This DRM allowed us to calculate the total number of ducks which could be sustained (a proxy for carrying capacity) by dividing the total energy available on the landscape by the energy required by an average duck (most models use a Mallard as reference) over a 180-day wintering period (mid-September to mid-March). We used the 2020 CVJV plan to inform total habitat area (11635.5 ha), foraging threshold (32.1 kg/ha), and total metabolizable energy of wetland seeds (2.5 kcal/g), and estimated the daily energy needs of a duck (Mallard) to be 356.8 kcal/day (Miller and Eadie 2006, Soulliere et al. 2007). We adjusted total seed abundance estimates to only include seeds consumed by waterfowl (Fig. 1.6), which resulted in the exclusion of tidal wetland acreages as total seed abundance was below foraging thresholds (Hagy and Kaminski 2012, CVJV 2020). Based on these assumptions, the DRM indicated Suisun Marsh can currently meet the energetic needs of 37,441 ducks. While this simple DRM ignores many important factors (such as decomposition, temporal variability, and invertebrate food resources) present in the more complex bioenergetic model (TRUEMET) used by the CVJV, it provides a back-of-the-envelope indication that current wetland habitats in Suisun Marsh are far from supporting the goal population of 244,600 dabbling ducks outlined by the CVJV (CVJV 2020).

This DRM is very simple and we caution that planners use this only as an indication that more rigorous assessments of carrying capacity are needed. To do so, we are evaluating the methodology used to derive seed abundance estimates, conducting additional studies to assess the spatiotemporal variability of seed abundance, and developing a more sophisticated bioenergetic model. Our analysis of soil core samples indicates that inconsistencies in sampling depth could influence the accuracy of seed abundance estimates, potentially leading to biased estimates (bias 19.6% high) (Smith et al. in preparation). However, accounting for this bias in our DRM, only further reduces the estimate of the number of ducks that could be supported by Suisun Marsh to 27,021. One primary assumption of our DRM is that peak seed abundance occurs as wetlands are flooded in fall, which while true in other seasonal wetlands may not apply to Suisun Marsh. Our ongoing investigation of seed abundance throughout winter suggest seeds from some plant species increase until mid-December. This increase in seed abundance over the first half of winter would not be captured in our sampling, nor in the DRM. As we complete and coalesce the results of our on-going studies, we will use a more biologically informed agent-based bioenergetic model to provide an updated evaluation of waterfowl carrying capacity for the Suisun Marsh that addresses many of the uncertainties and assumptions of the DRM (Blenk et al. in preparation).

CONCLUSION

Extensive anthropogenic induced changes – primarily between the mid-1800s to early 1900s – to the complex tidal system of Suisun Marsh have negatively impacted multiple wildlife species (Moyle et al. 2014). As part of an effort to mitigate these impacts, several managed wetlands are being converted into tidal marshes in Suisun Marsh (SMP 2013). Ideally, restoring complex tidal marsh structure and hydrological linkage with larger sloughs and bays within Suisun Marsh would provide additional areas of high prey abundance and predator avoidance, important factors that increase native fish recruitment and survival which are not present in seasonally managed wetlands (Durand 2015, Colombano et al. 2020, 2021). Increased tidal marsh acreage is also expected to ameliorate the impacts of sea level rise within Suisun Marsh by allowing for sediment accretion while requiring minimal levee maintenance, which is needed for managed wetlands (SMP 2013). However, whereas tidal marsh provides many benefits to wildlife, recent studies on waterfowl use in Suisun Marsh indicate that waterfowl rarely utilize tidal marsh (Coates et al. 2012, Casazza et al. 2021), and our results show that tidal areas do not provide meaningful food sources used by waterfowl (Burns 2003, Satter unpublished).

Despite the potentially conflicting needs of wintering waterfowl and other wildlife species, recent research has found synergies between managed wetlands and tidal conservation goals. Plant species that wetland managers target for waterfowl are also consumed by the endangered salt marsh harvest mouse (Smith and Kelt 2019, Aylward et al. 2022). Additionally, managed wetlands mimic floodplain conditions which produce high abundances of zooplankton, macroinvertebrates, and small fish; and the draining of these wetlands exports these food resources into adjacent tidal sloughs and channels which are consumed by fish (O’Rear and Moyle 2014, Aha et al. 2021, Willaimshen et al. 2021). The multiple flushing/draining cycles use to reduce managed wetland soil salinities in spring can be used to increase food abundances during critical periods for salmonids and other rearing pelagic fishes (Kimmerer 2004, Aha et al. 2021). Additional seasonal wetland management strategies can be explored to determine if adjustments can be made to provide additional benefits to fish and other species of concern without reducing waterfowl benefits, as has been done in similar systems (Isola et al. 2000, Tori et al. 2002).

Historically, the diverse tidal marsh habitats of pannes, ponded areas, and semi-permanent water were able to produce food resources that supported large populations of non-breeding waterfowl (Moyle et al. 2014). However, the tidal marshes presently available do not provide abundant annual seed resources and are rarely used by waterfowl (Casazza et al. 2021). There is evidence that ponded areas within tidal marshes are used by some waterfowl, but it is unclear as to what factors make these sites appealing (Casazza et al. 2021). Many of the tidal wetland areas we sampled were near-monotypic stands of dense *Schoenoplectus* sp. and *Phragmites* sp., often near the edges of sloughs and channels. Vegetation cover at many sites was tall and extremely dense, likely prohibiting waterfowl from foraging. As additional information continues to become available regarding the value of tidal restoration sites within Suisun Marsh, a critical evaluation of conservation goals needs to be conducted to determine if current actions are providing the desired outcomes.

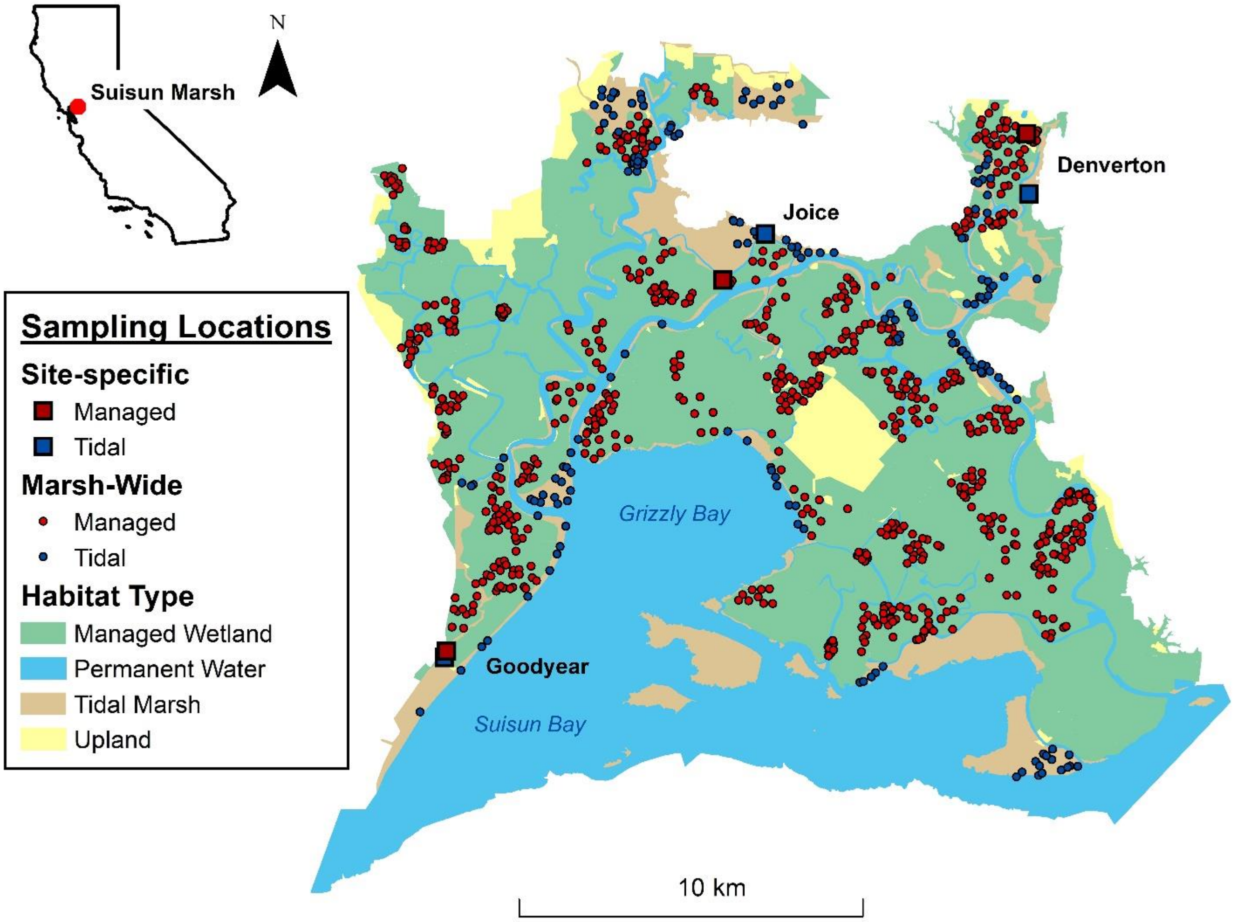

Figure 1.1: Sampling locations within Suisun Marsh for both sampling protocols. Colors for both sampling protocols indicate the wetland type, managed (red), and tidal (blue); site-specific sampling areas are depicted by squares, marsh-wide sampling locations are indicated by circles.

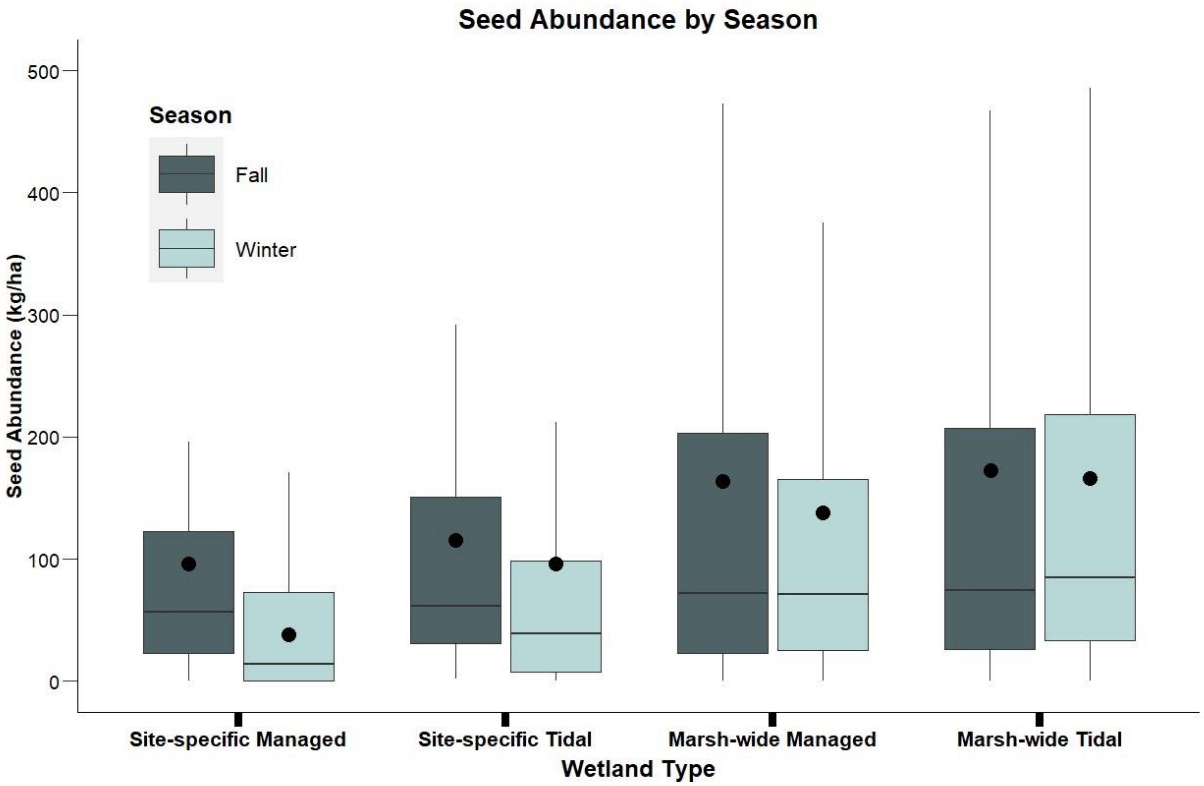

Figure 1.2: Box plots of seed abundance by season and wetland type. Site-specific and marsh-wide data are presented separately. Marsh wide data are combined across both sampling years. The horizontal line represents the median, black circles represent means, and boxes represent the inter-quartile range. Outliers are not shown.

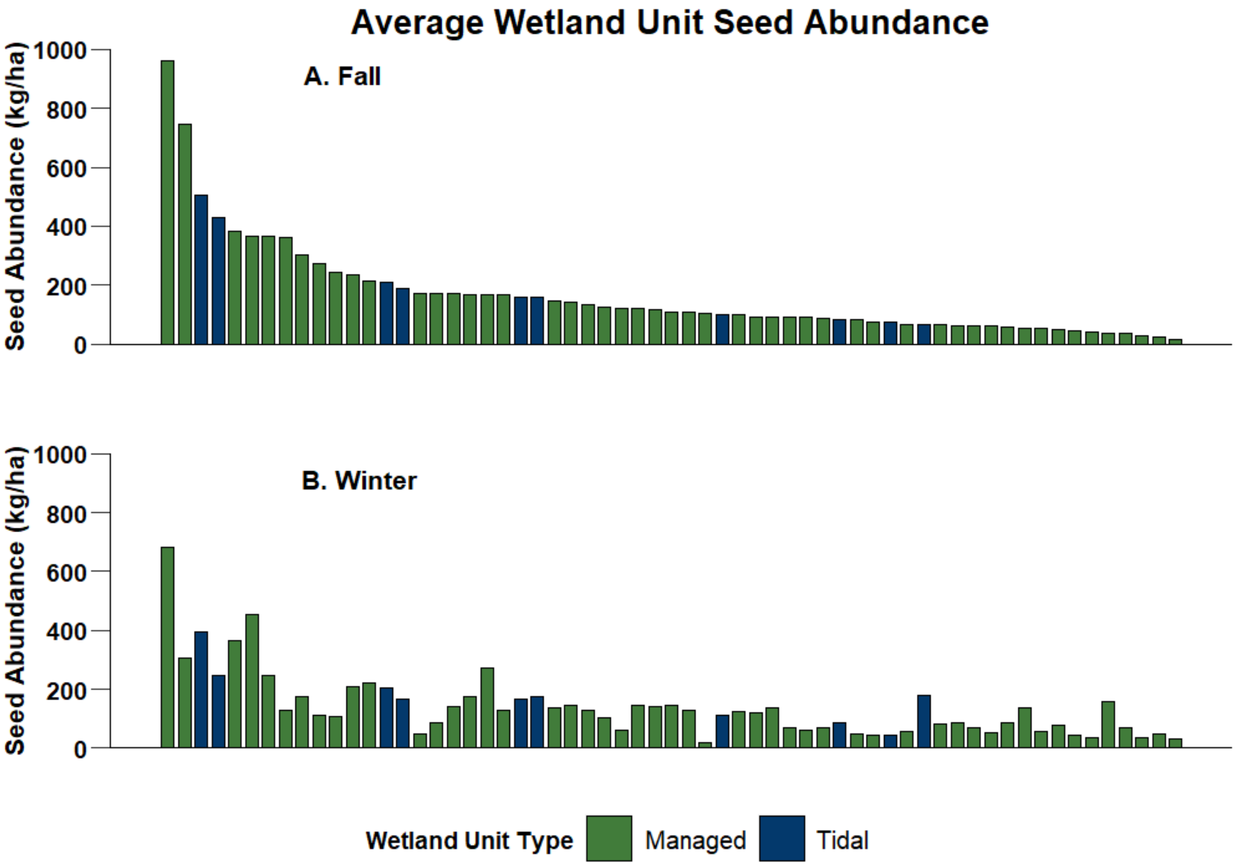

Figure 1.3: Mean seed abundance (kg/ha) for each wetland unit by season sampled in the marsh-wide assessment. Each wetland unit is represented by a bar in A and B, to show the change in average seed abundance between sampling periods. Managed wetlands are depicted by green, and tidal wetlands by blue. Only wetland units with at least 5 samples for each sample period (fall and winter) were included.

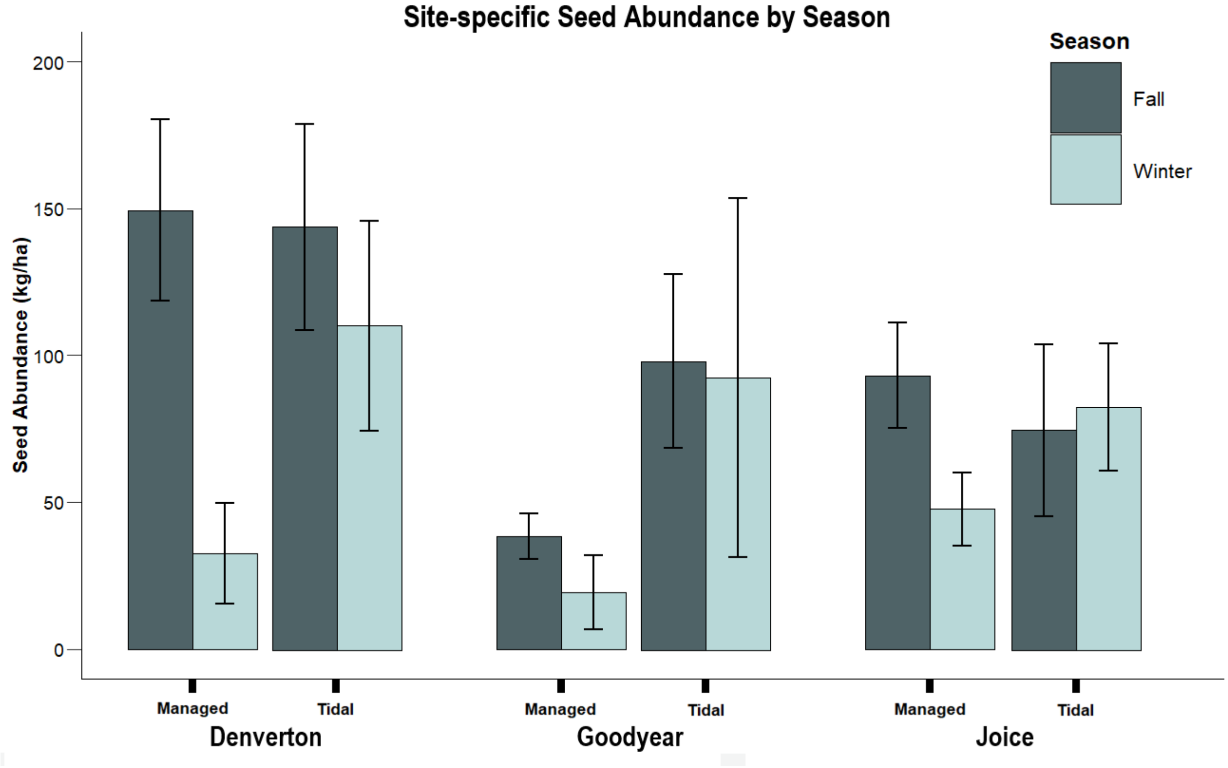

Figure 1.4: Mean seed mass (kg/ha, ±SE) at each of the paired (managed and tidal) site-specific sampling units. Fall samples (dark gray) were taken between November 19 and December 7, 2015, and Winter samples (light gray) were taken between February 2 and March 1, 2016, at each of the sites.

Figure 1.5: The most abundant species by mass, separated by wetland type (managed and tidal) and sampling scheme (site-specific and marsh wide). All unidentified species were grouped into a single category, which described less than 9% of total seed mass. Species comprising less than 1% of total mass were not included in the top five most common species but instead included into the 'Other' category.

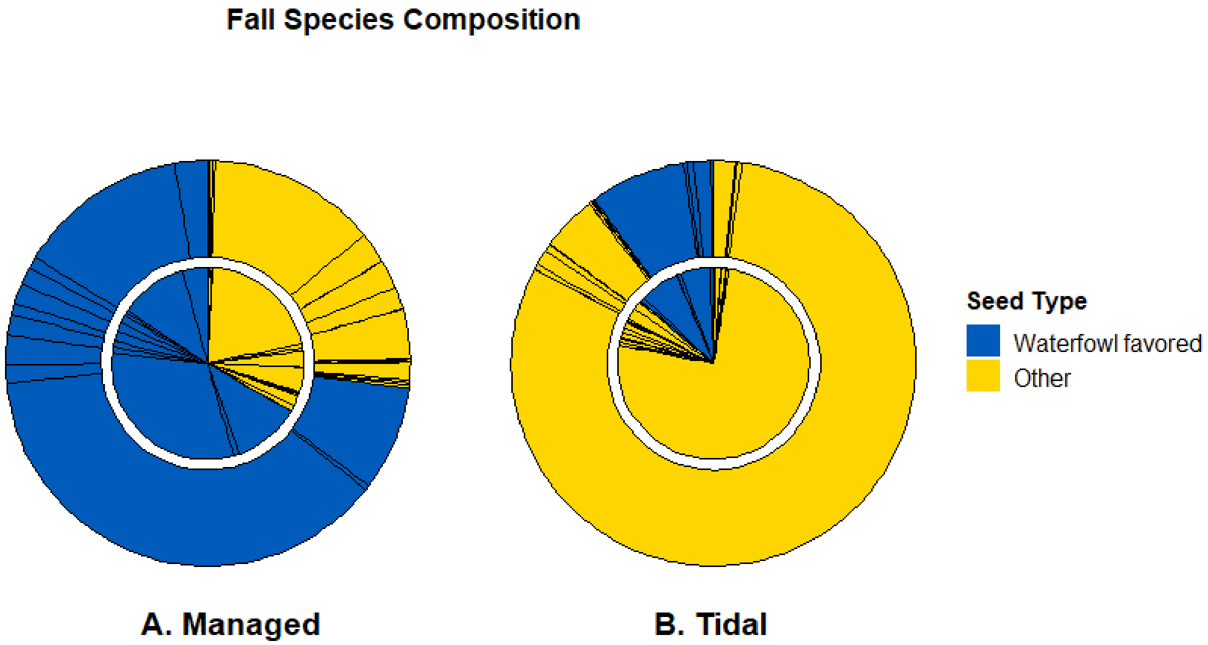

Figure 1.6: Fall species composition by wetland type from the marsh wide assessment. The inner circle represents the first sampling year (2017), and outer ring represents the second sampling year (2018). Seed were grouped into “waterfowl favored” (*Atriplex/Chenopodium*, *Bolboschoenus* spp., *Cotula coronopifolia*, *Crypsis schoenoides*, *Echinochloa crus-galli*, *Lolium multiflorum*, *Polygonum* spp., *Polypogon monspeliensis*, *Salicornia virginica*, *Sesuvium verrucosum*), and “other” categories using prior diet studies conducted in Suisun Marsh (George et al. 1965, Burns et al. 2003, J. Satter, UC Davis, in prep).

Table 1.1: Linear mixed model results for our marsh-wide and linear model results for site-specific assessments. The response variable for both assessments is log normalized seed abundance (kg/ha) for both assessments, and results are presented as they relate to the intercept. The marsh-wide model intercept is Wetland type [Managed], with wetland type, sampling season and collection year as fixed effects, wetland unit is included as a random effect. In the site-specific model the intercept is Site [Denverton], with sampling site, wetlands type, and sampling season as fixed effects.

	Seed Abundance [Log(ha/kg)]					
	Marsh-wide			**Site-specific**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	4.07	3.84 – 4.30	<0.001	4.13	3.63 – 4.62	<0.001
Wetland type [Tidal]	0.07	-1.44 – 1.58	0.928	0.64	0.15 – 1.12	0.010
Season [Winter]	0.04	-0.12 – 0.21	0.602	-1.31	-1.81 – -0.81	<0.001
CollectionYear [2]	0.11	-0.13 – 0.35	0.375			
Site [Goodyear]				-0.95	-1.50 – -0.40	0.001
Site [Joice]				-0.04	-0.66 – 0.57	0.889
Random Effects						
Residual Error (σ^2)			1.98			
Random Intercept Variance ($\tau_{00\ \text{Wetland unit}}$)			0.57			
Intraclass Correlation Coefficient (ICC)			0.22			
Number of Wetland Units			72			
Observations	1428			177		
Marginal R^2/Conditional R^2	0.001 / 0.225			0.190 / 0.172		

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CHAPTER 2 – Soil Core Volume Influences Estimates of Seed Abundance in Seasonal Wetlands but Not Tidal Marsh

ABSTRACT

Soil core sampling is commonly used to estimate seed abundance when assessing waterfowl habitat and population carrying capacities. Studies have evaluated the limitations and sources of bias associated with soil core sampling, but few have examined how variable sample volumes can influence estimates of seed abundance. We measured the soil volume of 1128 soil cores collected from managed wetlands and tidal marsh habitats to determine if seed abundance was correlated with the volume of soil sampled. We collected soil cores using a standard (6 cm diameter, 5 cm deep) soil coring device. Sampling depth was controlled by external flanges on the body of the device. We found collected soil volume to be highly variable; mean soil volume (215.6 ml) was 53% greater than the targeted soil volume based on the dimensions of the coring device (141.4 ml). Total seed abundance was positively correlated with soil volume in managed wetlands, but not in tidal marsh. Using a linear model, we found managed wetland samples contained an additional 42 kg/ha of total seeds for every additional 100 ml of soil collected. We determined that our estimates of total seed abundance in managed wetlands were 19.6% greater as a result of the relationship between seed abundance and soil volume. Estimates of waterfowl carrying capacity derived from soil core samples may be improved by considering the effect that variability in soil volume can have on estimates of moist-soil seed densities.

INTRODUCTION

Estimating seed abundance in habitats used by migrating and wintering waterfowl has been a major management focus for the last 30 years (Williams et al. 2014). Numerous studies have assessed the availability of foods in different wetland systems and agricultural lands

(Anderson and Smith 1999, Stafford et al. 2006, Drahota and Reichart 2015), evaluated the impact of wetland management practices on food production (Brasher et al. 2007, Stafford et al. 2011, Fleming et al. 2012), and determined how waterfowl deplete seeds over time (Greer et al. 2009, Hagy and Kaminski 2012). Seed abundance estimates often form the foundation of bioenergetic models, which have been employed extensively as habitat planning tools for waterfowl populations across North America (Goss-Custard et al. 2002, CVJV 2006, Williams et al. 2014).

Various techniques have been used to estimate seed abundance, including the assessment of inflorescences to estimating seed yield (Laubhan and Fredrickson 1992, Gray et al. 1999, Osborne et al. 2017), vegetation clipping (Low and Bellrose 1944, Haukos and Smith 1993, Reinecke and Hartke 2005), rapid visual assessment (Naylor et al. 2005, Fleming et al. 2012), and vacuum sampling (Penny et al. 2006, Evans-Peters et al. 2012). These techniques typically require species-specific calibration and/or provide only categorical assessments of seed abundance. Soil core sampling is the most commonly used technique as it can be used for a wide variety of habitat types and plant species. Soil core sampling involves a cylindrical device which is pushed into the substrate to collect a known volume of material (Swanson 1978, Naylor 2002). Following the collection of soil cores, samples must be washed and sorted, and then seeds must be identified, dried, and weighed – a time-consuming and laborious undertaking (Swanson 1983, Stafford et al. 2011, Livolsi et al. 2014).

Due to the continued and widespread use of soil core sampling, several studies have sought to evaluate and correct potential limitations of this technique. Researchers have addressed the substantial time cost associated with processing core samples by developing subsampling techniques (Kross et al 2008, Livolsi et al. 2014), and have developed frameworks to determine the number of samples required to minimize sampling cost and produce acceptable levels of variance (Behney et al. 2014, Ringelman et al. 2015). Additionally, bias in seed recovery rates due to seed size has been evaluated and correction factors have been developed to increase accuracy of estimates (Reinecke and Hartke 2005, Hagy et al. 2011). One component that has not been thoroughly addressed is the variation in the sample volume collected by soil coring devices. Despite the use of stoppers or other features that attempt to control sample depth, some variation in depth is unavoidable, leading to variable sample volumes. Additional factors such as soil saturation levels, soil composition, and general sampling error associated with the investigator transferring soil from the sampling device to a receptacle to either store or process the sample in the field can influence sample volume. These sources of variation may lead to bias in seed abundance estimates when investigators assume that all samples are of equal volume, compromising the accuracy of bioenergetic models or habitat assessments.

Sampling depth directly impacts the proportion of seeds collected, due to the logarithmic relationship between cumulative seed abundance and depth in wetland habitats — typically 70 – 90% of annual plant seeds occur within the top 5 cm of soil (Leck and Simpson 1987, Bonis and Lepart 1994, Evans-Peters 2010, Olmstead 2010). The vertical distribution of seeds within wetland substrate can be influenced by the plant species, hydrology, timing of sampling, and sedimentation rates (Leck and Graveline 1979, Leck and Simpson 1987, Csontos 2007). Similarly, common wetland management techniques that disturb the soil, such as discing, can rearrange seeds in the sediment horizon (Bonis and Lepart 1994, Csontos 2007).

There is no standard sampling depth for waterfowl foods, but the two most commonly used depths are 5 and 10 cm. The argument for sampling to a depth of 5 cm relies on the physical constraints of bill length for many species of waterfowl that utilize seed resources (~4.0 cm in mallards; Nudds and Kaminski 1984, Baldassarre and Bolen 2006); foraging to greater depths is energetically costly and unlikely to occur frequently in dabbling ducks (Santamaría and Rodríquez-Gironés 2002, Chen et al. 2019). Smith et al. (2011) experimentally assessed foraging depth and detected no consumption by waterfowl when seeds were buried 3.8 cm to 7.6 cm deep in flooded wetlands. However, studies on waterfowl species whose diets show the presences of tubers and animals that exist deeper in the soil typically sample to a depth of 10 cm (Sherfy et al. 2000, Kross et al. 2008). Regardless of the targeted sampling depth, controlling for consistent sampling depth is necessary for accurate comparisons and evaluations. Flanges or other fixtures on the exterior of the sampling device are often used to standardize sampling depth, yet these features have variable effectiveness, and such details are often not included in published reports.

Collecting soil cores to a consistent depth in flooded wetlands can be challenging due to turbid waters or vegetation, which can prevent an investigator from visually confirming the target depth was reached. Even with features such as flanges or collars which are designed to prevent sampling beyond the intended depth, factors such as roots or soil composition can result in investigators applying too much force and sampling too deep. Our objectives were to: (1) determine the precision and accuracy of collected soil volume using standard sampling methodology; (2) determine the influence of variable soil core volumes on estimates of seed abundance. To answer these questions, we measured the volume and seed abundance of 1128 soil cores collected in early and late winter, from managed wetland and tidal marsh habitats in the Suisun Marsh, California over two wintering periods. We estimated sampling depth by dividing our volumetric measurements by a constant (πr^2). Additionally, we compiled data from five studies which directly examined how seeds were distributed through the soil profile.

Together, these findings provide insight into the effect and magnitude that variable sampling volume has on seed abundance estimates.

STUDY SITE

Suisun Marsh is a mosaic of brackish managed seasonal wetlands and tidal marsh habitats that lies between the Sacramento-San Joaquin Delta and San Francisco Bay. The marsh contains 32,000 acres of managed wetlands –75% of which are managed privately by 150 private duck clubs – and 7,600 acres of tidal marsh (Gill & Buckman 1974, CVJV 2006, SMP 2013). The soils in Suisun Marsh are spatially variable and diverse in composition; primary soil types are Joice muck (20%), Reyes silty clay (18%), Suisun peaty muck (8%), Tamba mucky clay (22.5%), and Valdez silty clay loam (11.2%) (NRCS Web Soil Survey). We classified managed wetlands as those contained within man-made levees and where water was managed using infrastructure such as water control gates and/or pumps. We classified wetlands as tidal marsh when they were flooded solely through their exposure to the tidal cycle.

METHODS

We determined sampling locations using a two-step process using the *spsurvey* package in the program R (Stevens and Olson 2003, 2004; Dumelle et al 2021). Wetlands were selected using generalized random tessellation stratification (GRTS), then sampling sites within each selected wetland were determined using GRTS. We collected 10 samples from each wetland twice, first in early winter (Nov. 1 – 14th of 2017 and 2018) and again in late winter (Feb. 1 – 14th of 2018 and 2019) to estimate initial seed abundance and measure changes over the wintering period (Swanson 1978, Haukos and Smith 1993, Naylor 2002).

Soil cores were collected at each sampling location using a device with an internal diameter of 6 cm and a depth of 5 cm (141.4 cm^3). The sampling device (Photo 1) was constructed out of mild steel. The body of the sampling device was 56.5 cm long. The handle was a 0.9 m long tube (1.7 cm external diameter) with a cross bar (also 1.7 cm external diameter tubing) attached 17.5 cm from the top of the handle. A 6 mm diameter rod (Push rod, Photo 1) with a threaded end ran through the center of the T-shaped handle. We attached a rubber stopper to the end of this rod using a washers and nuts, allowing the user to push the entire soil core out of the device. The top of the rod was bent at 90˚ to prevent the rod sliding through the handle. All cores were collected in flooded wetlands, often in turbid waters, making visual inspection of sampling depth impossible. Sampling depth was controlled by two flanges (2.5 cm wide, 5 cm long) attached to opposite sides on the exterior of the tube, located 5 cm from the opening that was inserted into the soil (depth flanges, Photo 1). These external flanges contacted the surface of the soil when the body of the core sampling device reached a depth of 5 cm, providing tactile feedback to the investigator by increasing the force required to push the core sampler deeper into the soil. We chose not to use the more common circular flange due to the challenges it poses when collecting samples in heavily vegetated areas with microtopographic variability.

Immediately after the sampling device was lifted above the surface of the water, a sample bag (Ziplock™ freezer quart bag) was placed over the open end of the device to catch any material falling from the device. The investigator then used the rod to push the rubber stopper through the sampling tube, extruding the material collected in the device. Sample bags were then sealed and placed within a freezer within 8 hours of collection to prevent the deterioration of seeds until they could be processed. Prior to processing samples in the laboratory, samples were thawed until they reached room temperature (typically 24 hours). We measured soil volume post hoc to determine how the typical core sampling process used to assess waterfowl foods generates, or encounters, variation in sampling volume while also not impeding typical field sampling.

Due to time and cost constraints (often facing similar projects), we used simple volumetric displacement to measure soil core sample volume. We placed all but the bag's opening in water, then manipulated the sample to force out all air. We then placed the bag with containing the sample into a 1000 ml volumetric beaker and added water until the sample was fully submerged and the water level was at a measurement line. All samples were contained in the same type of plastic bag (Ziplock™ freezer quart bag). We then measured the water remaining in the volumetric beaker using a graduated cylinder. Subtracting the volume of water remaining from initial volume (sample plus water volume) provided the sample volume. All volumetric measurements were taken at ~ 23˚C to ensure consistent water densities. The sample was removed from the bag and placed into a 250 µm mesh sieve to allow water contained within the sample to drain. To increase the amount of water removed, a waterproof plate with a 2.5 kg weight was placed on top of the sample to provide consistent force as water was separated from the soil. The water that passed through the sieve was collected and measured in a graduated cylinder. The final soil volume was calculated by subtracting the volume of water that passed through the sieve from the total sample volume.

After taking all volumetric measurements, we washed samples through a series of sieves (mesh sizes of 4.00 mm, 2.36 mm, and 250 µm) to separate soil from seeds. Seeds and material too large to pass through the sieves were transferred to a 4 ml container and stored in a ~70% ethanol until they could be sorted. Samples were sorted by hand using a stereo dissecting microscope to aid in identification and removal of seeds. Seeds were placed in aluminum dishes, and dried at 80 °C until constant mass was achieved (typically 48 hours) before being weighed to the nearest 0.0001 g.

ANALYSIS

We analyzed the correlation between $\log_e$-transformed seed abundance and soil core volume using linear regression for each wetland type (managed wetland or tidal marsh) separately. We included season as a fixed effect and the interaction between soil volume and season (Fall [n = 606] or Winter [n = 264]). We used step-wise regression to identify the influence of each variable; we removed season (Tidal: Estimate = -4.911, SE = 3.348, p = 0.144, Managed: Estimate = -0.630, SE = 1.967, p = 0.749) and the interaction between season and soil volume (Tidal: Estimate = 0.928, SE = 0.644, p = 0.151, Managed: Estimate = 0.103, SE = 0.365, p = 0.778) as they were not significant. All models were fit using the core function (lm) in program R (R Core Team 2022). Model fit was assessed with package *performance* in program R (Lüdecke et al. 2021), to check the normality of residuals, homogeneity of variance, and multicollinearity between fixed effects and determine the quality of model fit.

We used our linear model results to determine the effect of soil volume on seed abundance estimates for managed wetland samples. We multiplied the slope of the line by the difference between the target soil volume (141.2 ml) and the measured soil volume for each sample to determine the portion of seed abundance described by the correlation between seed mass and soil volume.

We assumed that a substantial portion of the variation in soil core volume was caused by variation in sampling depth — despite our methodology to standardize sampling depth — so we also provided an equivalent soil depth for our soil volume estimates (which we felt were more accurate) using the equation for the volume of a cylinder [depth = volume / (π r^2)]. All cores were collected using the same equipment constructed from steel, preventing any fluctuations in core diameter during sampling over the course of the study.

Previous studies

We compiled data presented in five previous studies that quantified seed abundance in relation to soil depth, to determine how sampling depth can influence the proportion of total seeds captured. We only included studies which took place in wetland systems that experienced periodic dry periods, and enumerated seeds at defined depths (no germination studies were included). We compared results from five studies using percentage values (or calculated percentage values if they were not present) to determine how seeds were distributed across the first 10 cm of soil. Data were collected from presented figures and tables, Grillas et al. (1993) from Table 3 for only angiosperms, Bonis and Lepart (1994) from Figure 1, *Chara* sp. were excluded, Olmstead 2010 from Table 2.1, Evans-Peters 2010 from Table 3.1, and Nielsen et al. (2018) was averaged across all 6 wetlands sites presented in Table 1.

Two studies examined unmanaged tidal marshes in spring (Grillas et al. 1993, Bonis and Lepart 1994). These studies examined seed distributions to depths beyond 10 cm and all three found very little (Grillas et al. 1993) or no seeds at depths beyond 10 cm (Bonis and Lepart 1994), sample sizes were small ($n < 15$). Evans-Peters (2010) and Olmstead (2010) collected samples from managed wetland systems in autumn and had larger sample sizes (≥ 50). Nielsen et al. (2018) collected samples from six wetland systems in spring and summer. We compared three candidate models – linear, logarithmic, and cubic – to determine the best fitting line for these data. Each model included study as a random effect. We selected the candidate model using AICc as model structure was fixed.

RESULTS

Geometric mean seed abundance across all soil cores was 1.95 e^{-2} g (71.22 kg/ha), with an arithmetic mean of 4.73 e^{-2} g (SE =2.18 e^{-3}) (173.13 kg/ha, SE = 2.23). Soil core volume varied considerably, from 45 ml to 560 ml, with a target volume (based on the sampling device dimensions) of 141.2 ml. Of the 1128 soil cores collected, 36 samples had volumes less than the target volume range (141.2 ml ± 10%) and 1074 had larger volumes. The geometric mean of soil volumes collected from tidal wetlands was 189.22 ml, whereas in managed wetlands it was 220.93 ml. Despite using the same soil coring device for all samples, estimated depth varied considerably, from 2 to 20.4 cm (55 to 570 ml) with 90% of samples occurring between 4.2 and 12.7 cm (119.4 ml to 358.7 ml). The arithmetic mean of estimated sample depths in tidal wetlands was 7.1 cm (SE = 1.44 e^{-1}); in managed wetlands it was 8.3cm (SE = 9.20 e^{-2}).

The correlation between $\log_e$ seed abundance and soil volume was statistically significant in managed wetlands (n = 870) (Fig. 2.1), with a slope of 6.36 e^{-1} (SE = 1.48 e^{-1} , $p < 0.001$), but not in tidal wetlands (n = 258) (Fig. 2.2), with a slope of -5.52 e^{-2} (SE = 2.75 e^{-1} , $p = 0.841$) (Table 2.1).

Mean seed abundance in managed wetlands was 169.1 kg/ha (SE = 9.24). The application of the linear correction ($y = 5.36\ e^{-2} + -3.29\ e^{-3}\ x$) reduced the mean seed abundance to 135.9 kg/ha (SE = 7.43), indicating that seed abundance in managed wetlands was overestimated by 33.2 kg/ha or 19.6%, due to increased sampling volume (82.1 ml greater than expected).

The data gathered from prior studies followed a similar general trend where the largest proportion of seeds existed in the top 5 cm of soil (Fig. 2.3). The cubic model had the lowest AICc value (109.8) of the three candidate models (linear AIC = 124.1, quadratic AIC = 131.5). Confidence intervals ($\alpha = 0.9$) were largest at depths near 8 cm, and much smaller at lower depths (< 4 cm).

DISCUSSION

We measured the volume of 1128 soil cores collected over two wintering periods in Suisun Marsh and examined the relationship between seed abundance and soil volume. Despite our efforts to standardize sampling methods and the inclusion of external steel flanges (Photo 2.1) to facilitate consistent sample core depth sampling, the actual sampling depths varied considerably, from 2 to 20.4 cm. We found mean sampling volume was approximately 53% larger than intended and highly variable. Although standard soil core sampling methodology likely generated a significant portion of this variation, our process of measuring soil volume also likely introduced additional variability. All soil cores were collected from flooded wetlands and contained water. We could not definitively assign a source to this water, as it could have been in the soil or come from the water column. We attempted to standardize water content by placing samples into a 250 µm sieve with a 2.5 kg weight placed on top of the soil. This method was effective at removing water from samples, yet it also removed small soil particles and undoubtedly influenced soil compaction, likely biasing soil volume measurements negatively. Despite this concern we encountered significantly larger soil volumes than expected, suggesting that we collected samples that went deeper than our target depth of five centimeters.

We found a positive relationship between seed abundance and soil volume in managed wetlands (Fig. 2.1), whereas no trend was present in tidal wetlands (Fig. 2.2). Sampling season had no effect on seed abundance, nor did season have an interaction effect with soil volume on seed abundance. Seed abundance varied by 32% over the range of soil core volumes actually sampled in managed wetlands, despite our attempts to target the same depth (5 cm) and volume (141.2 ml). Applying the results of the linear model to our samples to correct for the volume bias showed mean seed abundance in managed wetlands was increased by approximately 20%. Due to low levels of observed seed abundance (< 225 kg/ha) this volume bias resulted in decreasing landscape level estimates of seed abundance by 33.2 kg/ha (169.1 – 135.9 kg/ha). However, if this same degree of bias occurred in rare areas with high seed abundances (e.g., over 1000 kg/ha) (Naylor 2002, Kross et al. 2008) the impacts could be substantial. The unintentional increase of sampling volume could have a large impact on both local and landscape level estimates of available seed resources.

The collection of soil cores in flooded wetlands at a constant depth can be challenging due to the inability of the investigator to see the core sampler interact with the soil. Instead, the investigator must rely on familiarizing the tactile feedback of the sampling device with reaching the intended depth, which is provided by flanges or another type of external feature on the core sampling device interaction with the surface of the soil. However, this tactile feedback varies due to soil saturation, compaction, soil type, and vegetation coverage, all of which were highly variable both within and among the wetland units sampled. These factors also influence how well soil is retained within the coring device; fully saturated, silty or sandy soils with low percentages of clay are harder to contain and transfer to storage bags. In these conditions, cores were often sampled to deeper depths which improved soil retention within the core sampling device. Typically, with these loose substrates, observers cover the end of the core sampler with a hand or other device when removing samples from wetland. Moreover, in heavily vegetated areas cutting through surface vegetation or roots requires significant force often leading to deeper soil cores unless the sampling device has a serrated edge (Swanson 1983).

Sampling depth and seed distribution

Prior studies examining wetland seed distribution across depth found a logarithmic relationship, where 79 to 95% of the cumulative total of seeds exist in the top 5 cm (Leck and Simpson 1987, Grillas et al. 1993). We found a cubic model best described the data we compiled from the literature (Fig. 2.3), following the more broadly applicable trend of seed abundance declining monotonically with depth (Shiferaw et al. 2018). Variation in how seeds are distributed across depth can be due to seed size and density, plant reproduction characteristics, time of year, and soil disturbance (Leck and Simpson 1987, Yenish et al. 1992, Shiferaw et al. 2018). These diverse factors prevent a broadly applicable percentage of cumulative seed to be assigned to any specific depth, even within similar habitat types. However, shallow target depths (< 5 cm) will experience larger fluctuations in the percentage of cumulative seeds collected as a result of variation in collected sample depth (Fig. 2.3). Sampling to a greater depth (≥ 8 cm) would limit the variation in total seeds collected as a result of variation in sampling depth, providing more consistency in seed abundance estimates.

Although we did not directly measure sampling depth, we estimated depth by dividing the volume measurements by a constant (πr^2). We found our estimated mean sampling depth was 8.3 cm, while our target depth was 5 cm. Given the trend between seed abundance and soil volume determined from our linear model, larger soil cores (likely a result of sampling beyond 5 cm) resulted in overestimating arithmetic mean seed abundance by 19.6%. Comparing our observed and linear corrected seed abundance estimates to the data in Fig. 3 suggests the managed wetlands we sampled had a cumulative seed abundance to depth curve most similar to the quadratic line, where the difference in seed abundance encountered at 5 cm compared to 8.3 cm would be 14.7%. These results were very similar to that of Evans-Peters (2010), which took place in managed wetlands with similar plant communities, disturbances, and collection periods to our study. The lack of a relationship between seed abundance and soil volume in the tidal marsh samples suggests a higher proportion of seeds occurred near the surface, similar to what Bonis and Lepart (1994) encountered in seasonal marshes within river delta, and Grillas et al. (1993) in estuarine seasonal marshes (Fig. 2.3).

Foraging pressure and management practices in managed wetlands likely influenced the relationship between seed abundance and sample volume (depth) we encountered in both wetland types. Foraging waterfowl can deplete seeds from wetlands at high rates (Nolet et al. 2006, Greer et al. 2009, Hagy and Kaminski 2015), and most sites had been flooded for over 30 days prior to sampling. It is likely that waterfowl and other granivores consumed seeds at or near the soil surface in managed wetlands, altering the observed distribution of seeds across the soil profile such that a higher proportion of seeds occurred at greater depths. Conversely, as most waterfowl species overwhelming prefer managed over tidal areas in the Suisun Marsh, a lack of waterfowl foraging in tidal marsh likely corresponds with higher proportions of seeds at or near the soil surface (Casazza et al. 2021). Moreover, managed wetlands within Suisun Marsh are often disked to create disturbance (limited to 20% of total acreage annually to conserve habitat for sensitive species), enhancing the germination of annual plants wetland managers are targeting. This soil disturbance also moves seeds deeper into the soil profile, typically to a depth between 2-10 cm (Yenish et al. 1992, Mohler et al. 2006, DeVictor et al. 2007). The seasonal flooding cycle, with limited flow-through, likely reduced seed export out of managed wetlands compared to tidal wetlands. As a result, seeds are retained in managed wetlands and exposed to disturbances that can move seeds to deeper depths more quickly than in tidal marsh, where infrequent soil disturbance combined with the semi-diurnal tidal cycle of Suisun Marsh reduces chances for seeds to move deeper in the soil profile (Leck and Simpson 1987, Cappers 1993, Neff and Baldwin 2005).

The implicit assumption when using soil core samples to assess waterfowl foods is that all seeds collected are available to waterfowl. The current practice is to estimate seed abundance only using the area sampled (i.e., the circular area of soil encompassed by the core sampler, πr^2); depth is only considered relevant regarding waterfowl foraging abilities and is treated as constant. Yet, neither foraging depth nor soil core sampling depth are constant. Foraging depth is mediated by several factors, including soil type, water depth, and overall food abundance (Santamaría and Rodríquez-Gironés 2002, Hagy et al. 2010, Smith et al. 2011), which rarely stay constant throughout a study location or study period, leading to additional variation in already ‘noisy’ data sets. Furthermore, although researchers attempt to collect soil cores at a fixed target depth, variation in core depth is inevitable, as we observed in our study. Efforts to evaluate sample volume and/or standardize to a constant depth using modified techniques or equipment, as well as post hoc assessments may improve seed abundance estimates. In our study where overall seed abundance was considered low, and the corresponding error in landscape level estimates of carrying capacity may be small, the bias was nonetheless substantially high. We caution that managers should consider seed abundance estimates from soil cores that do not correct for depth as highly variable and potentially imprecise, and accordingly be more conservative in assessing current carrying capacity for waterfowl in conservation planning efforts as our estimates of seed availability would have been biased 19.6% high without applying a volume correction factor.

CONCLUSION

The drawbacks of soil core sampling have been well described; they are tedious, costly, and time consuming (Stafford et al. 2011, Williams et al. 2014, Ringelman et al. 2015), it is challenging to determine optimal sampling sizes (Reinecke and Hartke 2005), and there are seed recovery biases due to sample processing (Reinecke and Hartke 2005, Hagy et al. 2011). Yet core sampling still provides a quantitative estimate of food available that can be applied across a variety of wetland habitats without requiring species-specific or regional calibration. If core sampling continues to be used for estimates of landscape level seed abundance, we suggest standardizing soil volume or soil depth via both experimental design (static core volume) and statistical analysis (adjusting seed abundance based on the sample's soil volume or soil depth) to acknowledge the potential error that can occur using standard sampling methods. Our examination of prior studies also suggests that sampling to a target depth between 8 and 10 cm would reduce the sensitivity of seed abundance estimates to fluctuations in depth, while still providing investigators the ability to adjust seed abundance estimates to accurately represent the seeds that fall within waterfowl foraging ranges.

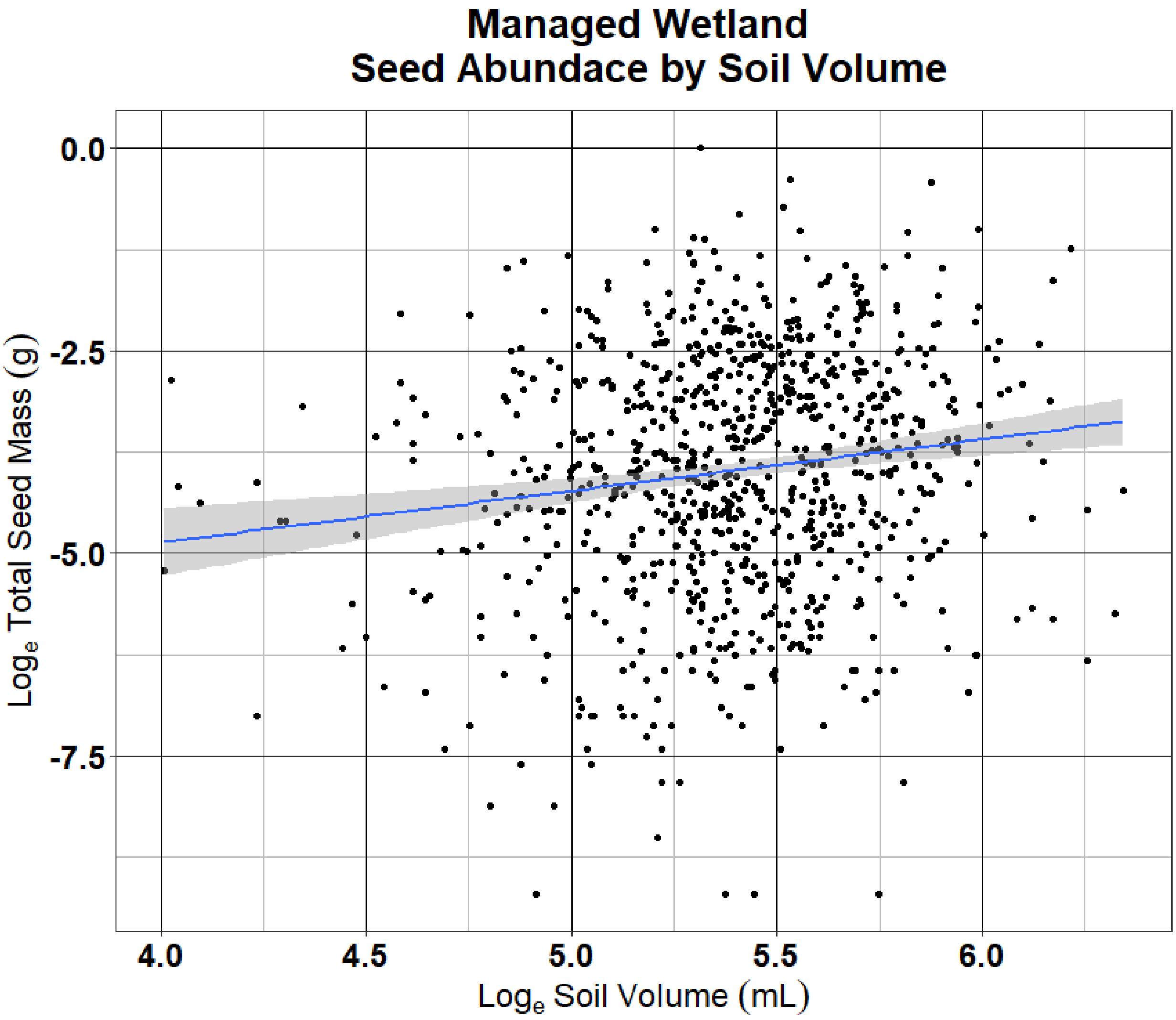

Figure 2.1: Log_e total seed mass (g) correlated with log_e soil volume (ml) for samples collected from managed wetlands in Suisun Marsh during November of 2017 and 2018 and February of 2018 and 2019. The linear regression line is shown in blue with the gray shaded area representing the 95% confidence interval.

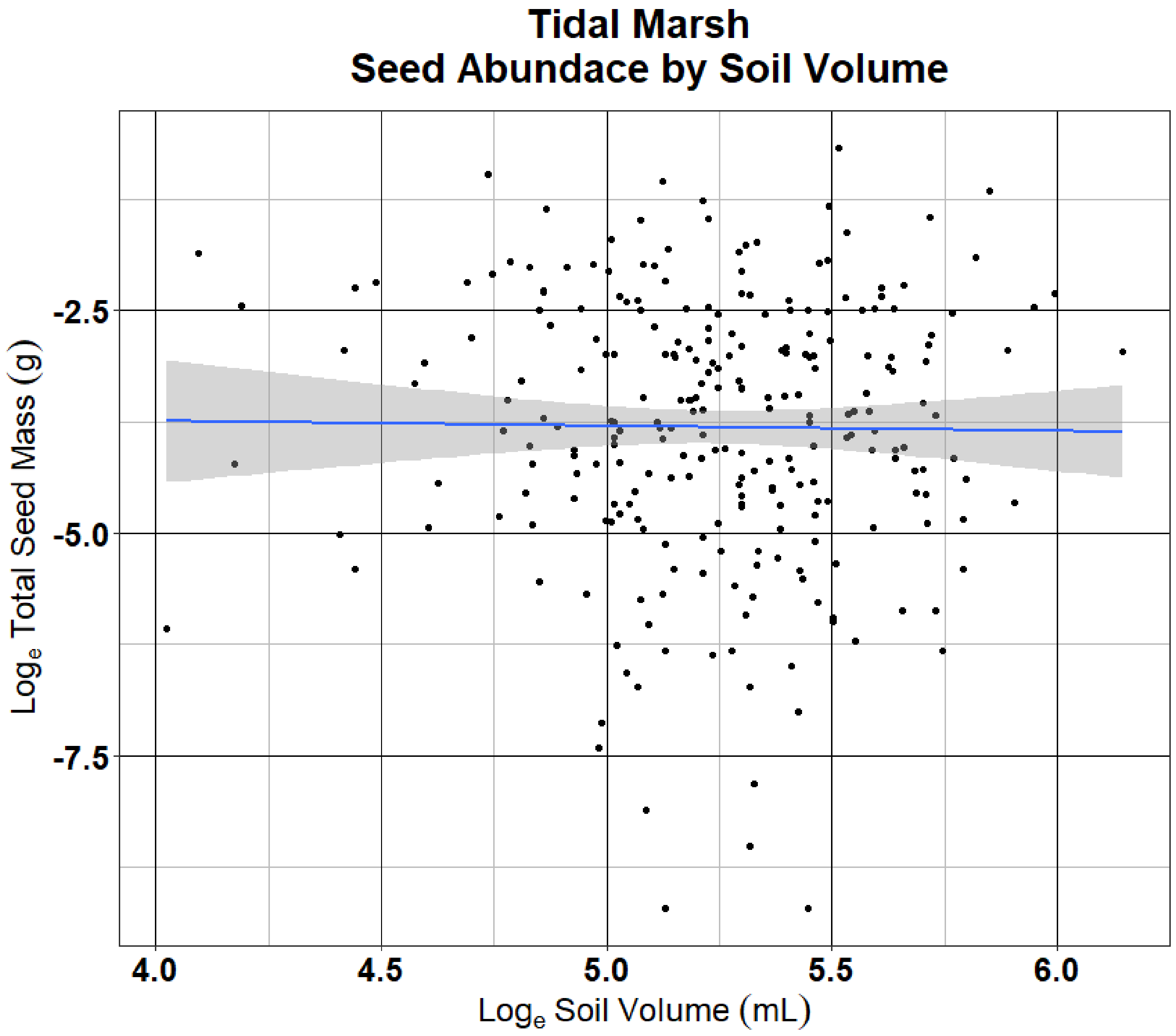

Figure 2.2: Log$_e$ total seed mass (g) correlated with log$_e$ soil volume (ml) for samples collected tidal marshes in Suisun Marsh in November of 2017 and 2018 and February of 2018 and 2019. The linear regression line is shown in blue with the gray shaded area representing the 95% confidence interval.

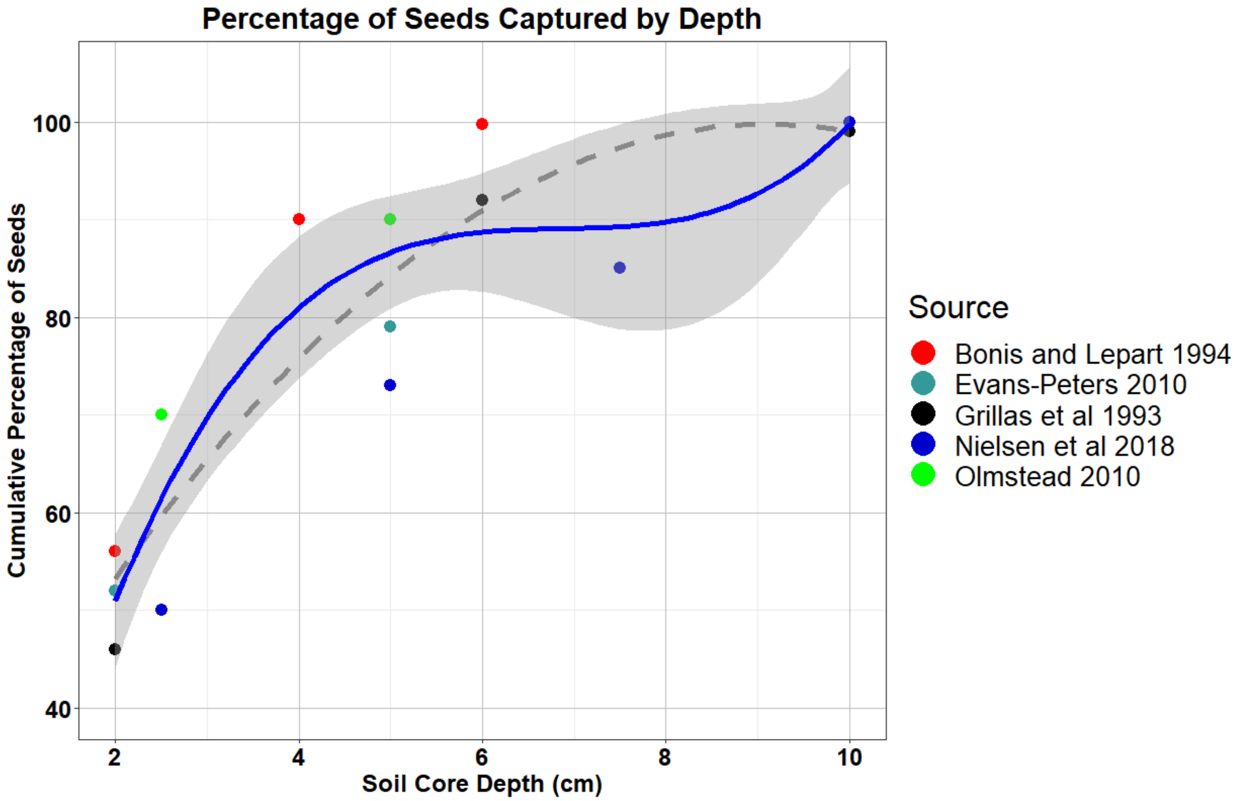

Figure 2.3: Cumulative percentage of total seeds captured by soil core depth (cm) from various studies. Two lines were fit to the data with source as a random effect. The blue line shows cubic fit (AIC = 101), shaded area shows 90% confidence interval. The gray dashed line shows the quadratic fit (AIC = 119).

Table 2.1: Linear regression model results of $\log_e$ seed abundance and $\log_e$ soil volume for both managed and tidal wetland samples.

Managed Wetland Linear Model

Coefficients	Estimate	Std. Error	t value	Pr(>|t|)
Log_e Seed Abundance (Intercept)	-7.41	0.80	-9.26	< 2e-16
Log_e Soil Volume	0.64	0.15	4.30	1.93E-05

Residual standard error: 1.478 on 868 degrees of freedom
Multiple R-squared: 0.02083, Adjusted R-squared: 0.0197
F-statistic: 18.46 on 1 and 868 DF, p-value: 1.929e-05

Tidal Wetland Linear Model

Coefficients	Estimate	Std. Error	t value	Pr(>|t|)
Log_e Seed Abundance (Intercept)	-3.52	1.45	-2.44	0.0155
Log_e Soil Volume	-0.06	0.28	-0.20	0.8413

Residual standard error: 1.503 on 256 degrees of freedom
Multiple R-squared: 0.000157,Adjusted R-squared: -0.003749
F-statistic: 0.0402 on 1 and 256 DF, p-value: 0.8413

Photo 2.1: Soil core sampling device constructed by the author

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CHAPTER 3 – Environmental and Wetland Management Influences on Seed Occurrence and Abundance in Seasonal Wetlands within the Suisun Marsh

ABSTRACT

The number of non-breeding waterfowl within the Suisun Marsh has dropped far below conservation objectives over the last decade. A recent evaluation found waterfowl food resources (primarily seeds) were less than half of what was predicted to be available in seasonal wetlands. Although prior research has found relationships between the occurrence of wetland plants (which produce the majority of seeds waterfowl consume) and wetland management actions, no direct evaluation of environmental and management practices using seed abundance has been conducted. We assessed 730 soil cores collected from 71 managed wetlands to determine how seed occurrence and abundance was correlated with region (habitat zone), salinity, wetland management infrastructure, soil type, disking, and overall management intensity. The occurrence of several species was correlated with salinity, management intensity, and disking. The best predictor of total seed abundance was habitat zone, which is defined by shared physical factors known to impact vegetation growth and production. Our results indicate that management can influence the occurrence and composition of important food plant species, but location had the greatest influence on the overall abundance of seeds in managed wetlands. These regional differences in seed abundance have implications for tidal restoration efforts, as the loss of seasonal wetland acreage within more productive regions could have a disproportionate impact on total food availability. Moreover, our data suggest that current management practices cannot enhance wetland conditions to dramatically increase seed abundance.

INTRODUCTION

The Central Valley of California is a critical area for waterfowl in the Pacific Flyway, supporting six million ducks and geese each winter, despite having lost over 90 percent of the area's historic wetlands (Gilmer et al. 1982, Mitsch and Gosselink 2007, CVJV 2020). Waterfowl have been sustained through habitat management efforts focused on meeting the energetic needs of overwintering populations (USFWS 1986, Williams et al. 2014, CVJV 2020). Seasonal wetland management techniques have enhanced the abundance of important food plants, the seeds of which provide essential carbohydrates and nutrients during fall and winter. The flooding of post-harvest agriculture fields – primarily rice – has increased access to additional food resources such as waste grain over winter (Fredrickson and Taylor 1982, Reinecke et al. 1989, Eadie et al. 2008, Petrie et al. 2016, CVJV 2020). However, increased frequency and duration of droughts in the Central Valley have reduced seasonal wetland acreages, seed abundance, and winter flooded rice over the last decade (Petrie et al. 2016, Matchett and Fleskes 2018, Matthews et al. 2022). Waterfowl populations are likely to decline throughout California as continued water reductions limit winter flooding and impact the growth of food resources that waterfowl rely on, unless improved wetland management techniques offset this loss (Petrie et al. 2016, Wilson et al. 2022).

Suisun Marsh is a complex of tidal marsh and managed seasonal wetlands located at the outlet of the Sacramento–San Joaquin River Delta (Delta) and provides a powerful example of how declining waterfowl populations may be correlated with reductions in food abundance (SMP 2013, Moyle et al. 2014). Unlike other wetland basins in California, Suisun Marsh contains no agriculture and supports the energetic needs of waterfowl with food resources produced exclusively in seasonally managed wetlands (Burns 2003, CVJV 2020, Casazza et al. 2021). An evaluation in 2017-2018 found the abundance of wetlands seed within Suisun Marsh was approximately 168 kg/ha, half of the seed abundance that was projected to be available (CVJV 2020, Chapter 1). Mid-winter surveys in the Suisun Marsh over the last decade revealed that waterfowl numbers have declined dramatically and are currently 50% below conservation objectives (Moyle et al. 2014, CDFW 2020, CVJV 2020). The reduction of food resources for waterfowl is likely to be exacerbated as 15% (2,500 ha) of the Suisun Marsh's seasonal wetlands are to be converted to tidal marsh over the next thirty years, and these tidal wetlands contain little to no food resources utilized by waterfowl (subfamily Anatinae) (Burns 2003, SMP 2013, Chapter 1). Given these multiple challenges, improved wetland management will be needed to restore waterfowl populations within the Suisun Marsh and compensate for the loss of seasonal wetlands due to wetland conversion (SMP 2013).

Improving wetland management techniques requires evaluating how environmental and management variables influence seed production. Current management recommendations within Suisun Marsh are founded on the results of studies examining the effect of salinity on vegetation composition (Mall 1969; Rollins 1973, 1981). However, to date there has not been a direct evaluation of how management factors or environmental conditions influence seed abundance. Our goal was to answer two questions about wetland management in Suisun Marsh: (1) Are higher salinities associated with lower abundances of waterfowl-preferred seeds? and (2) are management actions (such as disking) increased the abundance of waterfowl-preferred seeds? To address these questions, we used field samples to estimate the abundance of seeds in 71 managed wetland units, across all eight regions of the Suisun Marsh, and over two winter periods. Using these data, we conducted the first comprehensive assessment examining how seed abundance and species occurrence were correlated with salinity (CDEC 2017), water management infrastructure (Chappell et al. 2018), soil types (SURRGO), extent of disking, and management intensity. Our results help to evaluate the effectiveness of current management practices and provide insight into how the composition and abundance of food resources for waterfowl might be influenced by changing environment conditions.

STUDY SITE

The majority of food resources used by waterfowl in the Suisun Marsh occur in the 11,635 ha of managed seasonal wetlands, approximately 75% of which are privately owned and managed, while the California Department of Fish and Wildlife (CDFW) manages the remainder (Gill and Buckman 1974, Burns 2003, SMP 2013, Chapter 1). Levees and water control structures isolate managed wetlands from tidal inundation, allowing managers to manipulate flood regimes (Barthman-Thompson et al. 2005). These seasonal wetlands receive water from brackish sloughs and channels, typically remaining flooded between October and February (Rollins 1973, 1981, Barthman-Thompson et al. 2005). Classic wetland management techniques such as irrigation, disking, mowing, burning, and the use of herbicides are used to promote favored plant species and reduce undesirable species (Fredrickson and Taylor 1982, Rollins 1981). In addition to these seasonal wetland management techniques, there is a large focus on maintaining low soil salinities (Fredrickson and Taylor 1982, Barthman-Thompson et al. 2005). Wetland managers use leaching cycles, where low salinity water (often in early spring) is used to flood wetlands, saturate soils, and draw out salts before being drained back into neighboring sloughs and channels (Rollins 1973, 1981). Yearly variation in water quality, and regional diversity within Suisun Marsh, requires managers to consider a range of factors (water quality, ability to move water, current plant community, impacts to other species, costs, etc.) when attempting to implement wetland management actions.

The State Water Resources Control Board established salinity standards for channel water through the Water Right Decision 1485 in 1978 to maintain wetland conditions required for waterfowl plant food production (SWRCB 1978). In 1988, salinity control gates were constructed on the eastern part of Montezuma Slough (a major waterway running through much of Suisun Marsh); these gates use tidal action to draw low salinity water into Suisun Marsh (Sommer et al. 2020). Water salinities within the marsh vary spatially and temporally; the lowest salinities occur in February and increase throughout spring and often peak in late summer or early fall (Barthman-Thompson et al. 2005, Sommer et al. 2020). Two factors combine to create a north-east to south-west salinity gradient across Suisun Marsh.

There are two spatial salinity gradients across the Suisun Marsh, east-west and north-south. The east-west gradient varies in response to freshwater flows from the Delta to the east interacting with saltwater flows from the San Francisco Bay to the west (Barthman-Thompson et al. 2005, Sommer et al. 2020). The north-south salinity gradient is mediated by perennial and seasonal creeks – whose flows are influenced by rainfall – which feed into the north marsh, resulting in lower spring salinities in the north marsh (DWR 1995, Barthman-Thompson et al. 2005). Variation in salinities, a range of elevations, and the effects of management activities result in diverse wetland plant communities present within the marsh (Rollins 1981, Barthman-Thompson et al. 2005, Moyle et al. 2014).

METHODS

We used seed abundance data from Chapter 1. We collected soil cores (n = 730) from 71 managed units during the fall (late October, early November) in two consecutive years. Soil cores (diameter of 6cm, depth of 5cm) were washed through of series of sieves (4.00 mm, 2.36 mm, and 250 µm) to separate seeds from other material. Seeds were then identified, dried to constant mass at 80˚C and weighed to the nearest 0.0001 g (see Chapter 1 and 2 for details). The primary species encountered were, *Atriplex* sp., *Chenopodium* sp., *Bolboschoenus* sp., *Cotula coronopifolia*, *Crypsis schoenoides*, *Echinochloa crus-galli*, *Polygonum aviculare*, *Polygonum argyrocoleon*, *Salicornia pacifica*, and *Stuckenia pectinate*. We also found *Ruppia maritima*, *Cicuta maculate*, and *Cuscuta salina* in our samples but did not include them in our analysis due to infrequent occurrence and limited management value. We grouped *Atriplex* and *Chenopodium* due to the challenges in separating the two genera using only seed characteristics.

We explored relationships between our estimates of seed abundance and several management and environmental covariates, including; habitat zone, spring water salinity, soil type, drain speed, disking extent, and management intensity. We did not include mowing in our list of management variables, as it often occurs in fall to reduce standing vegetation structure. Similarly, we did not include burning because it is applied opportunistically across small areas (due to regulations required to minimize impacts to the peat soils present in Suisun Marsh and surrounding metropolitan areas).

Environmental and management variables

Habitat zones. The Suisun Marsh Resource Conservation District (SRCD) has defined eight habitat zones (Fig. 3.1), which are regional grouping of managed wetlands that share similar water sources. SRCD has outlined best management practices for each habitat zone, including target plant species that are best suited to the conditions present in each habitat zone, as well as guidance to adjust management under drought conditions or challenges with moving water. Despite sharing similar geographical locations and water supplies, considerable variation exists within each zone due to differences in elevation, management histories, and water control infrastructure.

Soil type. We assigned each soil core sample a soil type by referencing collection locations with soil survey data provided by the Natural Resources Conservation Service (NRCS) and stored on the Soil Survey Geographic (SSURGO) database (available at https://websoilsurvey.sc.egov.usda.gov/). Soil types represent the soil "map unit", which are named according to the taxonomic classification of the dominant soils. We used ArcGIS to spatially join soil types to each of our sampling locations. All of our sampling locations were contained within the Solano County, California (CA095) soil survey which was mapped using a scale of 1:24,000. Samples occurred within one of nine soil types (presented in descending order of frequency): Tamba mucky clay, Reyes silty clay, Joice muck (including the clayey subsoil), Valdez silty clay loam, Suisun peaty muck, water (flooded at the time of evaluation), tidal marsh, and Alviso silty clay loam. Most soil types we encountered were strongly acidic (pH 4.6-5.5) in the first 20 cm (Reyes, Joice, Suisun, and Tamba).

*Water salinity***.** We collected salinity data from nine California Data Exchange Center (CDEC) monitoring stations (Beldon Landing (BDL), Blacklock (BLL), Goodyear Slough (GYS), Hunter Cut (HUN), Ibis (IBS), Montezuma Slough (MSL), National Steel (NSL), Volanti (VOL), Sunrise Club (SNC)) (CDEC 2017). We assigned each wetland unit we sampled a CDEC station which was located nearest the water intake. The distribution of CDEC stations throughout the main waterways within Suisun Marsh resulted in some habitat zones containing multiple stations. Three habitat zones were covered by a single water monitoring station; zone 3 (VOL), zone 4 (BLL), and zone 7 (MSL). We calculated mean monthly salinities for each station by averaging daily high tide salinities using 15-minute data to best capture the water salinities being applied to wetlands in spring. We only included high tide salinities since this is when forcing pressures are highest, resulting in the largest water volume intake for wetland units. The twice daily high tide levels were identified using “river stage level” (in feet) readings that were paired with salinity data for each of the 9 CDEC stations. We identified high tide values with the R package *quantmod* and used the function *findPeaks* (Ryan and Ulrich 2022). We visually inspected graphical outputs for outliers and to ensure peaks were accurately identified. We then averaged salinity values associated with the identified peaks across each month.

*Drain speed***.** Water management infrastructure is a key component for successful wetland management. Conversion from natural tidal marsh to agriculture and seasonal wetlands has resulted in subsidence in many areas of the marsh (Barthman-Thompson et al. 2005, Moyle et al. 2014). Combined with topographical variation and wide distribution of upland areas within wetland management units, the effective conveyance of water into and out of managed wetlands is highly variable. In 2018 an assessment of water control structure elevations, pipe diameters, and target water levels was used to inform models which determined pond draining rates in days (Suisun Marsh Improvement Assessment, Chappell et al. 2018). These data (specifically, days to drain to one foot below target water levels) provided evaluations of the ability to drain wetland management units quickly, a key management function for effective leaching cycles. We assigned each sample a wetland unit drain speed (days to drain one foot) based on sampling location.

Disking. The extent of late summer disking was assessed by examining individual habitat management plans which landowners file with SRCD. Disking extent is voluntarily limited to 20% of total wetland unit acreage per year to reduce impacts to salt-marsh harvest mouse populations (SMPP 2013). Disking extent was assessed for the year prior to sampling, as spring disking would impact vegetation growth in the season following drawdown. We used percentage of disked acreage (acres disked divided by total wetland unit acreage) given the variable size of wetland units.

Management intensity. We used a qualitative evaluation (scored between one to four, using 0.5 increments) to assess overall management intensity due to the variety of wetland management techniques which often vary by region. A score of one corresponds to passive management, where the minimum effort of moving water to ensure a wetland was flooded during winter was undertaken. A score of four was given to wetland units in which an extensive effort was undertaken to improve both germination and seed production for target plant species, along with efforts to control undesirable plants, and these management actions were implemented every year. Management scores for private lands were determined by averaging responses across four SRCD water managers, who have practical experience working directly as habitat managers and provide guidance to private habitat managers throughout Suisun Marsh. State-owned and managed wetland units were assigned management scores by interviewing the state wildlife biologist for the Wildlife Areas contained within the Suisun Marsh.

ANALYSIS

We used a linear mixed model to determine if log-normalized total seed abundance (ln(1+ kg/ha)) was correlated with habitat zone, soil type, management intensity, average spring salinity, extent of discing in the prior year, and the number of days required to drain the wetland unit (by one foot of water depth). We included wetland unit as a random effect to capture the spatially clustered sample design. Only some wetland units had drain speed data (n = 416), so we first tested if drain speed had a statistically significant influence on total seed abundance. We found no strong evidence that seed abundance was correlated with wetland unit drain speed (estimate = - 0.024, SE = 0.016, df = 37, *p* = 0.146) so we excluded drain speed from our model to allow use of the full data set (n = 730). We made pairwise comparisons (estimated marginal means) of the categorical variables, habitat zone and soil type, to determine if levels within these variables were significantly different from one another using the program R package *emmeans* (Lenth 2022). Linear models were constructed using *lmerTest*, an extension of the *lme4* (Bates et al. 2015) package which provides *p* values for tests of fixed effects and approximate degrees of freedom using Satterthwaite's method in program R (Kuznetsova et al. 2017).

We used generalized linear models to test species-specific responses (logit transformed presence/absence data) to normalized values of management intensity, disking extent, and average spring salinity. We did not include the categorical variable of drain speed, soil type or habitat zone due to limited sample sizes and poor model fit. Generalized linear models were constructed using the base R function (citation). We assessed models for linear relationships, normality of residuals, homogeneity of variance, multicollinearity, and normality of random effects if present, using the R package *performance* (Gotelli and Ellison 2004, Lüdecke et al. 2021).

RESULTS

We analyzed estimates of seed abundance using 730 samples collected in two consecutive years (2017 = 420, 2018 = 310) during late October and early November, shortly after wetlands were flooded (Fig. 3.1). Mean seed abundance was 146.7 kg/ha over all samples, with no significant difference between sampling years (estimate = 0.00, SE: 0.42, df = 92, p = 0.99). We found that seed abundance varied by habitat zone; the highest mean seed abundance was in zone 3 (483.4 kg/ha) while the lowest was in zone 1 (77.0 kg/ha) (Fig. 3.2). Species occurrence also differed by habitat zone.

Habitat zone 4 contained the highest occurrence for *Echinochloa crus-galli* (found in 3.8% of samples), while *Crypsis schoenoides* occurred most frequently in zone 3 (22.0%). Overall, the most common species across all samples were *Sesuvium verrucosum* (73.4% occurrence), *Bolboschoenus* sp. (50.3% occurrence), and *Schoenoplectus* sp. (38.4% occurrence).

Most of our samples were collected from units with one of three soil types (Tamba mucky clay (29.2 %). Reyes silty clay (22.9 %), and Joice muck (16.9%)) while other soil types were less common (Valdez silty clay loam (9.9 %) Suisun peaty muck (9.6 %), tidal marsh (3.0 %), Joice muck clayey subsoil (2.5%), Alviso silty clay loam (0.4 %)). We also collected samples (n = 42) from areas which the soil survey classified as water, likely due to the soil survey encountering flooded areas being unable to evaluate the soils. Habitat zones 5, 6, and 7 had similar proportions of samples from the same soil types, while the remaining habitat zones were comprised of distinct combinations of soil types (Fig. 3.2). All soil types had similar seed abundance in our linear mixed model, as indicated by pairwise comparisons of means (Table 3.1).

We observed a mean of 4.7% of wetland unit acres being disked in the year prior (either 2016 or 2017 depending on sampling collection year) to our sampling. There were differences in disking extent by zone, with zone 3 having the greatest mean extent (13%) while no disking occurred in zone 8 (permanent water) (Fig. 3.2). We did not find any significant correlation between total seed abundance and disking in the year prior (-0.01 ± 0.02, df = 116, *p* = 0.68) (Table 3.1). However, there was a significant increase in odds of occurrence four food plant species (*Atriplex*/*Chenopodium* sp., *Crypsis schoenoides, Echinochloa crus-galli, Sesuvium verrucosum*) as disking extent increased, while the odds of occurrence declined for only one species *Polygonum aviculare* (Fig. 3.4)

Mean management intensity was 2.3, with zone 3 exhibiting the highest level of management (3.0), and zone 2 having the lowest level (1.8). Management intensity was not significantly correlated with total seed abundance (0.07 ± 0.12, df = 102, *p* = 0.55) (Table 3.1). However, higher management scores were associated with increased odds of occurrence for *Cotula coronopifolia*, *Polygonum argyrocoleon*, and *Polygonum aviculare* but reduced odds of occurrence for *Schoenoplectus* sp., *Stuckenia pectinate*, and *Typha* sp. (Fig. 3.4).

Average high tide spring salinity varied between 0.33 to 6.58 mS with a mean of 2.87 mS. Monitoring stations GYS and IBS reported the highest mean spring salinities (3.78 mS, 3.38 mS, respectively), while NSL and MSL reported the lowest (1.33 mS, 0.79 mS). The highest maximum salinity values occurred in June at the IBS (10.26 mS) and HUN (10.37 mS) stations. Habitat zone 1 (Western Marsh, Goodyear Slough) exhibited the highest observed mean salinity in spring (4.3 mS), while zone 7 (Southern Marsh, heavily influenced by SMSCG) exhibited the lowest mean (0.8 mS). We did not find a correlation between total seed abundance and average spring high tide salinity (0.04 ± 0.05, df = 248, *p* = 0.42) (Table 3.1). The odds of occurrence of one species, *S. pectinate,* increased with salinity levels, while the odds of occurrence for *Atriplex / Chenopodium* and *E. crus-galli*, declined (Fig. 3.4).

DISCUSSION

Seasonal wetlands within Suisun Marsh are managed using a range of techniques to encourage the growth of plants preferred by waterfowl while concurrently limiting the impact of environmental conditions such as salinity, which vary by region (Barthman-Thompson et al. 2005, Moyle et al. 2014). We found the occurrence (presence) of several species was correlated with spring salinity, management intensity, and disking, similar to results from previous studies examining vegetation composition in the marsh (Rollins 1973, 1981). However, we found no correlation between total seed abundance and several environmental and management factors including drain speed, disking, average spring salinity, soil type, and overall management intensity. Instead, the habitat zone/region within the marsh was the best predictor of total seed abundance in managed wetlands. Our results indicate that management can influence the occurrence and composition of important food plant species, but that location in the marsh has the greatest influence on the overall abundance of wetland seeds. These regional differences have implications for tidal restoration efforts, as the loss of seasonal wetland acreage within more productive regions could have a disproportional impact on total food availability. Moreover, our data suggest that current management practices cannot further enhance conditions in seasonal wetlands to dramatically increase seed abundance.

Habitat zones in the Suisun Marsh are defined geographically with an emphasis on shared water sources. These, in turn, strongly coincide with several common physical factors, such as salinity and pond elevations (which influence flood and drain speeds), which are known to impact vegetation growth and production (Rollins 1981, Fredrickson and Taylor 1982, Mushet et al. 1992, Chappell et al. 2018). We found the highest seed abundance in the northern most habitat zones (3 and 4), which typically have high elevations (fast flood and drain speeds) and low water salinities. Although seed abundance was similar among habitat zones, species composition differed. Zone 3 had the highest proportion of C. schoenoides and *Polygonum aviculare*, while zone 4 had higher abundances of *Echinochloa crus-galli* and *Polygonum argyocoleon*. The three habitat zones (5, 6, and 7) comprising the central and eastern parts of Suisun Marsh had similar seed abundances and species compositions to one another. The south and west zones (1 and 2) – which experience high salinities and typically drain slowly, or fail to drain completely, due to low pond bottom elevations – had the lowest seed abundances. Habitat zone 8, which is comprised entirely of permanently flooded managed wetlands, contained much higher rates of occurrence for emergent species (*Typha* sp., *Schoenoplectus* sp.), and *Stuckenia pectinate*, a submergent species. Overall, there was a general trend of declining seed abundance along a north-south gradient, and to a lesser extent, an east west gradient, corresponding with increasing salinity gradients (Barthman-Thompson et al. 2005). Except for the southwestern zones (1 and 2), the variance in seed abundance within habitat zones was large, suggesting that even within zones, a diversity of conditions exist.

Water salinity has been an ongoing concern to wetland managers in the Suisun Marsh for decades due to the expansion of upstream water diversions and increased periods of high salinity, leading in turn to reduced growth and production of waterfowl foods (Rollins 1973, Mushet et al. 1992). We did not find a strong correlation between salinity and total seed abundance, but we did observe the occurrence of two waterfowl-preferred plant species (*Atriplex* / *Chenopodium* sp., *E. crus-galli*) declined as salinity increased. The lack of a stronger effect of salinity is likely due to the low salinities which coincided with our sample collections. Our first year of sampling followed the wettest water year on record for the Northern Sierra Precipitation 8-Station Index, at 94.7 inches, or 178% of the mean precipitation, while our second year occurred after a water year that saw 79% of normal precipitation. As a result, we observed a maximum average slough salinity of 10 mS/cm in June, yet during drought periods salinity levels can exceed 15 mS/cm in May, with pond salinities typically 2-10 mS higher (Barthman-Thompson et al. 2005). The impacts of salinity on vegetation are most pronounced during drought years, as increased evaporation in the ponds combined with reduced freshwater availability increase salt concentrations within the soil following summer dewatering (Rollins 1981, DWR 2001). Although many of the plant species within managed wetlands are adapted to brackish conditions, severe drought can elevate salt concentrations to levels which kill vegetation and prevent germination (Rollins 1981, DWR 2001, JFP 2022). Managers use leaching cycles to reduce soil salinity levels in spring, but their effectiveness depends on access to fresh water (Rollins 1973, DWR 2001).

The implementation of best management practices to produce critical food resources for waterfowl requires consideration of the effort/expense a manager is able to expend (Rollins 1981, Fredrickson and Taylor 1982). To determine the effect of management effort relative to other factors, we used a qualitative score of overall management intensity. As with other factors, such as salinity and disking, we did not find a statistically significant correlation between total seed abundance and management intensity score. We did find higher management intensity scores corresponded with increased occurrence of some preferred plant species, and the reduction of undesirable plant species (from a food value perspective) (Fig 3.4). These results indicate a higher level of management effort can increase the potential availability of preferred food species even if the physical conditions may not be optimal. However, even extensive management actions do not appear capable of overcoming drought and other physical conditions in the marsh, and consequently, the more productive regions can be expected to have higher seed abundances - even with a lower intensity of management - than regions with greater management challenges and poorer conditions for preferred plant species.

Increased disking was correlated with increased occurrences of many waterfowl-preferred foods (*Atriplex / Chenopodium* sp., *C. schoenoides, E. crus-galli,* and *S. verrucosum*). Disking is a commonly used technique to introduce disturbance to seasonal wetlands and results in a shift in species composition (Fredrickson and Taylor 1982). Most preferred species are annual plants, which respond well to disturbance. Moreover, salinity-tolerant perennials (*Distichlis spicata, Salicornia* sp., and *Schoenoplectus* sp.) will outcompete annuals over time without some disturbance (Rollins 1981, Fredrickson and Taylor 1982). Disking, which incorporates standing vegetation into the soil, is used to maintain ratios of open water to standing vegetation (often 50:50, e.g., hemi-marsh) which are favored by waterfowl (Kaminski and Prince 1981, Masto et al. 2022). Due to concerns for threatened and endangered species, the extent of disking in the Suisun Marsh is voluntarily limited to a maximum of 20% of the total wetland acreage each year. Although this self-imposed limitation may reduce the total number of acres disked, thoughtful application over multiple years could provide multi-species benefits which outweigh the benefits of a more extensive approach.

We found no significant correlation between total seed abundance and soil type, although our linear model estimates of seed abundance in mucky soils (Joice, Suisun, and Tamba) were higher than silty soils (Reyes and Valdez). A previous study found no consistent association between soil water salinity and soil type (DWR 2001), and it is likely that other factors have a larger effect on seed production. The effects of soils could be masked by the relatively large impacts of other factors, such as salinity. Wetland drain speed influences wetland salinities and the ability of managers to implement irrigations and leach cycles; however, limited data prevent us from conducting a more detailed assessment with seed abundance and species occurrence (Rollins 1973).

CONCLUSION

The Suisun Marsh comprises 15% of the seasonal wetlands in the Central Valley and is protected in perpetuity (SMP 2013, Moyle et al. 2014, CVJV 2020). Although overall seed abundance was low, some regions contained very productive wetlands. Maintaining and improving these productive regions is key to supporting wintering waterfowl, as their loss will be extremely difficult to recover through enhancement to other regions. Although management may not be able to overcome environmental conditions, it does increase the presence of waterfowl-preferred foods. Recent work has indicated that improving aging wetland infrastructure will increase the effectiveness of many management actions (Chappell et al. 2018). Reductions in flood and drain times can improve seed production by increasing the effectiveness of irrigations and leach cycles (Chappell et al. 2018).

Projected increases in the severity and frequency of drought throughout the Central Valley are likely to lead to reductions in water availability in spring and winter, further exacerbating declines in abundance and quality of the remaining wetland habitats (Diffenbaugh et al. 2015, Petrie et al. 2016, Matchett and Fleskes 2018). The Suisun Marsh has provided critical habitat for waterfowl in drought years due to its location at the outlet of the Sacramento–San Joaquin River Delta. However, water salinities are increasing due to frequent droughts, resulting in increased salt intrusion from the San Francisco Bay (Chappell et al. 2018, Durand et al. 2020, Beakes et al. 2021). Increased salinity levels in Suisun Marsh will likely further reduce already low seed abundances and drive a shift in plant community composition in seasonal wetlands (Rollins 1981, Chapter 1). These forthcoming and growing challenges highlight the critical need to enhance seasonal wetlands within the Suisun Marsh to support the potential of even greater wintering waterfowl use in the face of declining wetlands in neighboring basins.

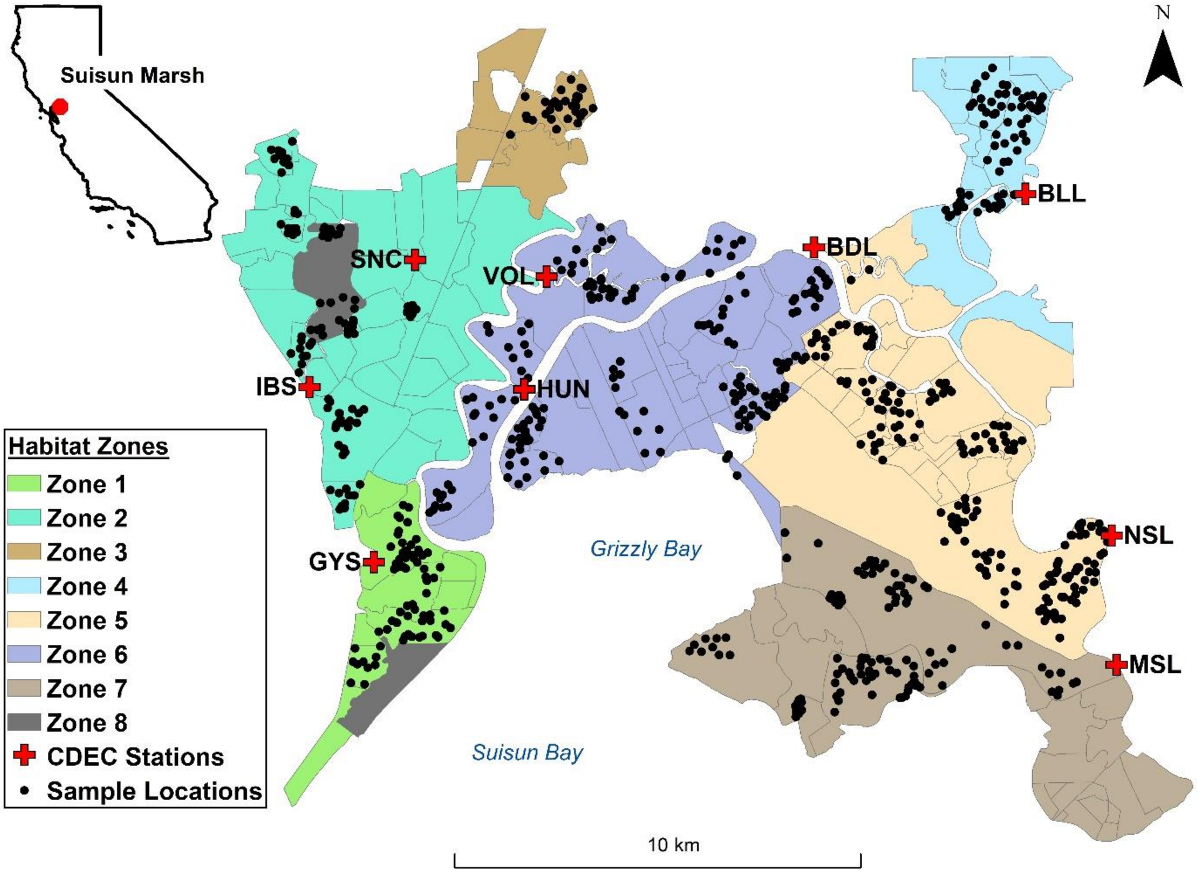

Figure 3.1: Sampling locations (black circles) within the eight habitat zones defined by the Suisun Resource Conservation District. The California Data Exchange Center (CDEC) water monitoring stations are shown as red crosses with each site’s three letter acronym.

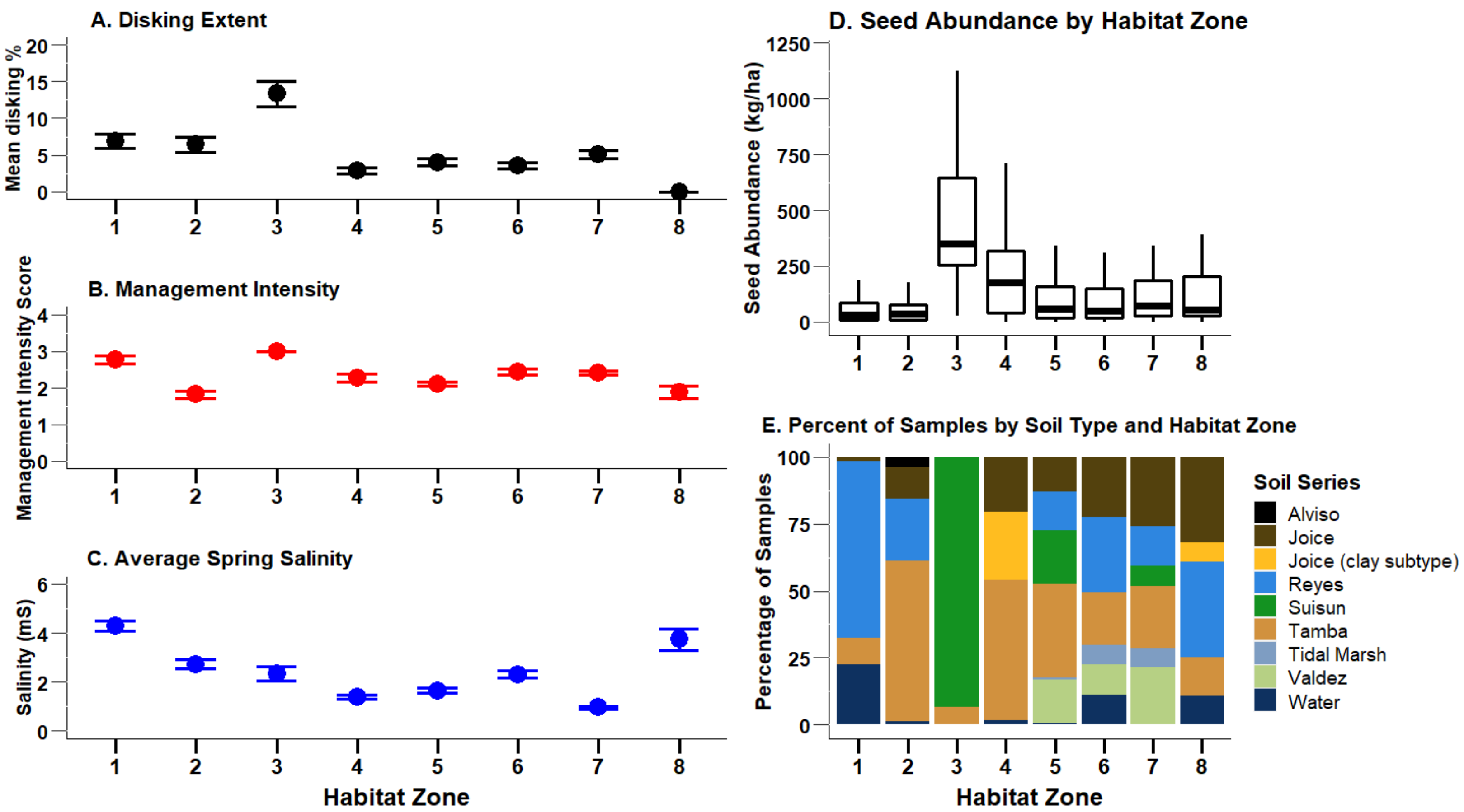

Figure 3.2: Disking extent (**A**), Management intensity score (**B**), and high tide salinity in spring (**C**) means by habitat zone are represented by circles, and standard errors are shown as vertical bars. Seed abundance (kg/ha) by habitat zone is presented as a box plot (**D**), and the percentage of samples located within each of the primary soil types are presented by habitat zone (**E**).

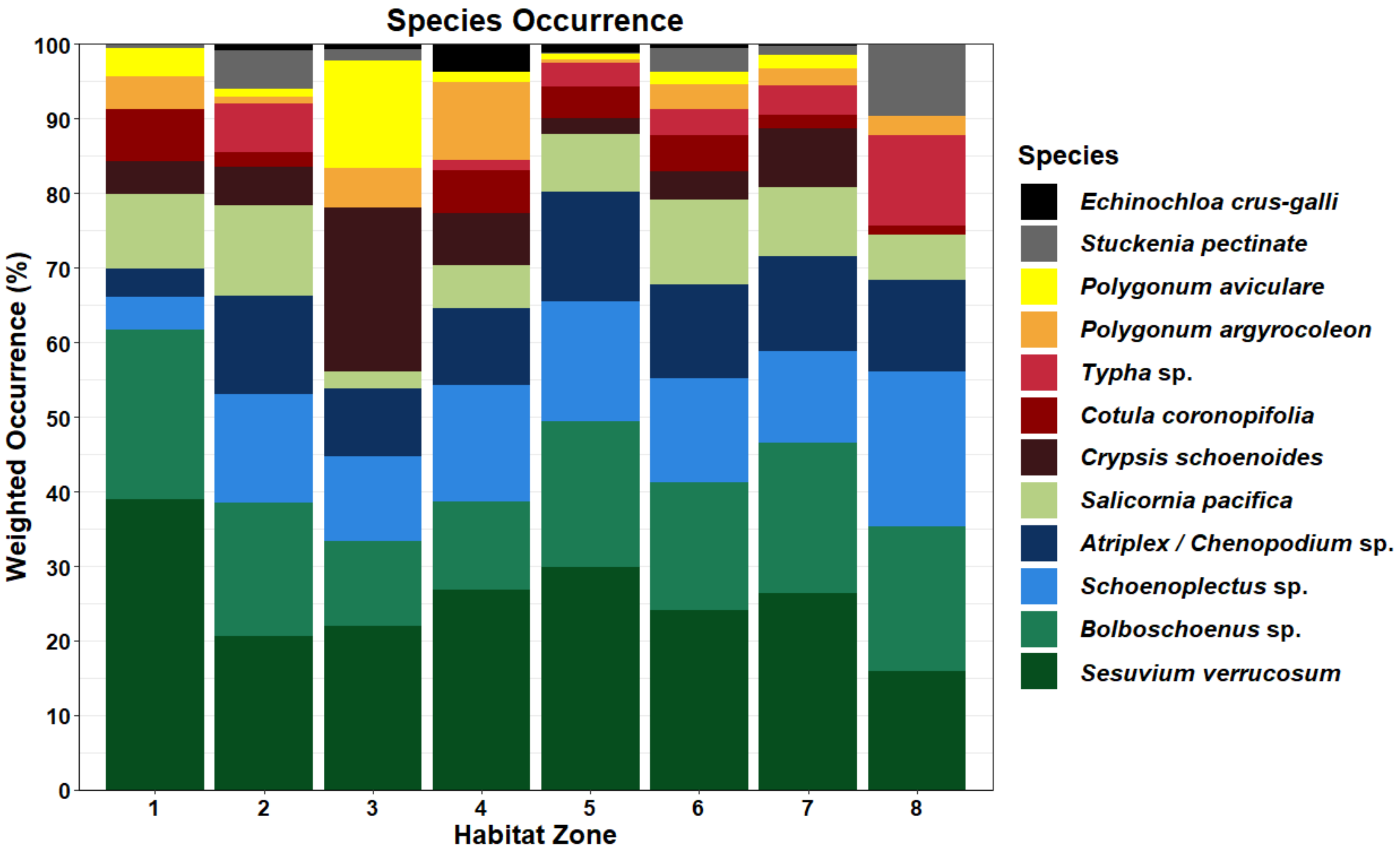

Figure 3.3: Proportional plant species occurrence by habitat zone. We included 12 species of primary management concern, and excluded *Ruppia maritima*, *Cicuta maculate*, and *Cuscuta salina* due to infrequent occurrence.

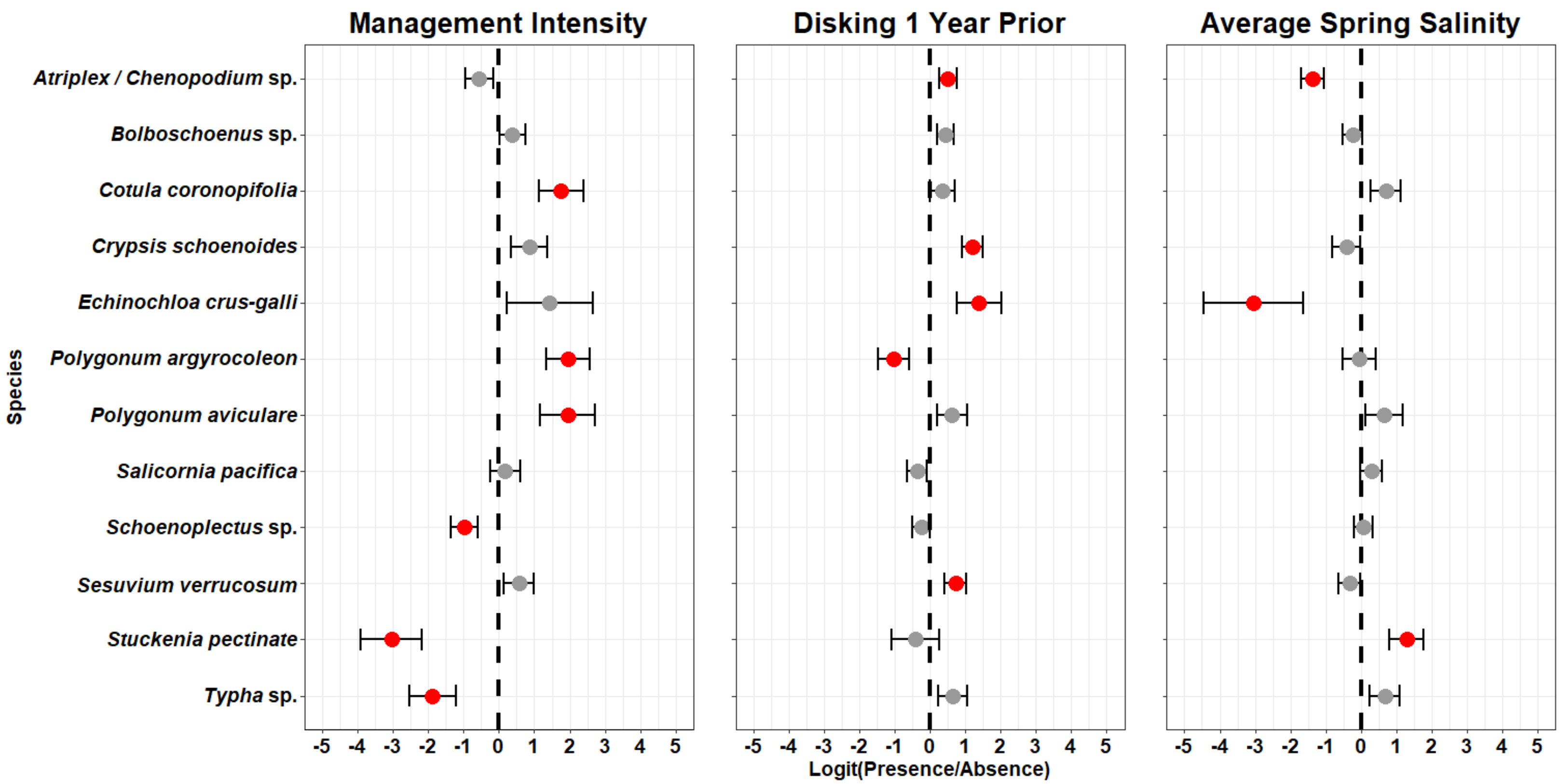

Figure 3.4: Species-specific responses to management intensity (left panel), disking (middle panel) and average spring salinity (right panel). Presence/absence data were logit transformed, and each main factor data were normalized to aid interpretability. Statistically significant values are presented in red, and the bars represent standard error.

Table 3.1: Total seed abundance (log-normalized kg/ha) by habitat zone, average spring salinity, disking in the previous spring, overall management intensity, and soil type. Statistically significant values are bolded, CI represents confidence interval. Wetland unit was included as a random effect. Pairwise Tukey contrasts were performed for habitat zones and soil types. Groups sharing the same letter are not statistically different and sequential lettering increases with the value of the predicted mean.

Predictors	Estimate	Std. Error	CI	df	"t" value	"p" value	
Habitat Zone [1](Intercept)	0.88	1.08	-1.34 – 3.10	345.95	0.78	0.44	a
Habitat Zone [2]	0.44	0.54	-0.75 – 1.63	55.48	0.73	0.47	a
Habitat Zone [3]	**2.55**	**0.69**	**1.13 – 3.97**	**70.94**	**3.53**	**<0.001**	**b**
Habitat Zone [4]	**1.50**	**0.58**	**0.23 – 2.77**	**67.58**	**2.32**	**0.02**	**ab**
Habitat Zone [5]	0.75	0.48	-0.42 – 1.92	67.74	1.26	0.21	ab
Habitat Zone [6]	0.89	0.47	-0.14 – 1.93	56.83	1.69	0.09	ab
Habitat Zone [7]	1.12	0.51	-0.20 – 2.43	72.09	1.67	0.10	ab
Habitat Zone [8]	0.95	0.65	-0.33 – 2.23	53.05	1.45	0.15	ab
Soil [joice muck]	**1.98**	**0.94**	**0.13 – 3.83**	**704.95**	**2.10**	**0.04**	**a**
Soil [joice muck clayey subsoil]	**2.45**	**1.04**	**0.42 – 4.49**	**688.99**	**2.37**	**0.02**	**a**
Soil [reyes silty clay]	**1.80**	**0.93**	**-0.01 – 3.62**	**710.37**	**1.95**	**0.05**	**a**
Soil [suisun peaty muck]	**2.20**	**0.97**	**0.30 – 4.10**	**703.63**	**2.28**	**0.02**	**a**
Soil [tamba mucky clay]	**1.99**	**0.94**	**0.15 – 3.83**	**702.38**	**2.13**	**0.03**	**a**
Soil [tidal marsh]	**2.07**	**1.03**	**0.04 – 4.10**	**646.09**	**2.01**	**0.05**	**a**
Soil [valdez silty clayloam]	1.76	0.96	-0.13 – 3.65	698.30	1.83	0.07	a
Soil [water]	**1.98**	**0.96**	**0.09 – 3.86**	**709.22**	**2.06**	**0.04**	**a**
Management intensity	0.07	0.12	-0.17 – 0.32	99.90	0.59	0.55	
Disking 1 year prior	-0.01	0.02	-0.04 – 0.02	114.95	-0.42	0.68	
Average high tide salinity	0.04	0.05	-0.22 – 0.30	126.62	0.32	0.75	
Year 2	0.00	0.42	-0.82 – 0.82	92.04	0.01	0.99	

Random Effects	
σ2 (residual variance)	1.97
$\tau00_{\text{Wetland unit}}$ (random intercept variance)	0.50
ICC (intraclass correlation coefficient)	0.20
$N_{\text{Wetland unit}}$	71
Observations	730

Marginal $R^2 = 0.124$, Conditional $R^2 = 0.302$

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CHAPTER 4 – Determining Peak Seed Abundance, Decomposition, and Apparent Depletion Rates of Waterfowl Foods in a Brackish Wetland

ABSTRACT

To effectively conserve wildlife, managers must identify key factors that influence population dynamics (Hanya and Chapman 2013). Food resources have critical implications for populations, specifically during periods of low availability, such as winter. The winter food limitation hypothesis (WFLH) states that the abundance of food during resource-poor periods limits populations of migratory birds (Fretwell 1972, Sherry et al. 2005). Three lines of evidence provide support for the WFLH in waterfowl. First, waterfowl body condition (a metric of endogenous lipid reserves) has been found to correlate with available food resources (Delnicki and Reineck 1986, Heitmeyer 2006, Moon et al. 2007). Second, body condition has been found to be correlated with survival (Bergan and Smith 1993, Moon and Haukos 2006), the timing of migration (Heitmeyer 1988), and breeding success and recruitment Raveling and Hietmeyer 1989, Guillemain et al. 2008, Anteau and Afton 2009). Third, waterfowl distributions tend to be correlated with resource (food) availability (Nichols et al. 1983, Hepp and Hines 1991, Pearse et al. 2012). The evidence in support of the WFLH has formed the foundation of waterfowl and wetland habitat conservation in North American for the last 35 years (Reinecke et al. 1989, Williams et al. 2014, CVJV 2020).

In response, wetland managers have focused efforts to systematically evaluate the availability of food resources in wintering areas to determine whether sufficient energy is available to support existing (or targeted) waterfowl populations (Naylor 2002, Kross et al. 2008, Petrie et al. 2016, Williams et al. 2014). The information from these evaluations is used to develop and parametrize bioenergetic models, which enable managers to anticipate the number of individuals a food supply can support (Goss-Custard et al. 2002, CVJV 2006, Williams et al.

2014). These models, combined with habitat assessments, have guided the conservation and management of nearly 8 million hectares of wintering habitat for waterfowl in North America (Reinecke et al. 1989, Williams et al. 2014, CVJV 2020). Researchers have worked to improve the accuracy of these models by incorporating more sophisticated processes of habitat selection, bird movement, and foraging behavior to better estimate energy gains and expenditures (Miller et al. 2014, DeAngelis and Diaz 2019). However, most models rely on assumptions which have not been fully (or even partly) evaluated, often due to challenges associated with obtaining realistic parameter estimates from the field (Goss-Custard et al. 2002, Miller and Eadie 2006, Williams et al. 2014). One common but extremely important assumption is that the standing stock of food that is present when waterfowl arrive on the wintering grounds in fall represents peak food abundance, such that the table is "set" when birds arrive. Thereafter, food abundance is assumed to decline over winter due to decomposition and depletion, and managers seek to estimate how much remaining food is available to support populations as winter progresses (Goss-Custard et al. 2003, Petrie et al. 2016).

This "table is set" assumption is typically applied to seeds produced by plants that grow in wetlands or agricultural crops, which dabbling ducks depend on as a primary source of energy and nutrients throughout winter (Fredrickson and Taylor 1982, Delnicki and Reinecke 1986, Hagy and Kaminski 2012). The assumption of peak food availability occurring in fall (before waterfowl arrive) appears to fit well with the phenology of seed production by annual plants, which germinate, grow, and ultimately produce seeds when seasonal wetlands are dry (Fredrickson and Taylor 1982, Haukos and Smith 1993, Reinecke and Hartke 2005). Seeds are retained in these wetlands over winter due to water management infrastructure which acts as a boundary, not only containing seeds but also preventing seeds from entering in high quantities from adjacent areas (Fredrickson and Taylor 1982, Middleton 2000, Hagy and Kaminski 2012). Consequently, most studies which evaluate the abundance of seeds for waterfowl do so only at beginning of the wintering period, assuming it represents the peak abundance of food (Naylor 2002, Kross et al. 2007, Greer et al. 2009, Chapter 1). A second sample is often collected at the end of winter to evaluate the depletion of food resources attributable to waterfowl foraging, and decomposition (Naylor 2002, Kross et al. 2007, Greer et al. 2009). Decomposition rates often are considered to be a source of background loss, as they remain relatively constant over time, whereas rates of seed removal by waterfowl vary over time and can be substantially larger (Nelms and Tewdt 1996; Hagy and Kaminski 2012, 2015). This approach, which implicitly assumes seed dynamics over winter are inconsequential to evaluations of abundance, tends to find higher abundances of seeds in fall compared to winter. However, without evaluating seed resources more frequently, managers could be failing to detect important trends which could impact the precision of bioenergetic models.

Precise estimates of seed densities are difficult to obtain in wetlands due to the heterogenous distribution of seeds (Stafford et al. 2006, Straub et al. 2012, Ringelman et al. 2015); estimates of seed abundance often exhibit large coefficients of variance with many sample locations containing few or no seeds, while others contain copious amounts. Sampling rarely produces reliable estimates of how patchy seed resources are and what causes this heterogeneity. Some of this variability is likely the result of hydrochory – the dispersal of seeds by water (Leck and Simpson 1987, van den Broek et al. 2005, Middleton 2000). The distance by which hydrochory can move seeds depends heavily on the species, habitat structure, and water flow (van den Broek et al. 2005, Nilsson et al. 2010, Sommers et al. 2013). Species-specific buoyancy determines if seeds float for extended periods of time (> 210 days), of if seeds will disperse in the water column, or across the substrate with sediment (Merritt and Wohl 2006, Gurnell 2007, van den Broek et al. 2005). Habitat structure such as microtopography, irrigation ditches (common in managed wetlands), and emergent vegetation can mediate water flows and provide structures which capture seeds (van den Broek 2005, Markwith 2014, Truong et al. 2015). At larger spatial scales, broader spatial diversity may lead to highly variable estimates of seed density (Peterson and Baldwin 2004, Stafford et al. 2006, Ringelman et al. 2015).

This inherent difficulty in obtaining reliable estimates of seed (food) abundance has important implications for habitat and population management based on bioenergetic models. Carrying capacity predictions made by bioenergetic models can be very sensitive to relatively small changes in food availability estimates (Miller and Eadie 2006, Miller et al. 2014), but spatial and temporal variation often results in seed density estimates varying by 100-400 kg/ha (Naylor 2002, Kross et al. 2008); even a difference of 25 kg/ha over a small area (1000 ha) can change predicted carrying capacity by > 1,000 dabbling ducks (Ringelman et al. 2015, Chapter 1). Managers currently lack the information to determine how seed dynamics influence estimates of seed density in wetlands. Without knowing how seed abundances change over the wintering period, particularly in the absence of waterfowl foraging pressure, bioenergetic models that assume a constant or homogeneous distribution of seeds may provide inaccurate estimates and misinform management efforts.

To determine how the spatial and temporal variability of food resources may impact our ability to accurately evaluate the abundance of food resources, a more temporally intensive sampling structure is required. One approach is to explore seed dynamics at a smaller local scale, where it is possible to employ small-scale, high frequency sampling of wetlands in combination with the use of foraging exclosures. In so doing, we may better be able to determine when peak seed abundance occurs, evaluate the heterogeneity of seed distributions in space and time, and assess the extent of seed removal due to waterfowl foraging relative to other seed consumers and decomposition. In short, whereas most studies employ large spatial scale but small temporal scales, complementary efforts are needed at smaller spatial scale, but over longer temporal scales and ideally with more frequent assessment. Furthermore, such analyses should be coupled with experimental controls and assessments of foraging depletion and seed decomposition.

We performed an in-situ analysis to determine if seed dynamics influence assumptions central to bioenergetic models used to assess waterfowl habitats. We specifically tested three predictions: (1) Food abundance estimated at the beginning of fall represents peak food availability; (2) Decomposition rates are constant, vary by plant species, and comprise a small proportion of total seed loss; (3) Foraging by waterfowl represents the greatest source of seed depletion, can be estimated in the field, and varies by waterfowl abundance and patch use. We conducted repeated sampling (5 intervals) at small-scale study locations within a single 230-acre wetland to determine how seed abundance changes over time. We evaluated declines in seed abundance by partitioning the two major sources of seed loss, depletion by waterfowl and decomposition. We stratified small-scale sampling locations by waterfowl use (high and low), determined by using GSM-GPS locations from marked dabbling ducks, to capture a range of foraging rates. Each sampling location included an exclosure which allowed us to compare the impact of waterfowl foraging on seed abundance estimates. We directly assessed seed decomposition rates for three waterfowl-favored species (*Bolboschoenus* sp., *Echinochloa crus-gal*, and *Crypsis schoenoides*) to determine background rates of seed loss (Burns 2003, Satter et al. in prep.). We also evaluated seeds at a broader, wetland unit scale, providing us with a comparison to determine how sampling scale is influences by seed dynamics.

METHODS

Decomposition

We assessed seed decomposition rates for three species favored by waterfowl (*Bolboschoenus* sp., *Echinochloa crus-gal*, and *Crypsis schoenoides*) over the non-breeding season in three managed brackish wetlands (Nov. 7, 2019, to Feb. 27, 2020) (Burns 2003, Satter in prep). We collected mature seeds in August and September by hand at two sites within Suisun Marsh (Wings Landing and Denverton). Seeds were dried to a constant mass at 80˚C, vegetation (stalks, leaves, and glumes) and damaged or partially developed seeds were removed, and seeds were stored at 0˚C until they placed into decomposition tubes. Decomposition tubes (10 cm in diameter, 5 cm tall) were constructed of acrylonitrile butadiene styrene (ABS) plastic, with fiberglass mess (0.3 mm aperture) covering both ends, and the bottom was covered with an additional 0.05 mm aperture mesh, similar to Nelms and Twedt (1996). Each tube contained 2.5 grams of seeds from a single species. Thirty decompositions tubes (10 tubes for each species) were deployed at each of three sites across the western portion of Suisun Marsh (Wings Landing, Joice Island, and Goodyear; 90 tubes in total) (Fig. 1). The decomposition tubes for each site were contained within a 0.6 by 1.5-meter chicken wire envelope (decomposition array) that was held to the bottom of the wetland using wooden stakes, ensuring tubes would not float or be dispersed over the course of the study. Each decomposition array also included two temperature loggers (iButton thermochron), one inside a decomposition tube, and another which was loose within the envelope. We removed a decomposition tube for each species from each sites every 14 days; because wetlands drained before we were able to sample all tubes, we only completed eight sampling intervals (e.g., 72 of 90 decomposition tubes). Decomposition tubes were kept in a cooler on ice until they taken back to the lab. Seeds were removed and rinsed with water to remove any material from seeds that entered the decomposition tube before being dried at 80˚C until constant mass and weighed.

Depletion

We examined apparent seed use at four locations – two that received high waterfowl use, and two that received low waterfowl use – within a single 230-acre wetland unit using foraging exclosures (3.0 m in diameter, 0.6 m high) and paired open sites between early November and late February. We quantified waterfowl use with GPS-GSM location data from marked dabbling ducks between 2016 and 2019 (inclusive). We included only nocturnal locations, as dabbling ducks typically forage nocturnally in winter (Jorde et al. 1984, Miller 1985). We converted point locations to rasters using ArcGIS, then classified the data into high use (top 10% of raster values) and low use (bottom 10% of values). Paired open sites were placed within 10 meters of each foraging exclosure, constrained to presenting a similar vegetative community to that in the exclosure. We collected three soil core samples from each site (exclosure and open) every 28 days between Nov. 11, 2019, to Feb. 26, 2020 (5 sample periods). Our first sampling event occurred 14 days after the wetland unit was flooded.

We estimated seed abundance at the wetland unit level by collecting 20 soil core samples at the beginning, middle, and end (Nov. 6, 2019, Jan. 1, 2020, and Feb. 26, 2020, corresponding with exclosure sampling periods 1, 5, 9) of the wintering period. Sample locations were determined using a generalized random tessellation stratification (GRTS) method, which provides a spatially balanced selection, using the *spsurvey* package in program R (Stevens and Olson 2003, 2004; Kincaid et al. 2016, Dumelle et al. 2021).

Sample collection and processing

All soil cores were collected using a soil coring device with a diameter of 6 cm and a depth of 5 cm (Haukos and Smith 1993, Naylor 2002). Soil cores were washed through a series of sieves

(4.00 mm, 2.36 mm, and 250 µm) to separate seeds from other materials. We identified all seeds contained within each soil core using a stereo dissecting microscope, then separated seeds by species and dried at 80˚C until constant mass (typically 48 hrs) and weighed to the nearest 0.0001 gram. We grouped all *Schoenoplectus* sp., *Bolboschoenus* sp., *Rumex* sp., *Lotus* sp., and *Typha* sp. to genus to avoid misidentification, and we combined *Atriplex* and *Chenopodium* into a single group as identifying features (bracts and seed coats) were often missing.

ANALYSIS

Decomposition

We used a paired t-test to determine whether temperatures within the decomposition tubes differed from temperatures within the array. Although temperature did not vary greatly across sites, it did vary over time and therefore we included it as a site-specific covariate. We included site-specific averaged tube temperatures for each sample period as a covariate in our linear models examining decomposition. We specified 10 linear models to assess decomposition (grams lost) using species, sample period, site (Wings, Joice, Goodyear), and temperature as covariates (Table 1). We included only data from the first through sixth sampling period (first 84 days) in our linear models since our temperature loggers did not record past 84 days. We specified combinations of these variables as fixed effects and included interactions between these factors to determine the model that best fit the data. We also included curvilinear models (natural log of sample period) because our calculations of daily percentage of mass loss declined over the course of the study. We compared all models using AICc (Hurvich and Tsai 1989). We used the core function (lm) in program R to fit all linear models (R Core Team 2022).

Exclosures/open sites

We analyzed the correlation between total seed abundance in exclosures and open sites and among sampling periods using linear regression. We $\log_e$-normalized seed abundance (e.g., ln(1+

kg/ha)), and included sampling period, site type (open and exclosure), and waterfowl use (high and low) as categorical fixed effects. We included an interaction term between sampling period and site type to account for the crossed study design. We used the R package *performance* to assessed model fit by checking for heteroscedasticity and assessed residuals for normality (Lüdecke et al. 2021). We found no indication of temporal autocorrelation when inspecting residuals.

Apparent seed use by waterfowl

We used methods described by Hagy and Kaminski (2012) to estimate apparent waterfowl seed use in open sites. To avoid overestimating available food resources, we used diet data (Satter et al. in prep) to determine which seeds waterfowl consume commonly (Hagy and Kaminski 2012). Nine genera/species (*Atriplex / Chenopodium*, *Bolboschoenus* spp., *Echinochloa crus-galli*, *Lolium multiflorum*, *Polygonum* spp., *Polypogon monspeliensis, Salicornia virginica, Sesuvium verrucosum*, and *Crypsis schoenoides*) comprised 97% of the total aggregate wetland seed mass in dabbling duck diets (n = 549) collected in Suisun Marsh (Satter et al. in prep). We grouped these species as '*waterfowl preferred foods'* and determined their aggregate mass at each sampling period. We then applied our average daily decomposition rate (0.17% mass lost/day, see below) to determine expected rates of seed loss over the study period. By taking the difference of expected seed mass from observed seed mass at each timestep following peak seed abundance we were able to calculate apparent seed use by waterfowl.

RESULTS

Seed decomposition

Seed decomposition was best described by the linear model which included species and sampling period as fixed effects, with an interaction effect between the two factors (adjusted r^2 = 0.97) (Table 2). The inclusion of site and temperature increased AICc and BIC values significantly (> 5). *Echincochloa crus-galli* exhibited the highest average rate of decomposition (0.27%/day), followed by *Crypsis schoenoides* (0.18%/day) and *Bolboschoenous* sp. (0.06%/day) after being submerged for 102 days (Fig. 2). The averaged percentage of mass loss per day across the three species was 0.17%. Both *C. schoenoides* and *Bolboschoenus sp.* exhibited a significant loss in mass in the first 14 days (0.50 - 0.93%/day), after which the slopes between sampling periods were reduced (Table 2, Fig.2). Following this initial loss of mass, *Bolboschoenus* sp. exhibited no significant decline in mass for the remainder of the study. Conversely, there was a relatively constant increase in total mass lost across all sample periods for *E. crus-galli*.

Hourly temperatures inside the decomposition tubes were lower across all sites when compared to the temperatures adjacent to the tubes at the bottom of the wetlands. The largest hourly temperature difference occurred at Goodyear (0.337 ± 0.013˚C, $t = 9.2$, $p = < 0.01$), followed by Wings (0.160± 0.023˚C, $t = 13.3$, $p = < 0.01$) and Joice (0.060 ± 0.036˚C, $t = 18.3$, $p = < 0.01$). We compared mean temperatures by site and found Goodyear (10.7-11.7˚C) was significantly warmer than both Joice (9.65-10.6 ˚C) and Wings (9.21-10.2 ˚C). However, given that the accuracy of the Termochron is ± 1 ˚C, we cannot be confident that these differences are entirely attributable to the location.

Seed composition and mass over time

We used mean dry mass of seeds to assess species composition at the wetland unit level. *Crypsis schoenoides* was the most abundant species, comprising over 65% of total dry mass across all sampling scales, and it experienced the largest decline over the winter period (Table 3). The average dry mass of *Bolboschoenous* sp., *Sesuvium verrucosum,* and *Atriplex / Chenopodium* sp. increased across all sampling scales over the course of the study. *Echinochloa* *crus-galli* was very rare in our small-scale sampling, comprising less than 0.2% of aggregate seed mass and occurring only in the high waterfowl use exclosure (Table 3). Our wetland unit sampling encountered the greatest amount of *E. crus-galli*, and virtually all of the initial seed mass was gone by our final sampling period.

Decomposition rates did not predict the net changes in species-specific mass over the course of the study (Table 3, Fig. 3). Although the observed total seed abundance and predicted total seed abundance were very similar in the high waterfowl use exclosure, and the low waterfowl use open site at the end of the study period, the trends that the observed and predicted mass had over the course of winter were very different. In exclosures, seed abundance increased until day 42 in low waterfowl use areas, and until day 70 in high use areas (Fig. 3). In open sites, seed abundance remained constant (low waterfowl use), or increased (high waterfowl use) by day 42. The increases in seed abundance in open sites were due to increased *Bolboschoenous* sp., whereas the increase in exclosures was driven by *C. schoenoides*. In contrast, decomposition predicted steady declines in seed abundance.

Low waterfowl use areas had significantly lower $\log_e$ total seed masses compared to high use areas (Table 4). Initial estimates of average seed abundance in open sites and exclosures were similar; however, low waterfowl use areas had lower means (open sites: 445 kg/ha, SE = 131; exclosures: 776 kg/ha, SE = 166) than high waterfowl use areas (open sites: 835 kg/ha, SE = 252; exclosures: 964 kg/ha, SE = 173). At a broader marsh-wide scale, seed abundances were most similar to high waterfowl use areas (916 kg/ha, SE = 168) (Fig. 4).

Following initial estimates, seed mass increased until day 70 (0.59 ± 0.27, p = 0.03) in exclosures while seed mass in open sites remained unchanged until day 42 (-0.27 ± 0.37, p = 0.47) (Table 4). The largest difference in mean total seed mass between open sites and exclosures occurred in high waterfowl use areas on day 70, when the exclosures contained 2047 kg/ha more seeds than the open sites (Fig. 4, Table 5). By the end of the study period, day 126, average total seed mass was between 264-300 kg/ha in all open sites, while exclosures in both low and high use areas contained higher average seed masses (high waterfowl use: 876 kg/ha, SE = 204; low waterfowl use 384 kg/ha, SE = 70) (Table 5). Marsh-wide mean seed mass was very similar to open sites in both low and high waterfowl use areas at each timestep.

Apparent seed use by waterfowl

Seeds that are preferred by waterfowl comprised a decreasing proportion of total seeds over time in our wetland unit assessment (91.4% at day 14, 84.1% at day 70, 65.4% at day 126) (Table 3, and 5). Apparent waterfowl foraging (declines in seed abundance beyond that predicted by decomposition alone) accounted for a decline of 316.3 kg/ha between day 14 and day 70, and 489.1 kg/ha between day 70 and day 126 in our marsh wide estimate (7.2 kg/ha removed per day).

Waterfowl-preferred seeds increased in abundance in our small-scale assessments (10% and 16% increase in high- and low-use sites, respectively) until day 42. Following day 42, average apparent foraging rates varied by waterfowl use types; high use areas declined by an average of 491.7 kg/ha every 28 days, while low use areas declined by an average of 157.9 kg/ha every 28 days. Daily rates of seed removal attributable to foraging ranged from 17.6 kg/ha (high use sites) to 5.6 kg/ha (low use sites).

DISCUSSION

To fully understand the dynamics of seed abundance and food availability in brackish wetlands, we needed to better understand the spatial and temporal patterns of seed abundance.

We evaluated the declines in seed abundance due to decomposition and waterfowl foraging and accounted for gains due to seed movement due to flooding. We assessed decomposition rates for three species (*Bolboschoenous* sp., *Echinochloa crus-galli,* and *Crypsis schoenoides*) favored by waterfowl using controlled evaluations in different locations within the marsh. This was essential to determine if declines in seed abundance exceeded expected losses due to decomposition, which could be attributed to waterfowl foraging. We quantified seed abundance and depletion in locations within a wetland unit with both high and low waterfowl use areas and compared these areas to the wetland-wide estimates. And finally, we compared changes in seed abundance inside and outside of foraging exclosures. Our results show that seed abundance initially increased, contrary to expectation, before declining after 42 (low waterfowl use) or 70 (high use) days, suggesting that some rethinking of how seed abundances change over winter is needed.

We observed temporal changes in seed abundance which contradict the assumption that peak seed availability occurs shortly after wetland flooding, which conflicts with the “table is set” hypothesis. Initial increases in seed abundance could be due to hydrochory, as water may have moved additional seeds into sampling locations before declines were observed. Following peak abundance, decomposition rates for the three species we examined (which accounted for 77% of the wetland unit aggregate seed mass) predicted higher abundances of seeds than we observed, which suggests waterfowl were removing seeds. Our estimates of apparent foraging rates correspond with our classification of waterfowl use; apparent foraging rates were much higher in high use areas (17.6 kg/ha/day) than in low use areas (5.6 kg/ha/day). When we examined species-specific changes in seed abundance at the wetland level, we found that waterfowl-preferred seeds comprised a much larger proportion of total seeds at the beginning (91%) compared to the end of our study (65%). These trends raise questions about the optimal time to sample brackish managed wetlands to capture peak seed abundance. Our data also indicate waterfowl foraging rates were spatially variable, suggesting that more complex bioenergetic models will be needed to account for these factors and produce more accurate estimates of habitat carrying capacity.

Decomposition

To properly evaluate how many seeds remained available to waterfowl over winter, we first had to determine the rate at which seeds would decompose over time. We selected three species (*Bolboschoenus* sp., *Echinochloa crus-galli*, and *Crypsis schoenoides*) which represent a majority of seeds within our study site, and are commonly consumed by waterfowl (Burns 2003, Satter et al. in prep). We assumed that due to warm (10˚C) and brackish conditions in Suisun Marsh, decomposition rates would differ from previous investigations conducted in cooler, fresh water, seasonal wetlands (Neely 1956, Shearer et al. 1969, Nelms and Twedt 1996). Instead, we found similar rates of decomposition for *Echinochloa* (0.27%/day compared to 0.26%/day in Nelms and Twedt 1996), and average decomposition rates across all species we examined (0.17%/day compared to 0.18%/day) (Neely 1956, Shearer et al. 1969, Nelms and Twedt 1996). We found no effect of temperature, or wetland site on decomposition rates. Although the highest temperatures did occur within the first two weeks of the study, which coincided with very high decomposition rates (0.50 - 0.93%/day). Our measurements of hourly temperature suggest there was no discernible difference between temperature inside the decomposition tubes and temperatures outside the decomposition tubes. Therefore, decomposition tubes did not significantly influence temperature. Although observed declines in seed abundance were poorly predicted by decomposition rates, they allowed us to evaluate the extent of seed loss not attributed to decomposition.

Why does seed abundance increase and decrease within exclosures?

We anticipated that seed abundance within exclosures would only decline after our initial assessment, given the prevailing expectation that seed abundance peaks shortly after wetland flooding – the "table is set" hypothesis. In contrast, we found seed abundance increased for up to ten weeks following flood-up in exclosures. This was unexpected as the majority of vegetation was submerged two weeks after flooding began, making it unlikely that additional seeds were becoming available. Hydrochory can be caused by wind and water flow, as seeds float on the surface of water, within the water column, or across the substrate, distributing seeds over the initial flooding period (Parolin 2005, Merritt and Wohl 2006, Brown and Chenoweth 2008). It is unlikely that seeds entered the study site from neighboring areas, as all managed wetlands were flooded at approximately the same time. We also found no seeds from species which grow in the adjacent tidal marshes, suggesting we did not encounter an influx of seeds from external sources. Our sampling method, soil core sampling, involves pushing a tube through the water to collect the top few centimeters of substrate (Olmstead 2010, Evans-Peters 2010). Soil core sampling poorly captures seeds on the water's surface, and thus could miss seeds, that despite being in the sampling locations, have yet to sink (van den Broek et al. 2005, Nilsson et al. 2010, Markwith et al. 2014).

After the unexpected increase in seed abundance within the foraging exclosures, seed abundance declined at rates which far exceeded (5-10 times greater) our measured rates of decomposition. While it is possible other (smaller) foragers could access seeds within our foraging exclosures, this is unlikely because most of the other common granivores in the marsh (passerines and rodents) do not forage under the water. Water depth in this wetland was shallow (< 30 cm) and we did not observe fish, or invertebrates in high densities within the exclosures during our visits (every 14 days). Hydrochory could explain the initial increase and then sharp decline in seed abundance in the exclosures where most seed consumers were absent. The distance by which seed are dispersed by hydrochory is variable but heavily dependent on water movement (Nilsson et al. 2010). The distance seeds would have to travel to exit our small-scale sites is minimal; exclosures were circular with a diameter of 3 meters; assuming a seed moved across the diameter over a two-week period, the seed would travel approximately 150 cm/week, or 21.5 cm/day. If a seed was located at the center of the exclosure, it could exit the exclosure in just 28 days moving at 5.4 cm/day (2.25 mm/hour). Thus, it is feasible that hydrochory could be responsible for the movement of seeds out of exclosures and sampling locations, and thus reducing seed abundances at those locations.

Water flow-through and wind may have caused seeds to travel these distances over short periods of time (Soomers et al. 2013, Markwith et al. 2014). A typical seasonal wetland, managed for waterfowl, is hydrologically isolated following initial flooding. However, wetland managers maintain water flow-through in the brackish wetlands within our study region to ensure that salinity levels do not dramatically increase over winter. Flow-through rates fluctuate based on tides and rainfall, as increased water depth within a wetland increases outflows rates. Our study site consistently experiences wind speeds over 7 m/s which, in addition to moving seeds on the water surface, could also create water movement below the surface due to the shallow depth (~ 25 cm) of our sampling sites (Van Dorn 1953). However, these two sources of seed movement may have been attenuated by obstructions, such as submerged and emergent vegetation, as well as the foraging exclosures themselves (Nepf 1999, Truong et al. 2015).

We would expect variation in seed movement, both in speed and direction, over the course of the wintering period. However, if we consider a conceptual model wherein a constant and unidirectional flow of water/wind drives the movements of seeds, we can pose a viable explanation as to how seed abundance within the foraging exclosures increased and decreased (Fig. 5). In this hypothetical model, hydrochory would move seeds into the foraging exclosure from surrounding areas over the first few weeks. Once in the exclosure, cage effects might then limit the rate of hydrochory and thus increase the residence time for seeds within the cage. Over time, foragers reduce the abundance of seeds outside the exclosures, resulting in fewer seeds moving into the exclosures (Fig. 5B). Coinciding with this reduction of seeds entering the exclosures is the continued movement of seeds out of the exclosure. The declining input over time, combined with continuous export of seeds, results in a bell-shaped curve of overall seed abundance when sampled over time.

This hypothesized process could explain the patterns observed for our small-scale estimates of seed abundance over time. Seeds in open sites began declining on day 42, which reduced the number of seeds moving into exclosures. The differential rates of hydrochory (exclosures = slower) created an apparent lag effect, where seed abundance peaked in open sites 28 days (or one sampling interval) before exclosures (Fig. 3). Peak seed abundance in exclosures (day 42 in low use, 70 in high use) coincided with the largest difference in normalized seed abundance with open sites. This difference in seed densities between open sites and exclosures likely led to a net movement of seeds out of the exclosure. As the difference in seed densities between open sites and exclosures is reduced, the rate of seeds lost from exclosures also declines. This can be seen in in Figure 3, as the slope between days 98 and 126 is less than the slope between days 70 and 98. Although trends between open sites and exclosures were similar across waterfowl use, peak seed abundance occurred later in in high use sites. One possible explanation for this difference is that hydrochory could be density dependent, as high use sites contained higher densities of seeds.

Improving carrying capacity estimates

The temporal changes in available seed resources we observed in our small-scale assessments suggest that sampling shortly after wetlands become flooded may fail to capture peak seed abundances. Although additional seeds are unlikely to be produced by annual plants following wetland flooding, seed dynamics create difficulties in detecting peak seed abundance. The species-specific changes in abundance over time (Table 3) may be correlated to the timing of seeds being released from vegetation, or different lengths of seed buoyancy (van den Broek et al. 2005). These changes in seed abundance may be more pronounced in estimates derived from soil core samples and using different sampling methods which better capture floating seeds could address these issues. Regardless, of sampling method, additional sampling periods at the start of the wintering season would provide a better evaluation of the total abundance of seeds available to waterfowl. Additional estimates of seed abundance over time can also be used to better approximate peak seed abundance, improving bioenergetic model accuracy.

Our assessments of seed abundance over time allowed us to determine peak seed abundance more accurately. To illustrate how our results can improve a simple bioenergetic model, we examined the daily ration model (DRM) which was applied to Suisun Marsh following a large-scale evaluation of waterfowl foods. The original DRM used estimates of landscape food abundance from samples collected shortly after wetlands were flooded (as per the "table is set" hypothesis). We show next that when we better characterize and quantify the delayed timing of peak seed abundance and the effects of foraging and seed movement, the original DRM estimates of carrying capacity are likely to be biased low.

Our small-scale evaluations of open sites indicated that seed abundance increased (10 to 16%) until 42 days after flooding. We expect waterfowl foraged occurred over this period, meaning this increase in abundance was co-occurring with reductions. Our assessment of seed reductions at the wetland unit level indicated apparent waterfowl foraging rates of 7.2 kg/ha/day, while our small-scale assessment of foraging rates ranged from 5.6 kg/ha/day in low waterfowl use areas to 17.6 kg/ha/day in high waterfowl use areas. Without a more detailed investigation into possible foraging rates across Suisun Marsh, it is difficult to extrapolate a reasonable foraging rate from a single wetland. Considering our study wetland had much higher seed production and waterfowl use compared to the marsh-wide average (Casazza et al. 2021, Chapter 1), we applied a conservative estimate of waterfowl foraging would be approximately half of our low use estimate (2.8 kg/ha/day). Accounting for this rate of foraging and a 10% increase in seed abundance over the first 42 days, the adjusted marsh-wide estimate of seed abundance would be 218.5 kg/ha (original estimate was 91.8 kg/ha). Using the same DRM parameters specified in chapter 1 and accounting for the adjusted peak seed abundance would result in a carrying-capacity estimate of 84,441 ducks, compared to the initial estimate of 27,021 dabbling ducks. This adjusted estimate is very close to the mid-winter waterfowl population estimate (82,000 ducks) conducted during the same time as the initial estimate of food abundance. Thus, without accounting for the more nuanced patterns of seed abundance and the effects of waterfowl foraging revealed through a more detailed small scale in-situ analyses of seed dynamics, our estimate of the number of birds that could be supported on existing food resources could be incorrect by 3-fold. We caution that these are simple calculations for illustration purposes, and we now intend to use these refined estimates in a more sophisticated agent-based bioenergetic model to evaluate carrying capacity for waterfowl in the Suisun Marsh (SWAMP; Miller et al. 2014, Blenk et al. in prep.).

CONCLUSION

Widespread acceptance of the winter food limitation hypothesis has underpinned a continental effort to manage food resources during winter to ensure sufficient food is available for waterfowl (Williams et al. 2014, CVJV 2020). Several bioenergetic models have been developed and applied to help guide habitat and conservation efforts, but these models require precise estimates of available food resources (such as seed abundance) to produce reliable predictions of habitat carrying capacity (Miller et al. 2014, Petrie et al. 2016). We observed an increase in seed abundance over three weeks in a recently flooded wetland. Our results indicate that the common assumption that the “table is set” at the beginning of fall shortly after wetlands are flooded may not be valid. Hydrochory can impact our ability to estimate peak seed abundance, particularly in brackish seasonal wetlands, by creating a spatial mismatch where soil core sampling is unable to effectively capture floating seeds. By accounting for hydrochory and waterfowl foraging, we can adjust estimates of seed availability using our results, consequently, DRM predictions of carrying capacity more than tripled. This dramatic change in estimated carrying capacity demonstrates the importance of accurately parameterizing food resources in bioenergetic models. Although our results could be specific to brackish wetlands, or the management of water, we need additional assessments to be sure similar trends are not occurring in other wetland habitats. If we continue to rely on bioenergetic models to guide conservation, additional research is needed to evaluate many of our assumptions regarding habitat food availability.

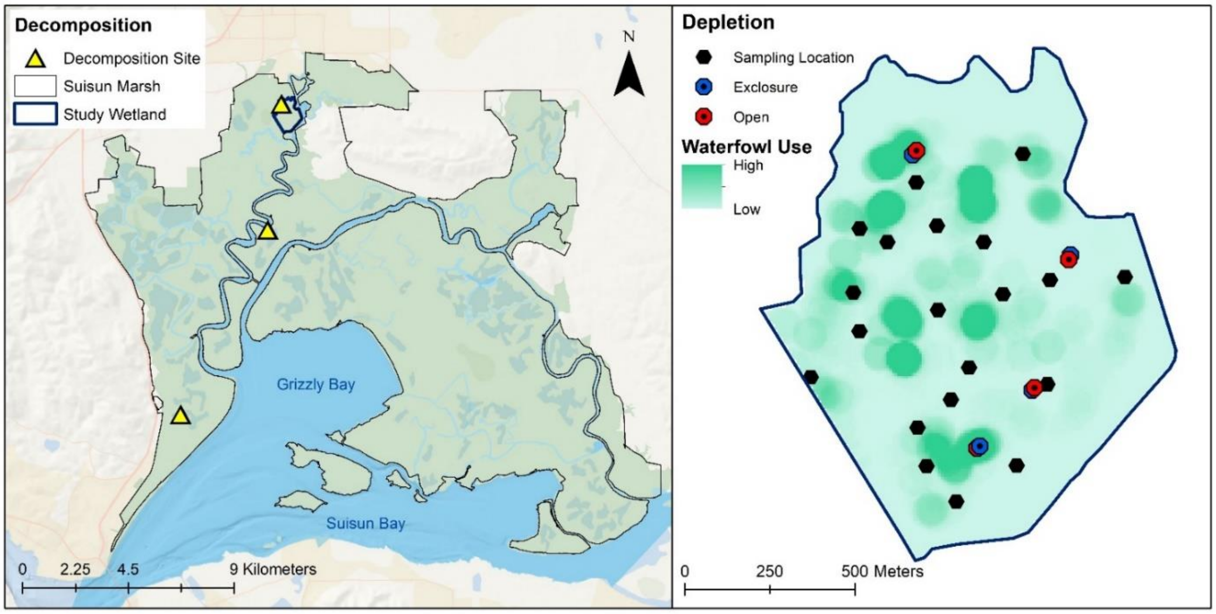

Figure 4.1: The left depicts the study site locations (yellow triangles) where decomposition arrays were placed in western Suisun Marsh. The right panel B shows the location of exclosures and the paired open sites (blue and red circles), as well as the sampling locations used to assess the entire wetland unit (black hexagons). Waterfowl use was determined using night locations from GPS-GSM marked birds over three years (2016-2019).

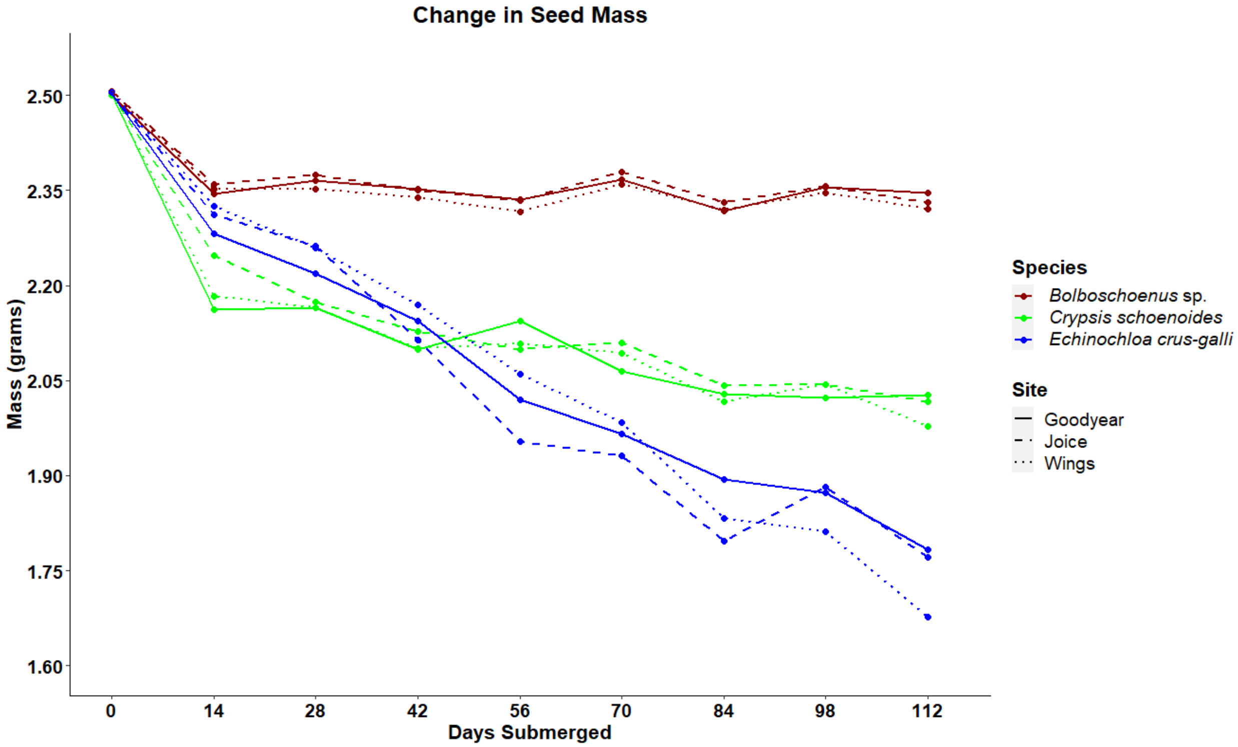

Figure 4.2: Mass (in grams) lost by each species (*Bolboschoenus* sp. *Echinochloa crus-galli*, and *Crypsis schoenoides*) over the wintering period at each site (Goodyear, Joice, and Wings). Species are represented by different colors, and sites are represented by different line types.

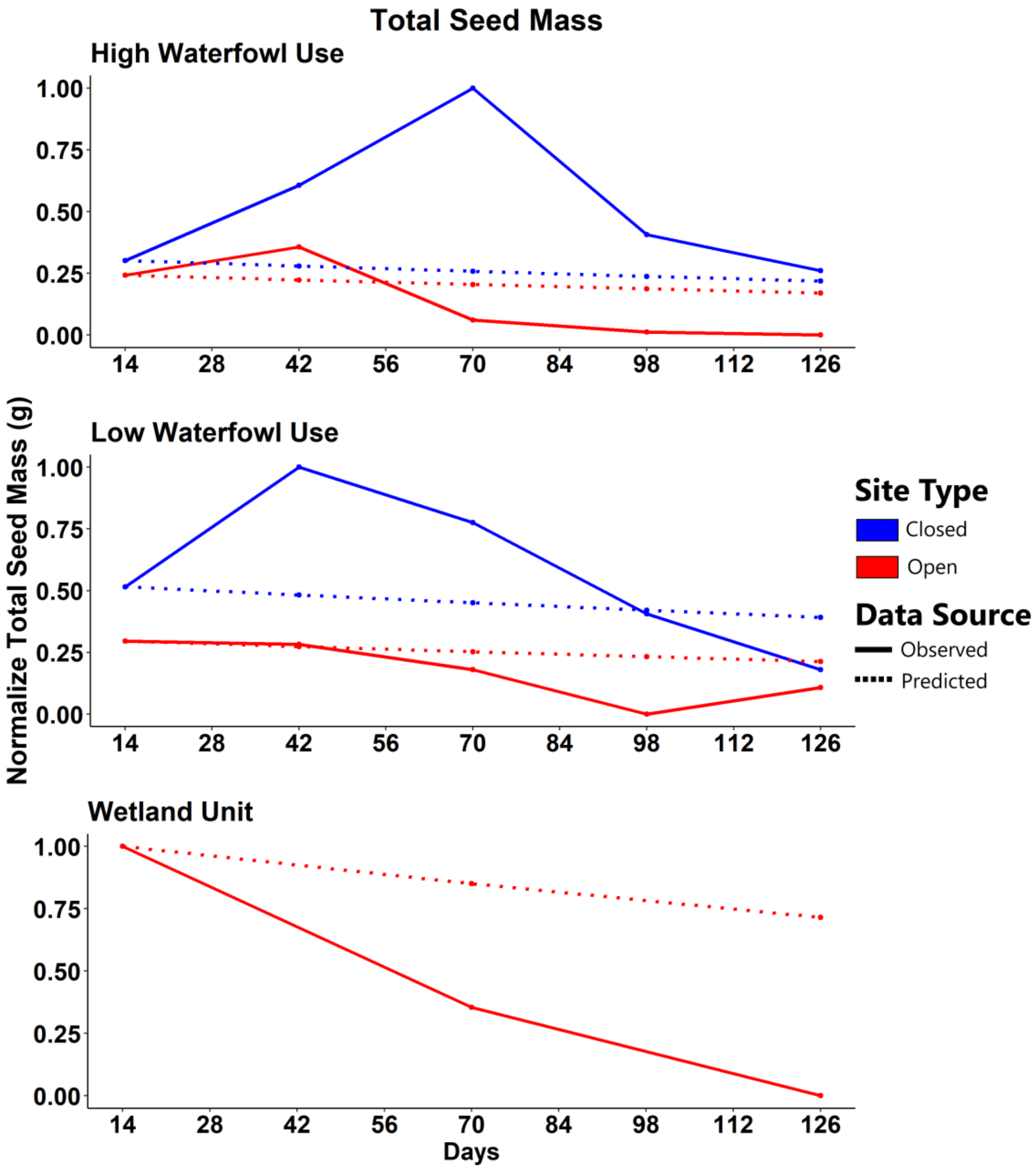

Figure 4.3: Changes in total seed mass within the open and closed (exclosures) sites, and within the entire wetland, during winter, 2019-2020. Exclosures are shown in blue, open sites (where waterfowl can access) are shown in red. Solid lines show observed changes in mass, assessed using soil cores. Dashed lines show expected declines in mass if initial mass is assumed as peak seed abundance, and seed loss is only due to decomposition. Daily decomposition rates represent an average rate across species (0.18%/day), based on previous studies (Neely 1956, Shearer et al. 1969, Nelms and Twedt 1996).

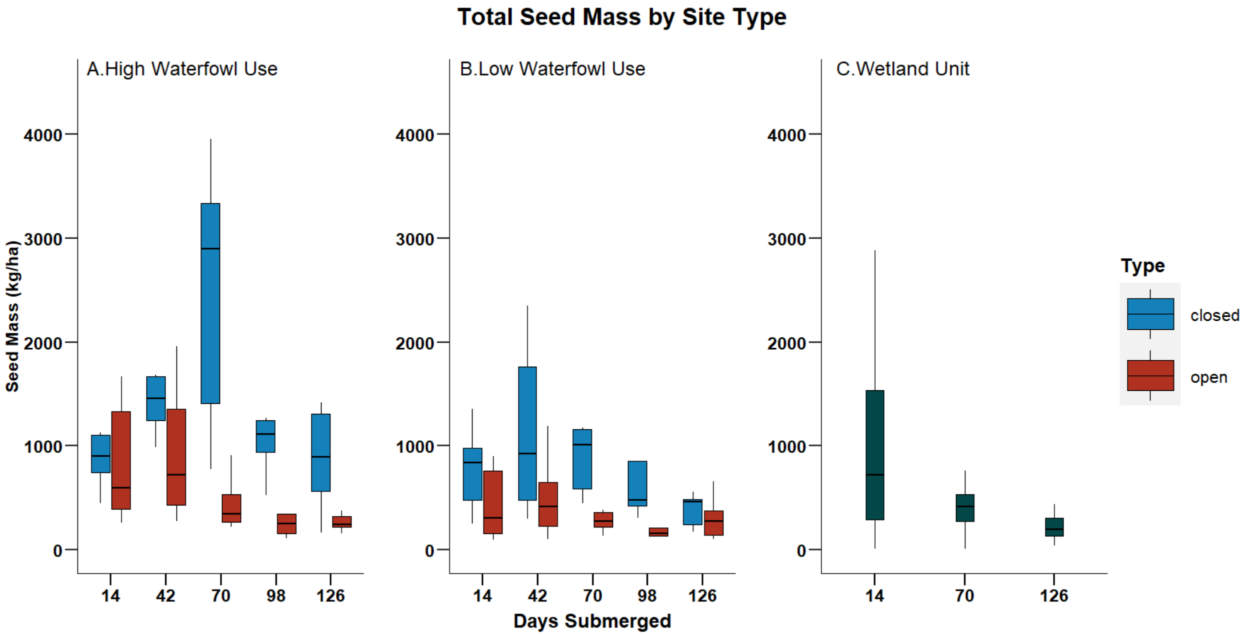

Figure 4.4: Total seed abundance (kg/ha) estimates derived from soil core samples separated by site type. **A**, sampling sites (open and closed) in areas that received high waterfowl use. **B**, sampling sites (open and closed) in areas that received low waterfowl use. Waterfowl use was assessed over a three-year period immediately prior to sampling. **C**, a random sampling effort conducted across the wetland unit. Open sites are shown in red, while closed sites (exclosures) are shown in blue. The marsh wide assessment is shown in gray. The box encompasses the first and third quartiles, the vertical lines show data extended 1.5 times outside of the inter-quartile range, and the horizontal line represents the median value.

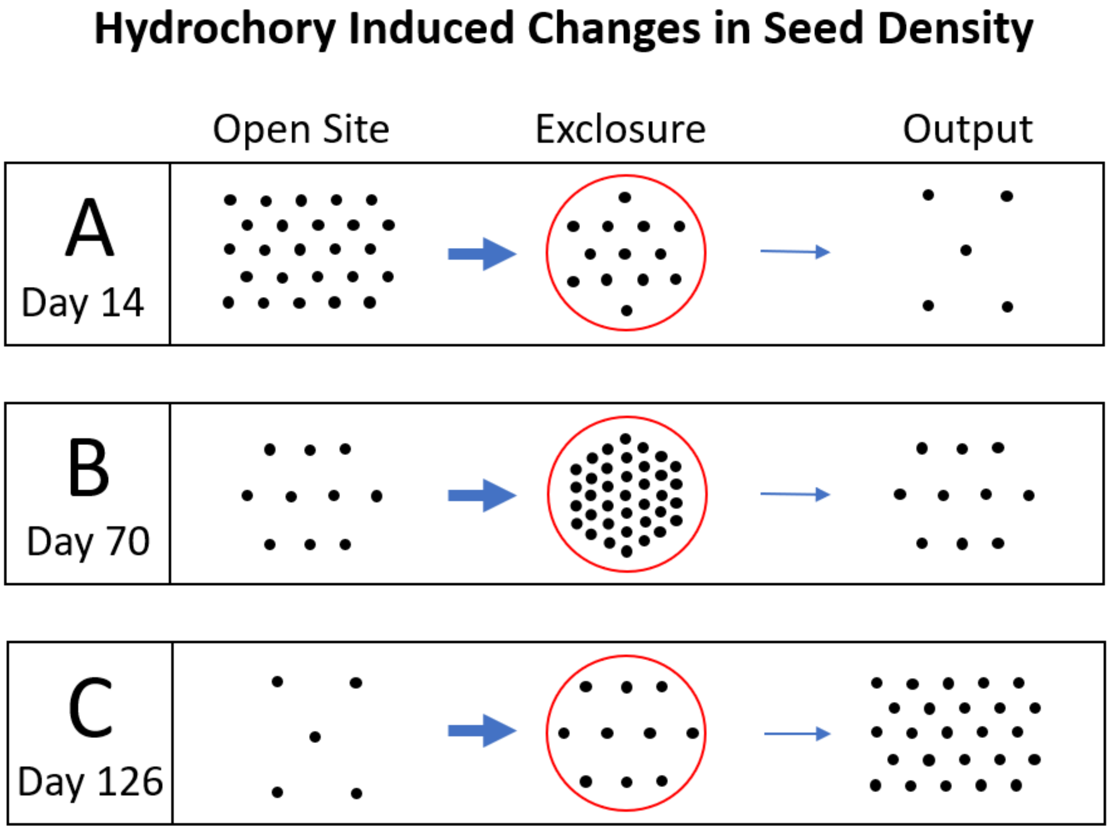

Figure 4.5: The influence of exclosures on seed abundance estimates. Black circles represent seed; the more numerous circles indicate greater densities. The large red circle represents the exclosure. Arrows represent that rate of seed movement; larger arrows represent a greater rate of movement.

Table 4.1: Decomposition Model Selection Table: A series of candidate models where the response variable, mass (grams) lost, is correlated with the covariates; species, sample period, site, and temperature. Model number 1 has the best support, which includes species and sample period as fixed effects and includes an interaction term to account for species-specific trends by sample period.

Model Number	Model Structure	df	AIC_c	BIC	Residual SE	Adjusted R^2
1	species*sampleperiod	19	-204.78	-189.34	0.025	0.973
2	species*sampleperiod + tubetemp	20	-201.90	-187.57	0.025	0.974
3	species*sampleperiod + site	21	-194.43	-181.53	0.026	0.971
4	species*sampleperiod + site + tubetemp	22	-192.90	-181.79	0.026	0.973
5	species*log(sampleperiod) + tubetemp	8	-190.49	-177.78	0.037	0.943
6	species*log(sampleperiod) + tubetemp + site	10	-187.22	-172.44	0.037	0.943
7	species*sampleperiod + site*tubetemp	24	-185.57	-179.22	0.025	0.974
8	species*log(sampleperiod)	7	-183.29	-171.80	0.040	0.933
9	species*log(sampleperiod) + tubetemp * site	12	-182.87	-166.61	0.037	0.943
10	species*log(sampleperiod) + site	9	-177.68	-163.87	0.041	0.93

Table 4.2: Linear model (Model 1 from Table 4.1) results for species-specific decomposition. Estimated species-specific mass (grams) lost at each time step (days) with confidence intervals (CI).

	Mass (g) Lost		
Predictors	Estimates	CI	p-value
species [*Bolboschoenus sp.*] (Intercept)	0.15	0.12 – 0.18	<0.001
species [*Bolboschoenus sp.*] * sample period2 [28 days]	-0.01	-0.06 – 0.03	0.49
species [*Bolboschoenus sp.*] * sample period 3 [42 days]	0	-0.04 – 0.04	0.9
species [*Bolboschoenus sp.*] * sample period 4 [56 days]	0.02	-0.02 – 0.07	0.274
species [*Bolboschoenus sp.*] * sample period 5 [70 days]	-0.02	-0.06 – 0.03	0.415
species [*Bolboschoenus sp.*] * sample period 6 [84 days]	0.03	-0.01 – 0.07	0.159
species [*C. schoenoides*]	0.15	0.11 – 0.19	<0.001
species [*C. schoenoides*] * sample period 2 [28 days]	0.05	-0.01 – 0.11	0.123
species [*C. schoenoides*] * sample period 3 [42 days]	0.09	0.03 – 0.14	0.006
species [*C. schoenoides*] * sample period 4 [56 days]	0.06	-0.00 – 0.12	0.055
species [*C. schoenoides*] * sample period 5[70 days]	0.13	0.07 – 0.19	<0.001
species [*C. schoenoides*] * sample period 6 [84 days]	0.14	0.08 – 0.20	<0.001
species [*E. crus-galli*]	0.05	0.00 – 0.09	0.035
species [*E. crus-galli*] * sample period 2 [28 days]	0.07	0.01 – 0.13	0.019
species [*E. crus-galli*] * sample period 3 [42 days]	0.16	0.10 – 0.22	<0.001
species [*E. crus-galli*] * sample period 4 [56 days]	0.27	0.21 – 0.33	<0.001
species [*E. crus-galli*] * sample period 5 [70 days]	0.36	0.30 – 0.42	<0.001
species [*E. crus-galli*] * sample period 6[84 days]	0.43	0.37 – 0.49	<0.001

Observations	54
R^2 / R^2 adjusted	0.982 / 0.973

Residual standard error: 0.02545 on 36 degrees of freedom
Multiple R-squared: 0.9819, Adjusted R-squared: 0.9733
F-statistic: 114.8 on 17 and 36 DF, p-value: < 2.2e-16

Table 4.3: Changes in species-specific mean dry mass by waterfowl use (low and high), and site type (open, exclosure, and wetland unit) over the entire sample period. Initial samples were collected 14 days after wetlands were flooded, and final samples were collected 126 days after wetlands were flooded. Observed loss is the quantity of mass lost over the 112 days between our initial sampling and final sampling event. Predicted loss was calculated by applying decomposition rates to initial mass values. Negative values indicate declines in mass, positive values indicate increases in mass.

	Average Dry Mass (mg)														
Species	**High Waterfowl Use**						**Low Waterfowl Use**						**Wetland Unit**		
	Open Sites			Exclosures			Open Sites			Exclosures					
	Initial Mass	Observed Loss	Predicted loss	Initial Mass	Observed Loss	Predicted loss	Initial Mass	Observed Loss	Predicted loss	Initial Mass	Observed Loss	Predicted loss	Initial Mass	Observed Loss	Predicted loss
Atriplex / Chenopodium sp.[a]	1.72	-1.02	-0.33	5.33	4.02	-1.02	0.04	1.51	-0.01	0.48	-0.13	-0.09	0.44	2.83	-0.08
Bolboschoenus sp.[b]	10.75	7.64	-0.75	4.35	34.83	-0.3	3.11	5.95	-0.22	2.25	2.67	-0.16	4.82	8.66	-0.33
Echinochloa crus-galli[b]	0	0	0	0	0.3	0	0	0	0	0	0	0	21.6	-21.5	-6.46
Polygonum aviculare[a]	15.83	-6.08	-3.01	21.7	-9.22	-4.13	18.77	-5.14	-3.57	3.3	1.73	-0.63	8.74	-4.27	-1.66
Sesuvium verrucosum[a]	5.75	-1.26	-1.09	5.57	2.07	-1.06	6.1	-2.02	-1.16	15.33	10.48	-2.92	19.71	-6.27	-3.75
Crypsis schoenoides[b]	192.73	-154.2	-38.64	225.68	-56.78	-45.24	82.56	-39.07	-16.55	161.48	-104.42	-32.37	166.83	-148.4	-33.45
Other[a]	1.62	-1.3	-0.31	0.93	0.6	-0.18	11.1	-1.12	-2.11	29.33	-17.62	-5.59	28.46	0.61	-5.42

[a] Mean decomposition rate observed across the three species we examined (0.17% mass lost)

[b] Species-specific decomposition rate based on our results (*Echincochloa crus-galli* = 0.27%/day, *C. schoenoides* 0.18%/day, and *Bolboschoenous* sp. 0.06%/day)

Table 4.4: Linear model results for our exclosure and open site assessment of seed abundance over the wintering period. Log normalized seed abundance (grams) was correlated with sampling period (days), waterfowl use areas (high and low), and site type (exclosures and open sites).

Log_e Total Seed Mass (g)

Coefficients:	Estimate	Std. Error	t value	p
sample period 1 [14 days] (Intercept)	-1.31	0.20	-6.53	<0.001
sample period 3 [42]	0.41	0.27	1.56	0.122
sample period 5 [70]	0.59	0.27	2.18	0.0312
sample period 7 [98]	0.07	0.28	0.26	0.7974
sample period 9 [126]	-0.45	0.27	-1.66	0.100
Type (Open)	-0.53	0.27	-2.01	0.0474
Use (Low)	-0.50	0.12	-4.14	<0.001
sample period 3 [42]: Type (Open)	-0.27	0.37	-0.72	0.4736
sample period 5 [70]: Type (Open)	-0.87	0.38	-2.30	0.0235
sample period 7 [98]: Type (Open)	-0.80	0.39	-2.07	0.0411
sample period 9 [126]: Type (Open)	-0.17	0.38	-0.46	0.6433

Multiple R^2*: 0.5008, Adjusted* R^2*: 0.4558*

Residual standard error: 0.6627 on 111 degrees of freedom

F-statistic: 11.14 on 10 and 111 DF, p-value: 5.712e-13

Table 4.5: Mean seed abundance at each sample period, separated by site type (open, and exclosure), and waterfowl use (high, and low). Wetland unit samples were not collected at 42 days and 98 days.

Mean Seed Abundance by Sampling Period

Site Type	Waterfowl Use	14 days		42 days		70 days		98 days		126 days	
		kg/ha	SE	kg/ha	SE	kg/ha	SE	kg/ha	SE	kg/ha	SE
Exclosure	High	964.07	173.88	1628.81	285.47	2487.22	535.06	1193.10	235.15	875.61	204.45
Open	High	835.43	252.77	929.44	254.97	440.70	108.30	336.15	120.40	263.99	29.36
Exclosure	Low	776.12	166.48	1151.73	307.05	1081.12	288.47	777.93	278.36	383.70	69.85
Open	Low	445.10	131.94	502.52	164.49	383.33	136.03	206.37	50.53	299.21	85.45
Wetland Unit		817.76	150.13	–	–	463.00	88.14	–	–	268.38	77.34

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