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Elizabeth Camarata for the degree of Master of Science in Environmental Sciences presented on May 23, 2019.

Title: Aquatic Plant Community Changes in Freshwater Ponds Recently Invaded by *Elodea canadensis* on the Western Copper River Delta, Alaska

Abstract approved:

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Establishment of a non-native plant species in new habitats beyond their native range is associated with inherent changes in ecosystem properties. These changes may be dramatic or subdued, and consequences may be positive or negative depending on characteristics and response of the resident ecosystem. Non-native aquatic plant species in the genus *Elodea* have demonstrated several adaptive characteristics which have led to a propensity for dominance where introduced. Species *Elodea canadensis, Elodea nutallii,* and their hybrid have recently become invasive in several waterbodies throughout the state of Alaska where this genus is the only documented non-native aquatic plant. In freshwater ponds of the Copper River Delta (CRD), the largest wetland complex in North America and critical habitat for fish and wildlife, infestation of *E. canadensis* has not homogenized all macrophyte communities over the last decade. Recent studies have described mechanisms of invasion of *Elodea* in other geographies; though, response of native plant species and native plant community dynamics in recipient habitats is still poorly understood. Wetland pond habitats on the CRD have undergone shifts in macrophyte community

assemblage and rapid succession resulting from a major tectonic event and include freshwater species tolerant of subarctic climatic conditions. Aquatic plants play an important role in structure and function of habitat. The purpose of this thesis is to advance the knowledge of aquatic plant community characteristics and patterns of variability to describe change which may influence higher trophic levels directly or indirectly. Species cover abundance, a population characteristic closely related to biomass, was utilized to assess changes in community structure, composition, and diversity by potential displacement of species due to recent occurrence of a non-native invasive species. Further, I investigated variability of species abundances at the resolution of the growing season and investigated how water temperature may mediate species interaction. This information was collected in five freshwater ponds, some with established populations of *Elodea canadensis,* positioned adjacent to two different drainages in the West CRD and analyzed then as individual cases to determine trends and identify patterns over a four-year snapshot of time in the species invasion.

Results of a community analysis employing non-parametric techniques for a multivariate dataset revealed no significant shift in community structure or composition in ponds where *E. canadensis* was present, never present, or eradicated among the four-year sample period. A pattern among ponds illustrating lack of trends at a yearly resolution suggested little influence exerted by the non-native species on the resident native assemblage at the levels of abundance in which *E. canadensis* has maintained over the time period. Investigation of temporal diversity at a yearly resolution revealed significant changes in individual species abundance and captured a pattern of shifts in species richness, evenness, and ordering of dominance. These results indicated a high level of variability within each growing season which may be explained by environmental parameters and their influence on species interactions. I concluded that, where there no overwhelming change in community characteristics has occurred over the study period, further investigation is needed to describe relationships between variability among species and physiochemical variables that may mediate the species interactions which structure aquatic plant communities. Establishment of these associations will allow further discernment of trends and aid in forecasting of community level changes.

Aquatic Plant Community Changes in Freshwater Ponds Recently Invaded by *Elodea canadensis* on the Western Copper River Delta, Alaska

by
Elizabeth Camarata

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Elizabeth Camarata, Author

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1.1 Aquatic Plant Communities and Exotic Species Invasion – An Overview

Establishment of an alien plant species in a new habitat beyond its native range causes inherent changes in ecosystem properties. These changes may be dramatic or subdued, and consequences may be positive or negative depending on impacts to conservation goals. Additions of plant species can increase diversity, structural complexity, and productivity (Kelly & Hawes, 2005; Thomas & Palmer, 2015; Schlaepfer, 2018); however, there are many examples of negative effects of exotic species on resident species performance which influence community characteristics such as biodiversity, structure, and function (Madsen et al., 1991; Parker et al., 1999). Recent studies have improved understanding of the patterns and mechanisms of invasion (Rejmánek et al., 2005; Levine et al., 2003), though impacts of non-native species to native plant community dynamics in recipient habitats is often poorly understood on a local level due to a lack of resources directed toward study of systems not yet in peril. Generally, the study of species invasions focuses on patterns of invasion and does not seek to elucidate sources of heterogeneity among invaded environments (Melbourne et al., 2007) which may be informative in explaining success of an invader or resilience of native community. It has also been recognized that only a small fraction of introduced species follow a trajectory of establishment, spread, and detectable impact (Williamson & Fitter, 1996).

Macrophytes are important primary producers in aquatic systems which act as substrate for epiphytic algae growth, an important food source for invertebrate grazers

(James et al., 2000). Dense aquatic macrophyte beds act as refuge for fish species (Valley & Bremigan, 2002) and affect movement of water and production-decomposition cycles which influence dissolved oxygen and other physiochemical conditions important for performance of higher organisms and food web dynamics (Carpenter & Lodge, 1986; Carter et al, 1991). Due to the importance submersed plant species in aquatic environments as service providers and ecosystem engineers (Jones et al, 1994), it is important to document trends over the course of the *Elodea canadensis* invasion on the Copper River Delta, an area of critical habitat for a variety of fish and bird species.

On this premise, I collected and analyzed aquatic plant community abundance data in several freshwater ponds on the Western Copper River Delta, recently infested by exotic species *Elodea canadensis*.

This chapter is an introduction into what is known about aquatic plant communities in the area and characteristics of exotic species *Elodea canadensis*. Species distribution on a landscape scale is driven by factors and gradients of a different spatial and temporal magnitude than distribution of species on a local scale where plant communities are influenced by some of these same factors yet structured by species interactions (Melbourne et al, 2007). Therefore, the scope of this research extends to a description of community patterns occurring at the same timepoint as infestation of a focal exotic species, *Elodea canadensis*, in the context of native aquatic species variation.

1.2 The Copper River Delta Aquatic Vegetation Communities

Prior to 1964, much of the delta was tidally influenced and included salt tolerant marsh plant communities. However, the 1964 earthquake resulted in uplift of the tidally influenced area shifted communities to freshwater macrophyte species. Community assemblages were influenced by alteration of water flow paths, deposition of sediment, erosional processes, and the biotic alteration of connectivity due to beaver activity (Boggs, 2000).

Due to this shift, macrophyte communities in the uplifted ponds are earlier in the stages of plant succession, though this has taken place rather rapidly (Boggs, 2000). Succession of communities has been characterized on the landscape scale, but little is known about the temporal diversity of these ponds. This work was done prior to the first reported occurrence of *Elodea* sp., the first and only reported invasive aquatic plant species in the state of Alaska to date.

The Copper River Delta, encompassing the project area, has been identified as a Critical Habitat Area by the State of Alaska as well as a Key Coastal Wetland by the United States Forest Service. These designations emphasize conservation of fish and wildlife which extends to suitability of their habitats.

1.3 Exotic Species Elodea canadensis

1.3.1 Taxonomy

Elodea canadensis is a submerged vascular aquatic plant belonging to the Hydrocharitaceae family. All species in the genus *Elodea* are submerged freshwater aquatic plants. Genetic analysis of *Elodea* samples from the CRD area revealed that only species *Elodea canadensis* Michx., or Canadian waterweed (Thum, 2015), is present.

1.3.2 Habitat and Distribution

Elodea spp. is found in lakes, ponds, and slow-moving waters and is tolerant of a wide range of water quality conditions (Spicer & Catling, 1988; Di Nino, Thiébaut, & Muller, 2005; Heikkinen et al., 2009; Grudnik & Germ, 2013). *Elodea* spp. generally occurs at intermediate water depths ranging from 0.1 to 8 m and is most often found between 0.1 and 1.5 m (Nichols & Shaw, 1986; Spicer & Catling, 1988; Mjelde et al., 2012). *Elodea* benefits from higher light levels in clear water, thus allowing it to grow to greater depth (Nichols & Shaw, 1986; Spicer & Catling, 1988; Lauridsen et al., 1994; Heikkinen et al., 2009).

Elodea is considered native to other places in North America such as most provinces of Canada and in the lower 48 states. This species is actively undergoing range expansion into higher latitudes from which it has previously been excluded. Range expansion of *E. canadensis*, *E. nuttallii*, and their hybrid is believed to have occurred in the 1980s. There are several examples of expansion and contraction of *Elodea* populations from Finland, Norway, Sweden, Germany, Czech Republic, and Japan (Lauridsen et al., 1994; Mjelde et al., 2012, Kadono, 2004; Simberloff & Gibbons, 2004). One potential mechanism for a population crash is depletion of iron or other nutrients in the sediment (Spicer & Catling, 1988; Kadono, 2004; Nagasaka, 2004; Simberloff & Gibbons, 2004). It is unknown whether its previous absence from the North American subarctic region is due to temperature limitations or simply geographic isolation. Populations of *E. canadensis*, along with similar species *E.*

nuttallii and their hybrid, are now present in several waterbodies throughout southcentral and interior Alaska.

1.3.3 Biology and Invasiveness

Previous studies have contributed to a pool of physiological knowledge on several *Elodea* species and the characteristics that contribute to their propensity for becoming dominant in areas of introduction outside their native range. In general, species of the genus *Elodea* have demonstrated phenotypic plasticity that allows it to adjust to a new environment (Thiébaut, 2007; Riis et al., 2010). The stem and vegetative buds of *E. canadensis* are fragile and easily broken, leading to dispersal through passive transport (Nichols & Shaw, 1986; Barrat-Segretain, 2005; Di Nino et al., 2005; Thiébaut, 2007; Xie et al., 2010; Sarneel, 2013). *Elodea* is able to store nutrients during winter dormancy, helping it grow early in the spring to outcompete native plants (Thiébaut, 2005). Photosynthesis of dense *Elodea* stands can create diel fluctuations of oxygen; observations have recorded as much as a 75% reduction in dissolved oxygen concentration throughout a day, dropping to levels harmful to fish and other aquatic organisms (1–2 mg/l). *Elodea* can also alter pH levels by respiration (Ondok et al., 1984; Mjelde et al., 2012). *Elodea* is considered stenothermic with optimum temperatures ranging between 10 and 25 degrees Celsius and it has a wide tolerance of pH levels ranging from 6.5 to 10. (Spicer & Catling, 1988; Heikkinen et al., 2009). As pH rises through the growing season, *Elodea* is able to use bicarbonate as a carbon source and maintain higher photosynthesis levels than other plants (Jones, Hardwick, & Eaton, 1996). *Elodea* is tolerant of desiccation and can survive being frozen in ice (Spicer & Catling, 1988; Kozhova & Izhboldina, 1993; Van Geest et al., 2005; Heikkinen et al., 2009; Barnes et al., 2013). None of these studies have been conducted in the sub-arctic ecoregion that includes Alaska, where 1) lentic waterbodies are glacial in origin, 2) geomorphic processes yield organic substrates, 3) diel cycles vary dramatically through the growing season, and 4) nutrients are overall limited.

Since introduction to the CRD, it has spread via flowing water, seasonally fluctuating water levels, and anthropogenic influences that include boats and float planes. These vectors have dispersed *E. canadensis* plants or fragments throughout the CRD lakes, ponds, and sloughs to create a landscape of well-established populations. Once present, it has been known to rapidly colonize through the mechanism of easily detachable apical fragments, which can easily root in substrate and reproduce vegetatively by stolons. Some individuals produce turions and dioecious flowers, but both are uncommon. Both male and female gametes need to be present to create a seedbank, but this is rare, and the most efficient reproductive strategy is usually clonal fragmentation. *Elodea* also has a wide tolerance to trophic conditions, as it is found across the full spectrum from oligo- to eutrophic ecosystems (Kozhova & Izhboldina, 1993; Greulich & Trémolières, 2006; Thiébaut, 2007).

Some studies have concluded that *Elodea* growth reduces algal diversity and productivity by increasing sedimentation, shading algae, and outcompeting algae for phosphorus, all of which favor other macrophytes (Perkins & Underwood, 2002). However, other studies have concluded that *Elodea* also provides habitat for epiphytic algae, and that this influences food web dynamics by reducing resources available to phytoplankton and other submerged aquatic vegetation (Carpenter & Lodge, 1986; Nichols & Shaw, 1986).

1.3.4 Invasion Timeline

Elodea is the first invasive submerged freshwater aquatic plant to be identified and documented in the state of Alaska. All species in the genus *Elodea* (*E. canadensis, E. nutallii,* and a hybrid are considered non-native and invasive in Alaska (Wurtz et al., 2013). In developed areas of the state, infestations have impeded float plane activity, a main mode of transportation, as well as reducing recreational activities. The first record of *Elodea* in Alaska was documented in 1982 as a small patch of plants in Eyak Lake on the West end of the Copper River Delta near the town of Cordova. In 2011 and 2012, the US Forest Service surveyed several locations throughout the lake, and found *Elodea* to be present in nearly all areas surveyed. Percent cover of aquatic vegetation was recorded by ocular estimation in several ponds and lakes across the delta over the 2015 and 2018 growing seasons. Surveys for the plant have not been conducted on all ponds and lakes of the delta as this is logistically impossible; however, many remote areas have been surveyed and monitored opportunistically. There is no hard evidence of exact introduction to the area and specific waterbodies in the study area, though the plant was detected in a number ponds adjacent to the Eyak River in years following initial detection in the upstream lake in 2011, and a flood event in 2009.

1.4 Study Questions

To shed light on changes in aquatic plant community structure over time and in response to efforts to eradicate *Elodea canadensis*, aquatic plant species abundance is being monitored by the USDA Forest Service (USFS) monthly over the growing season for four consecutive years. Physiochemical parameters were measured for use as predictor variables for explanation of variability.

In this thesis, I utilized species cover abundance, a population characteristic closely related to biomass, to assess changes in community structure, composition, and diversity by potential displacement of species due to recent occurrence of a non-native invasive species. Further, I investigated variability of species abundances at the resolution of growing season and investigated how water temperature may mediate species interaction. This information was collected in several freshwater ponds infested with *Elodea canadensis* and analyzed as individual cases over a four-year snapshot of time in the species invasion. The following section will address these questions:

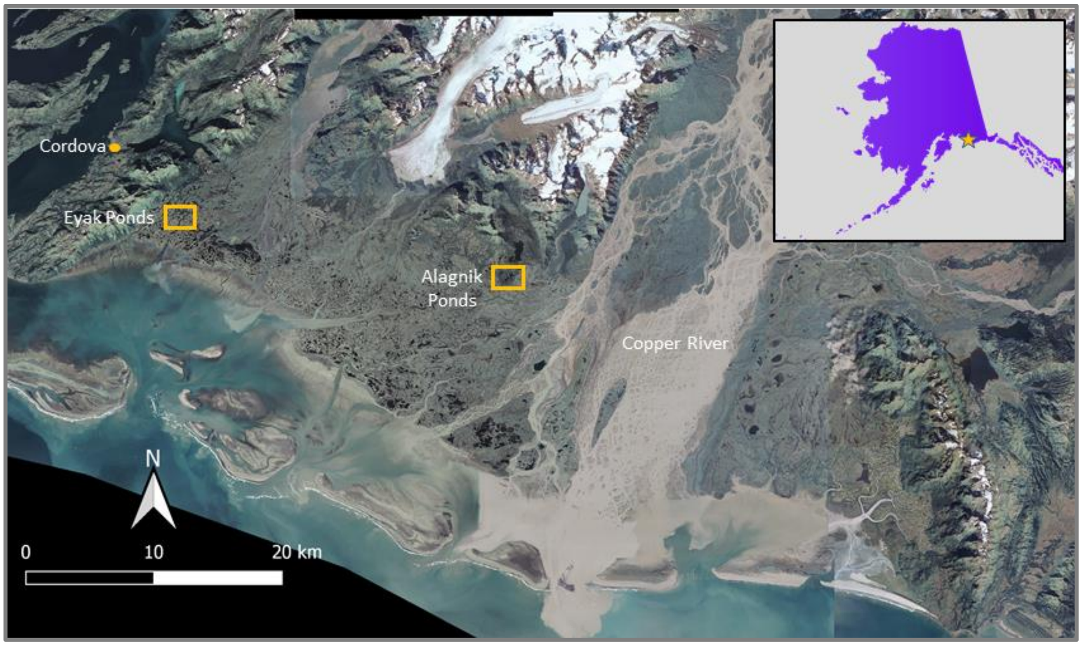
1) Did aquatic plant community characteristics change over a four-year snapshot in the infestation timeline? 2) How did diversity change from year to year; is there a pattern in year to year variation? 3) Was *Elodea canadensis* influential in structuring communities and in temporal dynamics of composition?

1.5 Methods Overview

1.5.1 Study Area

This study was conducted on the Copper River Delta (CRD), along the southcentral Gulf coast of Alaska bordered by the Chugach Mountains to the north and Prince William Sound to the west. The CRD is a discontinuous set of coastal deltas and alluvial piedmonts encompassing approximately 283,300 hectares comprising the largest coastal wetland complex in conterminous North America (Thilenius 1995). The project area is located east of the small fishing town of Cordova, within the CRD coastal wetland of south-central Alaska (Figure1.1). The region lies between 60°38’N to 60°00’N and longitude -145°52’ W. to 143°30’W. The average precipitation for the CRD is approximately 235 cm per year. Climate is characterized as wet and cool maritime. In general, the area lies within the Temperate Rainforest Ecoregion. Based on the hierarchical ecosystem classification, it resides in the Humid Temperate domain, Pacific Gulf Coast Forest and within the Meadow Province (Bailey, 1994). The delta is generally divided into rough types: the Uplifted Marsh area occurs closer to the Gulf of Alaska and is characterized by numerous shallow ponds containing fine marine sediment embedded substrates, separated by incised sloughs within a sphagnum moss ground cover and stands of alder and willow along channels; the Glacial Outwash Plain area is situated closer to the Chugach Mountains and is characterized by more infrequent ponds containing glacial sediment deposited substrate and spruce-hemlock forests (Boggs, 2000).

Figure 1.1 Study Area. Copper River Delta, Alaska, US. Study area is located within an uplifted deltaic wetland in the temperature rainforest of the southcentral coast.



1.5.2 Study Sites

Data was collected from five ponds spanning two pond complexes of differing geomorphological and hydrological characteristics (Table 2.1, Figure 2.1). Pond area and fetch length were measured from digital imagery in geographical information software. Pond depth measurements were averaged from water level readings at each sub-plot throughout the study. Shoreline complexity was calculated as the ratio of pond perimeter compared to a perfect circle of equal area.

The Eyak Cannery Pond complex is approximately 6 miles east of the town of Cordova and encompasses Eyak South Pond, West Cannery West Pond, and West Cannery East Pond; of which the latter two are hydrologically connected by a narrow slough yet are separated by a physical barrier to prevent flow through. These ponds are shallow with depths not often exceeding one meter. They are situated adjacent to the Eyak River and are perched above the river channel. Pond basins, which lie above river base flows most of the time, are ‘sealed’ by a thick silt layer, retarding ground water upwellings (Boggs, 2000). These ponds do not have direct connectivity to the Eyak River and water sources include largely precipitation and occasional spillover from flooding of the adjacent river. They cannot be considered ‘closed systems’ due to seasonal surface flood flows and potential ground water influence on recharge. The only fish species reported in this pond is Threespine Stickleback (*Gasterosteus aculeatus*). Ponds vary in size and shape but are rather similar in depth and bank slope. These ponds are in an open landscape with little allochthonous input from surrounding vegetation.

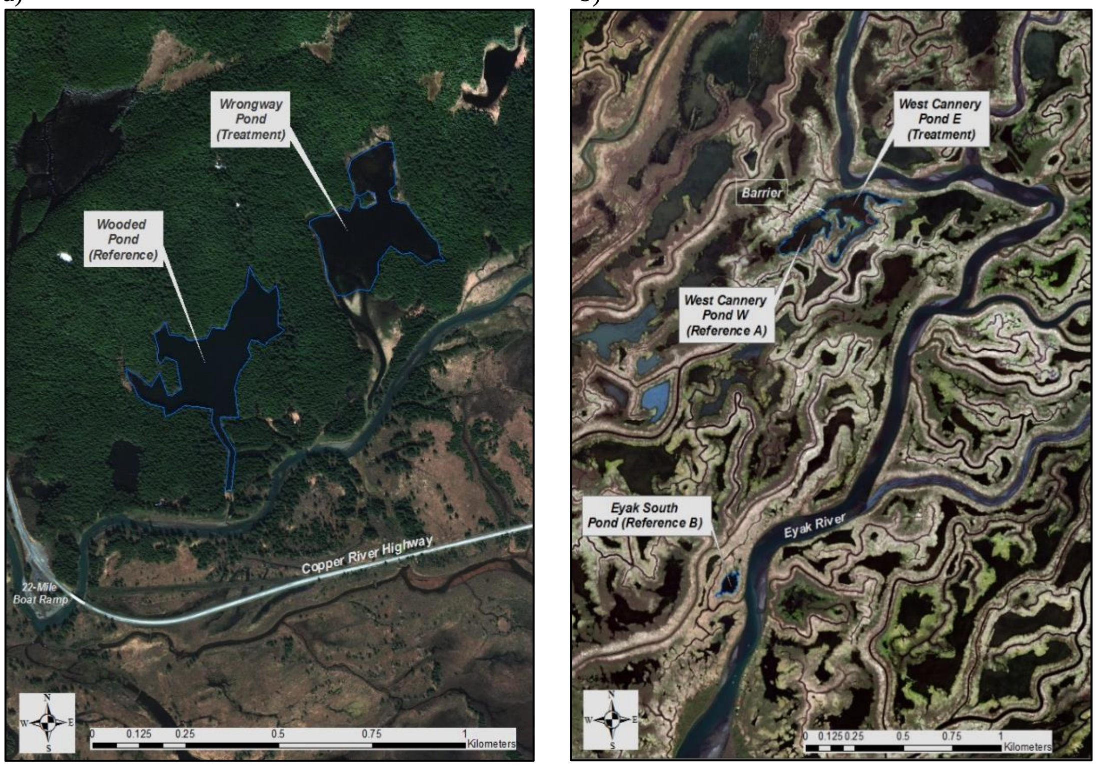
The Alaganik Slough pond complex is approximately 33 miles east of Cordova and encompasses Wrongway Pond and Wooded Pond, both of which are open system ponds with direct connectivity to the Alaganik Slough. The water source for both ponds is precipitation runoff from surrounding hills, glacier water from Saddlebag Creek, and backflow from Alaganik Slough which is fed by McKinley Lake. Both ponds are considered open systems because they are connected to the Alaganik River via sloughs. Several fish species migrate through these ponds including Coho Salmon (*Oncorhynchus kisutch*), Cutthroat Trout (*Oncorhynchus clarkii*), Dolly Varden (*Salvelinus malma*), Coastrange Sculpin (*Cottus aleuticus*), and Threespine Stickleback. These ponds are similar in size and shape yet vary in depth and thus bank angles which influence percent of littoral habitat. Wooded pond is substantially deeper in the middle portion of the pond. These ponds are surrounded by spruce-hemlock forest and receive allochthonous input from surrounding vegetation.

Table 2.1 Study pond physical parameters.

Site	Area (ha)	Depth Min (m)	Depth Max (m)	Depth Mean (m)	Shoreline Complexity	Fetch (m)
West Cannery West	2.3	0	0.9	0.56 ± 0.3	0.02	280
West Cannery East	3.5	0.02	0.7	0.48 ± 0.13	0.02	280
Eyak South	0.65	0.01	0.8	0.48 ± 0.17	0.01	130
Wrongway	8.5	0.05	1.7	0.92 ± 0.3	0.04	360
Wooded	6.5	0.02	3	0.92 ± 0.4	0.04	420

Figure 2.1 Study Ponds: a) Alaganik Slough; Wrongway and Wooded Ponds b) Eyak River; West Cannery West, West Cannery East, and Eyak South Ponds.

a) b)



1.5.3 Study Design

The study was conducted in five ponds adjacent to rivers occurring on the different drainages on the western portion of the CRD. Sampling was done using a nested-blocked design. Sample units (ponds) were chosen non-randomly based on logistically feasible access. Nested plots were sub-sampled at the quadrat level. Repeated sampling over four years comprised the blocking component.

Quadrat placement included (1) randomized plots within stratified areas of each pond, and (2) fixed plots occurring along permanently placed transects running perpendicular to shoreline chosen randomly but restricted to an azimuth unobstructed for the length of the transect. Randomized plots distributed throughout sections of each pond were stratified, based on zones of open water or complex littoral areas, to more accurately detect species richness within the whole pond with greater chance of capturing rare species, while also capturing distribution of *E. canadensis*. Plots fixed along transects were used to capture changes in abundance of individual vegetation patches over the growing season and year block by repeat sampling and serve to compare pre-and post-aquatic herbicide treatment measurements. An emphasis was placed on repeated measures provided by the temporal blocking component in local areas and achieving adequate precision by including sub-sampling.

Sampling intensity was set at an interval of once monthly throughout the growing season over the course four years. Site conditions in early and late season months such as ice, turbidity, and tannin staining of water dictated the ability to sample. Therefore, the only months which could be included in a balanced blocking design are June, July, August, and September.

The sample size was chosen in 2015 as 30 randomized sub samples per pond sample unit and repeated monthly based on the objective of providing initial survey data regarding infestation density within a given pond. However, sample size was adjusted based on logistical feasibility with access and effort despite a trade-off between confidence and precision with the time and cost of sampling. In 2016, a decision was made by the USFS include an herbicide treatment trial in one of the study ponds along with addition of transects to monitor effects of treatment by increasing ability for detection of changes in cover of *Elodea* relative to native vegetation, as well as pre- and post-herbicide treatment performance of native vegetation. Therefore, sampling effort was re-allocated to one 10-sub plot transect plot and ten randomized sub plots (Figure 2.2). To bolster detection of change and reduce variability, in 2017 an additional transect was added to each pond except Eyak South Pond due to its small area. This sampling effort was maintained in 2018. Sampling periods totaled twenty over four years.

Table 2.2 Sampling effort over the course of the study. Sampling effort increased over the course of the study based on available resources. Fixed Transect plots were initiated in 2016 while stratified random plots were sampled throughout the entirety of the study period (respective sample sizes denoted by “R” or “T” in the table). A total of 20 sample periods were implemented with a maximum number of subplots sampled of 180. Effort varied based on available resources and logistical constraints such as weather events.

Site		2015				2016						2017				2018					
		Jun	Jul	Aug	Sept	Apr	May	Jun	Jul	Aug	Sept	Jun	Jul	Aug	Sept	May	Jun	Jul	Aug	Sept	Oct
West Cannery West	R	3	10	10	8	5	10	10	10	-	10	10	10	10	10	10	10	10	10	10	10
	T	-	-	-	-	10	10	10	10	10	10	20	20	20	20	20	20	20	20	20	20
		N = 31				**N = 105**						**N =120**				**N =180**					
West Cannery East	R	6	18	18	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10
	T	-	-	-	-	10	10	10	10	10	10	20	20	20	20	20	20	20	20	20	20
		N = 52				**N = 120**						**N = 120**				**N =180**					
Eyak South	R	-	-	-	-	10	10	10	10	10	10	10	10	9	9	10	10	10	10	10	10
	T	-	-	-	-	10	10	10	10	10	10	20	20	20	20	20	20	20	20	20	20
		N = 0				**N = 120**						**N = 118**				**N =180**					
Wrongway	R	7	33	29	30	10	10	10	10	10	10	10	10	10	10	9	10	10	10	10	3
	T	-	-	-	-	10	10	10	10	10	10	20	20	20	20	20	20	20	20	20	20
		N = 99				**N = 120**						**N = 120**				**N =172**					
Wooded	R	10	11	11	11	10	10	10	10	10	10	10	10	10	5	10	10	5	9	9	4
	T	-	-	-	-	10	10	10	10	10	10	20	20	20	16	20	20	20	20	20	20
		N = 43				**N = 120**						**N = 111**				**N =167**					

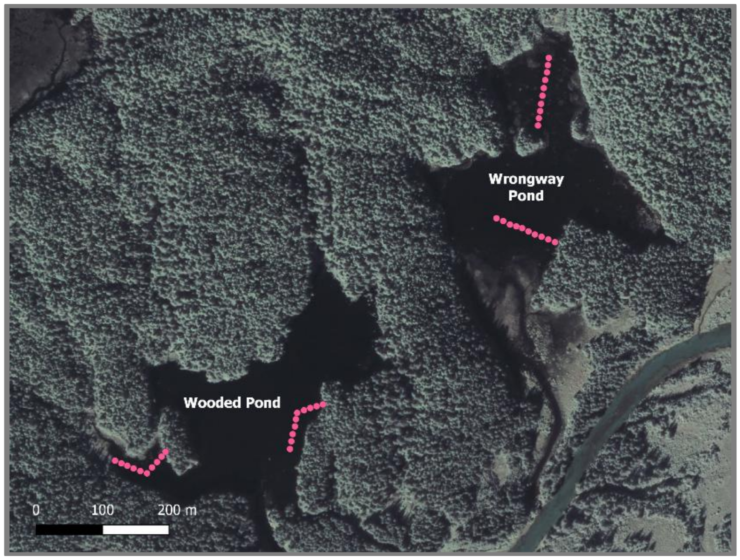
Dimensions of quadrats used in sub-plots were chosen as 1 m^2 to achieve adequate precision by capturing heterogeneity of the vegetation given typically occurring patch sizes in the ponds and detection of rarer species while maintaining a size manageable for transporting around a pond. Though quadrats with a rectangular shape generally improve precision by incorporating more variation in vegetation patchiness, sampling error in ocular estimations can increase due to difficulty of visualization. Position of random quadrats within the pond was determined using a stratified random scheme. Position of quadrats along transects was determined using a systematic interval scheme along the 100-meter plot at regular intervals of 10 meters apart along the base line resulting in 10 sub-plots per transect. 10 sub-plots yield a range of possible values that can be assumed from 0-100% by increments of 10%. The length of the transect was determined as 100 meters in order to achieve greater precision by capturing the inherent heterogeneity of the environment. The orientation of transects within the environment was selected based on capturing potential gradients in abundance of vegetation populations in the pond.

This sample design was chosen due to limited access for resampling remote areas and an understanding that landscape position is associated with variation in pond “types” across the delta landscape where the accepted classification is as follows: “Glacial Outwash” including Wooded and Wrongway ponds are situated adjacent to the Eyak River draining from Eyak Lake; and “Uplifted Marsh” including West Cannery West, West Cannery East, and Eyak South Ponds situated adjacent to the Alaganik Slough draining from McKinley Lake. The research questions presented here are restricted to drawing conclusions applicable to a narrow scope of inference due to a lack of replication.

Figure 2.2 Transect orientation in sample ponds: a) Eyak Ponds, b) Alaganik Ponds

a)

b)



One of the ponds, West Cannery Pond East, was treated with an aquatic herbicide in first June 2016 and subsequent months of each growing season thereafter. Regardless of repeated application, concentrations were not met and/or maintained for a duration long enough to affect plants in this pond until 2017, when concentrations spiked (Table 2.3). The herbicide used, fluridone, has a systemic affect on photosynthetic complexes and there is a substantial lag time between 30 and 90 days before mortality is induced depending on the time of year applied. Effects were not observed until 2018 when sampling indicated a disappearance of *Elodea canadensis*, the target species.

Table 2.3 Aquatic herbicide (fluridone) concentration (ppb) in Eyak Ponds. Adequate concentrations of herbicide were sustained for a duration necessary to affect vegetation beginning July 2017 and effects were not detected until May 2018 due to a lagged effect characteristic of the systemic herbicide.

	2016					**2017**				**2018**						
	7/19	8/16	8/31	10/05	10/20	7/16	8/14	9/11	10/13	4/26	7/11	8/29	9/12	9/25	10/12	10/24
W Cannery East **Treatment**	4	1.7	1.1	1.5	1.9	17.3	16.9	6.4	4.2	1.7	4.8	2.6	3.6	2.9	3.1	2.2
W Cannery West **Reference**	<1	<1	<1	<1	<1	1	1.6	1.3	1.3	<1	<1	1	1.7	1.5	<1	1.8

1.5.4 Physiochemical Data Collection

Information on environmental variables was collected during each macrophyte sampling period. Depth was recorded in meters at each macrophyte cover plot using a PVC rod marked in meter and centimeter increments. A YSI 556 MPS multiparameter meter unit was used for point sampling around the ponds in conjunction with samples being collected for associated macroinvertebrate and water chemistry studies by the USFS and other academic institutions. Point sampling included measurements of pH, temperature (C), dissolved oxygen (DO). Parameter measurements taken in the mid water column (metalimnion) were used. Sample points were located around the ponds coinciding with beds of differing vegetation composition. Replicates of metalimnion (middle column) samples were averaged to obtain whole values characteristic of a given sample period.

Water temperatures were recorded hourly using automated HOBO Pendant® data loggers (Onset Computer Corporation; manufacturer reported ± 0.2 °C accuracy) mounted on a t-post and placed in a central location in each pond. Data loggers were deployed at the beginning of each growing season and retrieved in the last few months of each year. Their position on the t-post was intended as an array for representation of three water column strata; however, less than three or two pendants were deployed in some ponds in some years based on availability of units. Malfunctioning and loss of loggers also occurred (Table A.1, Appendix A)

In these instances, gaps in water temperature data were modeled based on relationships to air temperature recorded at the Merle K "Mudhole" Smith airport, thirteen miles from the western edge of the CRD. These data were acquired by request from NOAA GHCN daily summaries. Daily maximum and minimum air temperatures were averaged to yield daily air temperatures (Figure A.1, Appendix A). Hourly water temperature data was averaged to yield daily water temperature values which were then compared to daily air temperature values by plotting the two against one and other and assessing correlation using coefficient R^2 (Table 2.4). This was done separately among years to reduce influence of confounding factors such as weather patterns and hydrologic events. In the year 2017, data loggers were deployed early in the season and without malfunction, and therefore modeling was not necessary.

Table 2.4 Correlation coefficients for air-water temperature relationships used for modeling missing water temperature data. *No modeling was needed for 2017 data.

Site		2015	2016	2017	2018
West Cannery West	R^2 =	0.7	0.8	-	0.5
West Cannery East	R^2 =	0.7	0.8	-	0.5
Eyak South	R^2 =	-	0.8	-	0.5
Wooded	R^2 =	0.5	0.7	-	0.6
Wrongway	R^2 =	0.7	0.6	-	0.5

Light intensity measured in Lux, the proportion of lumens over an area (1 Lumen/m2) was recorded on an hour interval using these sensors. Light sensors on the pendent loggers capture the whole range of visible light as opposed to more relevant sensors which measure down and upwelling light intensity along the photosynthetically active radiation (PAR) range of 400-700 meters. Data from loggers is useful for determining light extinction coefficients which can be a meaningful variable to compare with vegetation attributes. However, this was not possible for this study therefore light intensity was not considered. The study ponds are generally shallow and light attenuation did not exceed what was necessary for ocular estimations of plant cover, therefore this variable was not considered.

Data acquisition for Total Nitrogen (TN) was carried out by the University of Notre Dame. Field methods included collection of grab samples in Nalgene bottles (1 L) which were triple rinsed at each site before filling. Lab procedures include triple rinsing all glass amber storage bottles with filtered sample water. Bottles were filled with 60 mL of filtered water and 240 μL of concentrated hydrochloric acid for preservation purposes and stored in a refrigerator until samples could be analyzed to determine TN concentrations using chromatography. See Appendix A for water temperature, TN concentrations, and pH.

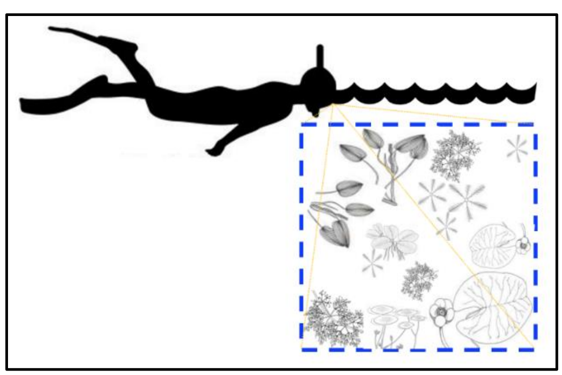
Herbicide concentration was determined by analyzing grab samples from the treated waterbody (West Cannery East Pond) as well as the untreated waterbody in close proximity (West Cannery West Pond). This variable is assessed for West Cannery East Pond, the only pond treated in the study set, and is denoted in the dataset with values representing fluridone concentration two weeks prior to the sampling period dates.

1.5.5 Aquatic Plant Species Abundance Sampling

Within pond sample units, sub-sampling was conducted in nested 1 m^2 quadrats. Abundance of each species was quantified by estimating the foliar cover of vegetation rooted within the plot frame. Ocular estimations of submerged plants were carried out by the observer snorkeling over the plot area (Figure 2.3). Cover values were expressed as a percentage of the plot area and recorded as actual values, as opposed to commonly used cover class methods. Cover estimates accounting for overlap is a standard practice in terrestrial environments; however, snorkel surveys allow for only an overhead view of vegetation cover and rarely provide a cross-sectional perspective of canopy strata. As a result, estimations were standardized to total 100% per quadrat including bare sediment and woody debris. A single observer quantified aquatic vegetation in 2015 and 2016 data to reduce variability introduced by observer bias; however, additional observers were added in 2017 and 2018. Sub-plot quadrats were positioned within the pond using a stratified random scheme, while a systematic interval scheme was used in the case of transects.

At each quadrat, individual plants were identified to species based on taxonomy and nomenclature current in the USDA PLANTS database (2016), the publication *Introduction to Common Native and Potential Invasive Freshwater Plants in Alaska* (2009) with reference to dichotomous key *Flora of Alaska and Neighboring Territories* (Hultén, 2009). Nomenclature at the time of 2015 sampling was recorded following a six-letter code convention consisting of the first three letters from both the genus and specific epithet based on Chugach National Forest vascular and nonvascular species lists from previous surveys. Species codes were recorded consistent with USDA plants database codes from 2016-2018.

Figure 2.3 Snorkel observer aerial perspective of ocular estimations.



SECTION 2: SHIFTS IN AQUATIC PLANT COMMUNITY CHARACTERISTICS AND TEMPORAL DIVERSITY IN SEVERAL FRESHWATER PONDS INFESTED WITH *ELODEA CANADENSIS*

2.1 Introduction

The effects of establishment by a non-native species on the native community differs among invaders and by the number of individual invasive species present at one time. However, in most cases, the invasiveness of a species at a point in time can be related back to its abundance surpassing that of natives. Some species do not need to achieve a high relative abundance to affect ecosystem processes by altering some functional aspect of the system; however, invasive strategies are often predicated on displacement of other species with which it competes for resources. Levine et al. (2003) concluded that ecological interactions rarely enable communities to resist invasion, but instead constrain the abundance of invasive species once they have successfully established. At the community level, the suppression of native plants is a result of the dominance an invasive species achieves in the invaded habitat (Daehler, 2003). A non-native plant exhibiting behavior characteristic of an invader will outperform co-occurring natives is expected to increase in relative abundance over time (Daehler & Carino, 1999).

Studying the community level impacts in the field is often accomplished by comparing invaded and uninvaded plots to identify potential effects of an invading alien species relative to natural random variation. However, with a lack of sufficient sample size, evaluation of impact by statistically testing for effects by comparison of invaded and uninvaded, or before/after invasion is not possible with this dataset. For this reason, a pattern analysis approach was used with his dataset treating each pond as a separate case contributing evidence toward answering several key questions.

Differences in structure and composition of communities were assessed by applying non-parametric hypothesis testing to multivariate components. This was done by summarizing the data and reducing correlations to measures of distance of each sample unit based on the species composition. Two of the research questions will execute hypothesis testing employing this data structure. Descriptive techniques were used to evaluate how diversity changed over time and which species contributed to stability of a site. A description of the magnitude and direction of variability in dominant species' abundances from year to year is provided using a variable representing a measure of change, as this attribute may be indicative of displacement of native species.

Research questions are: 1) Did aquatic plant community characteristics change over a four-year snapshot in the infestation timeline? 2) How did diversity change from year to year; is there a pattern in year to year variation? 3) Is *Elodea canadensis* influential in structuring communities and in temporal dynamics of composition?

2.2 Analysis Methods

2.2.1 Question 1 Methods: Did aquatic plant community characteristics change over a four-year snapshot in the infestation timeline, between 2015 and 2018?

Differences in community structure and composition were examined through community analysis using PC-ORD Software, version 7.02 (McCune & Mefford, 2016). Data was organized into multivariate matrices: 1) The primary matrix consisted of species arranged in columns and sample units arranged in rows with the response variable, abundance, populating the body of the matrix; 2) A secondary matrix containing environmental predictor variables in columns and sample units in rows corresponding to those in the primary matrix. Matrices were constructed using the reshape and "dplyr" packages (Wickham et al., 2017; Wickham, 2009) in R statistical software (R Core Team, 2017). Prior to applying modifications or transformations to data, data structure was explored by a descriptive summary of totals and coefficients of variance of rows (sample units) and columns (either species or environmental variables). Due to the prevalence of infrequently occurring plant species, several transformations of the raw data were evaluated in an attempt to reduce variance and improved data structure in both transect and random plot data; though, none were applied as no method was effective in further extracting new or stronger signals from the data. The raw data for both transects and random plots consisted of actual percent cover values of each plant species at each sub-plot (quadrat), summaries indicating great variation of species abundance values and weakly structured data. This was due to many zeros present in the dataset resulting from many infrequently occurring species. To assess changes in community structure, only data from fixed transect plots which were repeated between years, were considered. Separate species matrices were constructed and analyzed for each study pond as comparisons between ponds are not of interest in this analysis. A Mantel Test, performed in PC-ORD Software, version 7.02 (McCune & Mefford, 2016), was used to test significance of the congruence between two matrices by seeking linear relationship using randomization, which does not require the assumption of independence (McCune and Mefford, 2016). This method was employed to compare Sørensen distance matrices based on the raw data matrices between the same set of sample units for the month of July of two respective years. July was chosen due to this month having had equal sample effort among years, a requirement for the Mantel Test, as well as July representing the peak of the growing season when all species are occurring. Correlation of the two matrices is evaluated and compared to correlation coefficients generated by random reordering of the two distance matrices. The test statistic is a standardized Mantel statistic similar to Pearson's correlation coefficient (*r*), and a *p*-value is reached by measuring how likely the distance matrices are to have similar correspondence due to chance after 999 permutations. For each site, this test was applied to determine correlation of transect data from 2016, the first year transects were established, and 2018. Since only one transect had been established in 2016, data from the initial plots were used for this comparison. This method was repeated by site for comparison between data from 2017, when second transects were established, and 2018 incorporating information from both sets of transect plots. Explanation of the matrix dimensions for each species are reported with results (Table. 2.6).

Non-metric multidimensional scaling (NMS) (Kruskal, 1964; Mather, 1976) was used to visualize results from the Mantel Test using the same July 2016 to 2018 dataset balanced in sample size and sampling effort. No modifications to the data were applied to the 50 sample units and 21 species before proceeding in autopilot mode "medium" using the Sørensen distance measure. NMS performed 50 runs on actual data and 50 runs on randomized data using a random starting configuration and with no penalization for ties. Convex haul overlays that grouped years allowed for graphical examination of the relationships of sample unit distance configurations in species space for the same month across years.

To assess compositional change, raw data structure was aggregated by averaging percent cover values to species total mean percent cover for each sample month of each sample year to extract a signal of yearly differences. Differences in species composition between year groups repeatedly sampled by month were tested using a blocked multi-response permutation procedure (MRBP) (Mielke & Berry, 2001) and performed in PC-ORD Software, version 7.02 (McCune & Mefford, 2016). This is a nonparametric technique for testing group differences that produced pairwise comparisons for all year groups. Matrices based on Sørensen distance were used to test the hypothesis of no difference between groups which is expressed using a descriptive term for effect size termed "*A*" that identifies within-group agreement. When *A* is close to 1, the composition of the compared groups is identical; when *A* is close to -1, composition of groups is less homogenous than expected by chance. A *p*-value is generated to indicate the likelihood that observed group differences are due to chance. Euclidean distance was used for pairwise comparisons. Total mean cover, the average cover of each species across all plots sampled, and which included the cover of bare ground in plots, was chosen because it was important to know not only plant coverage, but also the amount of bare ground. Only months June through September were included in matrices due to unequal sampling effort across years in April, May, and October. Data from both transect and randomized plots were considered in MRBP analysis. Main matrices containing species data and secondary matrices containing environmental variables were constructed and analyzed for each study pond as comparisons between ponds are not of interest in this analysis. Explanation of the matrix dimensions of each species are reported with results (Table. 2.7).

Differences in compositions of year groups revealed by MRPB were described for each site using Indicator Species Analysis (ISA) performed in PC-ORD Software, version 7.02 (McCune & Mefford, 2016) to qualify the year groups by identifying species which characterize them. The ISA method (Dufrêne & Legendre, 1997) is used to illuminate the contrast in performance of species which are indicators of a group. This descriptive technique uses relative abundance and relative frequency to compute indicator values (IVs) for each species which are indicative of participation in year groups. The contribution of each species to structural components of the group can be assessed in this way. The significance of IVs for each species is qualified by a Monte Carlo test with 1000 randomizations.

2.2.2 Question 2 Methods: How did diversity change from year to year; is there a pattern in year to year variation??

Overall change in site diversity over years was accounted for using the Shannon Diversity Index which gives a variance measure of species abundance distribution indicative of the level of difficulty surrounding predicting the identity of a randomly sampled plant. Values were calculated using the “vegan” package (Oksanen et al., 2018) in R software (R Core Team, 2017).

Temporal dynamics of aquatic plant community abundance were investigated. Species richness, a diversity parameter, was translated to a measure of total turnover which is calculated as the sum of the number of species which appear and those which disappear between years divided by the total number of species observed over the two time points and is represented as a proportion (Collins et al., 2008; Cleland et al. 2013). These components of appearance of new species and disappearances of previously occurring species were used to evaluate turnover of species regardless of species identity within a site over a year pair. Regarding the question of species displacement, totals of species appearance and disappearance from the system is informative, but trends in reduction of abundance at the species level may also provide evidence of individuals in a species population being displaced over time.

Yearly changes in individual species' abundances was assessed and significant of changes were evaluated for each site. Relative abundance was used in this analysis because it represents a species' proportion relative to all species present at that time. Relative abundance values were calculated as the proportion of each species relative to total proportion of macrophytes and represented as a percent. Bare ground is also calculated and summarized as total mean abundance per plot or site. The combination of vegetation and bare ground cover total 100% cover. Bare ground was not factored in the calculation of plant abundance related to plant proportion. The mean of these values aggregated to yearly timesteps is more meaningful than mean total abundance, which can be highly influenced by lower values at the tail ends of the growing season and thus not representative. Significance of changes in species mean relative abundances between years was evaluated by first constructing 95% confidence intervals from the standard error of the mean using a summary function written in R Software (R Core Team, 2017), then plotting and observing overlap in confidence interval limits among years. This is an estimate of confidence that the expected population mean will fall between the upper and lower bounds based on the sample size and the standard deviation of values used to calculate the observed point estimate. While lack of overlap of confidence intervals is highly indicative of significance differences in group means, in this case yearly means, lack of separation does not always imply a lack of significance (Payton et al., 2003).

Rank abundance, the order of species based on their abundance, was also assessed over time. This was accomplished through calculating rank-shift values which quantify relative changes in species rank abundance as the total difference in ranks over consecutive time points. The result is mean rank shift values for each year pair. Shifts in species rank over time was represented using a rank-shift clock, a visual aid for observing the re-ordering of species in a community over time. Overall rate of change was assessed for each pond by analyzing differences in species composition between sample years over consecutively increasing lags in time. These functions were performed using R (R Core Team, 2017) package "codyn" (Hallett et al., 2016).

2.2.3 Question 3 Methods: How much influence does focal species *E. canadensis* have on community structure?

To assess the influence of *E. canadensis* on community characteristics, its contribution to community structure was tested by comparing sample unit distance measures with and without the exotic included. Sperate species matrices were constructed; the first included the exotic species, and the second excluded the exotic species by simple deletion from the dataset. A Mantel Test was performed on distances measures associated with each of the two matrices to investigate correlation, and a randomized permutation test was included to determine significance of correlation. Non-metric multidimensional scaling (NMS) (Kruskal, 1964; Mather, 1976) ordination was then used to visualize correspondence between the actual community, and the community fictitiously lacking the exotic species, by comparing separate structural representation in reduced space. NMS was run in PC-ORD Software, version 7.02 (McCune & Mefford, 2016) with autopilot mode medium and Sørensen distance measure selected. NMS performed 50 runs on actual data and 50 runs on randomized data using a random starting configuration and with no penalization for ties. Data visualization was accomplished using successional vectors which represents migration of sample units through species space over time. Direction and magnitude of successional arrow between the paired ordinations was evaluated. The raw data was aggregated by averaging percent cover values from quadrats to species total mean percent cover for month-year combinations.

2.3 Results

2.3.1 Question 1 Results: Community Structural and Compositional Shifts

Mantel Test

The results of the Mantel Test performed on fixed transect plot data from 2016 to 2018 showed an overall moderate to strong correlation between distance matrices calculated from dissimilarity between sample units based on their composition. Any observed congruency between groups of sample years was significant when compared to random chance. In West Cannery West Pond, there was moderate correlation (r = 0.4, $p = 0.04$) in the distance matrices reflecting consistency in community structure among all years. The site treated with herbicide, West Cannery East, also displays congruence between the first and last sample year and yielded a strong correlation of species matrices (r = 0.78, $p = 0.003$). The Eyak South Pond also demonstrated strong congruency between sample year 2016 and 2018. Correlation of distance matrices representing dissimilarity of sample units at both Wrongway and Wooded Ponds was moderately strong between 2016 and 2018 (r = 0.6, $p = 0.001$ and r = 0.56). See table 2.5 for full statistical summary.

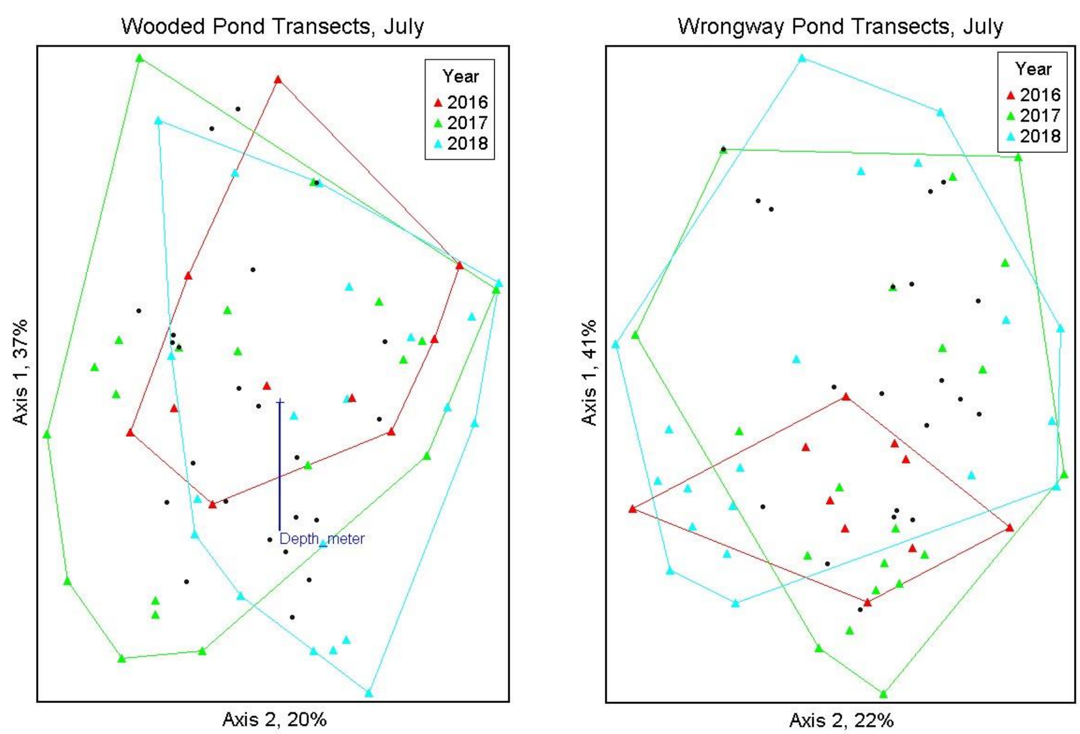
Table 2.5 Results of Mantel Test and description of matrices used. Comparisons made between 2016 and 2018 were based on 10 sample units, and comparisons made between 2017 and 2018 were based on 20 sample units based on presence of either one of two sets of fixed transect plots. Each pond displayed a significantly strong correlation of community structure between at least one year-pair including the last sample year.

Site	Comparison	SU	Species (1st, 2nd)	Transects Compared	r	*p*-value
West Cannery West	2016 v. 2018	10	14, 16	T1	0.4	0.04
	2017 v 2018	20	20, 16	T1, T2	0.4	0.001
West Cannery East	2016 v. 2018	10	14, 10	T1	0.78	0.003
	2017 v 2018	20	20, 16	T1, T2	0.4	0.001
Eyak South	2016 v. 2018	10	8, 9	T1	0.82	0.001
	2017 v 2018	-	-	-	-	-
Wrongway	2016 v. 2018	10	10, 10	T1	0.4	0.03
	2017 v 2018	20	21, 15	T1, T2	0.60	0.001
Wooded	2016 v. 2018	10	16, 20	T1	0.44	0.02
	2017 v. 2018	20	22, 20	T1, T2	0.56	0.001

Non-metric Multidimensional Scaling

Mantel Test results were reflected in configurations of NMS ordination plots (Figure 2.4). Convex haul overlays representing year groupings of sample unit aggregations were overlapping in species space for both Alaganik sites. Ordination yielded three-dimensional solutions for Wrongway and Wooded Ponds with final stress of 16.4 after 109 iterations (p = 0.02), and 16.1 after 76 iterations (p = 0.3) respectively. Wooded Pond axes explained 71% of the variation (axis 1 = 37%, axis 2 = 20%, axis 3 = 14%) with depth being the most correlated variable to axis 1 (r^2 = 0.4). Wrongway Pond axes explained 76% of the variation (axis 1 = 41%, axis 2 = 22%, axis 3 = 13%) with depth being the most correlated variable to axis 1 (r^2 = 0.6). No useful ordination solutions were found for Eyak River site due to weak structure in the data resulting from many rare species producing zeros in the dataset and lack of physical or temporal gradients. When each site is considered separately, the Eyak River sites lack strong physical depth gradients. The temperature variable has the potential to emerge as a temporal gradient when performing separate ordinations for each site as this variable would change in the same way over time among sample units within the site. If multiple sites are considered in the ordination, this variable has the potential for emerging as a spatial gradient as temperature within different sites may not change in the same way over time due to unique site-specific confounding factors. This portion of the analysis is comparing community structure at the peak of growing season over years thus considering only one isolated month. Therefore, no strong temporal gradient would emerge due to the temperature variable representing a monthly time step and similarity in July temperatures among years.

Figure 2.4 Non metric multi-dimensional scaling ordination plots describing results of the Mantel Test of correspondence between distance matrices. The two examples are from the Alaganik group ponds. The ordination plots represent the change in community structure over years at a site. The NMS procedure operated on the same data as the previous Mantel Test using a matrix of species abundances. The small triangles represent sample units, which are configured at distances from one and other according to their dissimilarities in species composition. The distance between two triangles represents the magnitude of dissimilarity. The colors correspond to the year with which the sample unit belongs. The overlaid polygons encompass all sample units for a given year. High overlap in groupings of sample units per year in species space. This illustrates the lack of change in community structure indicated by the Mantel Test results. If communities had shifted in the configuration of their composition, the different colored polygons would occupy separate regions in the ordination space.



Multi-Response Permutation Procedure

The results of the MRPB procedure to test for compositional differences among groups yielded, overall, mostly moderate agreement among groups at all sites. The site with the most homogeneity of composition in sample units among years was West Cannery West Pond (A = 0.3, p = 0.0007). Pairwise comparisons at this site reveal levels of agreement indicating that groups are more homogenous than expected by chance between the first sample year and the last sample year, 2015 and 2018 (A = 0.5, p = 0.03), though no statistically significant agreement could be found between 2015 and 2016 or 2017. Test results for West Cannery East Pond showed overall high agreement with the most homogenous species compositions being displayed between the first and last sample year, again, despite the herbicide treatment effectively removing the exotic species in 2018. Statistically significant pairwise comparisons were lacking for Eyak South Pond and Wooded Pond, though overall agreement was greater than expected by chance in the latter pond (A = 0.13, p = 0.003). This is likely due to a smaller sample size in these ponds; less plots in general in Eyak South as it is smaller, and barriers to sampling all plots in Wooded as water is tannic and visibility can be limited. See table 2.6 for full summary of results.

Table 2.6 Results of MRPB test and description of matrices used. Greyed rows represent year pairs where agreement between year groups is not significant ($p > 0.05$). In the context of ecology, an *A* statistic of 0.3 is considered high. Therefore, as the value exceeds zero and approaches the "high" end, there is a greater probability of non-difference between composition of species in different years than expects by natural variation.

	SU	Sp	Comparison	Months Included	*A*	*p*-val
West Cannery West	16	18	2015 v. 2016	June - Sept	0.11	0.12
	A = 0.3 *p* = 0.0007		2015 v. 2017	June - Sept	0.19	0.06
			2015 v. 2018	June - Sept	0.35	0.03
			2016 v. 2017	June - Sept	0.28	0.03
			2016 v. 2018	June - Sept	0.47	0.03
			2017 v. 2018	June - Sept	0.16	0.04
West Cannery East	16	28	2015 v. 2016	June - Sept	0.24	0.03
	A = 0.27 *p* = 0.0004		2015 v. 2017	June - Sept	0.18	0.05
			2015 v. 2018	June - Sept	0.44	0.03
			2016 v. 2017	June - Sept	0.10	0.14
			2016 v. 2018	June - Sept	0.36	0.02
			2017 v. 2018	June - Sept	0.24	0.03
Eyak South	12	17	No Sample in 2015			
	A = 0.08 *p* = 0.1		2016 v. 2017	June - Sept	-.005	0.41
			2016 v. 2018	June - Sept	0.14	0.08
			2017 v. 2018	June - Sept	0.03	0.32
Wrongway	16	30	2015 v. 2016	June - Sept	0.23	0.03
	A = 0.24 *p* = 0.00004		2015 v. 2017	June - Sept	0.24	0.03
			2015 v. 2018	June - Sept	0.34	0.02
			2016 v. 2017	June - Sept	0.22	0.02
			2016 v. 2018	June - Sept	0.24	0.03
			2017 v. 2018	June - Sept	0.20	0.03
Wooded	16	30	2015 v. 2016	June - Sept	0.10	0.16
	A = 0.13 *p* = 0.003		2015 v. 2017	June - Sept	0.14	0.08
			2015 v. 2018	June - Sept	0.17	0.04
			2016 v. 2017	June - Sept	0.03	0.3
			2016 v. 2018	June - Sept	0.17	0.03
			2017 v. 2018	June - Sept	0.07	0.1

Indicator Species Analysis

Few species emerged as significant indicators of year groups based on ISA analysis (Table 2.7). This is particularly true for the Eyak South pond, a site where the dominant species tend occupy the entirety of the plot are when sampled and thus the same species have approximately equal likelihood of membership to each year group resulting in no one species emerging as an indicator. The results of ISA analysis indicate that *Hippuris vulgaris* is dominant in the 2018 vegetation in Eyak South Pond (IV = 53.8, p = 0.03), no species emerged with significant indicator values for previous years so there is no comparison to be made regarding change over time. *E. canadensis* was not a significant indicator for any year groups at any of the sites, therefor no years can be characterized as dominated by the exotic species. The most perfect group membership is demonstrated by *Sparganium hyperboreum* at West Cannery East Pond in 2018, which is post *E. canadensis* eradication.

Table 2.7 Results of Indicator Species Analysis for year group characterization by species importance values (IV). Red text highlights insignificant IVs representing group membership less than is expected by chance for *E. canadensis.*

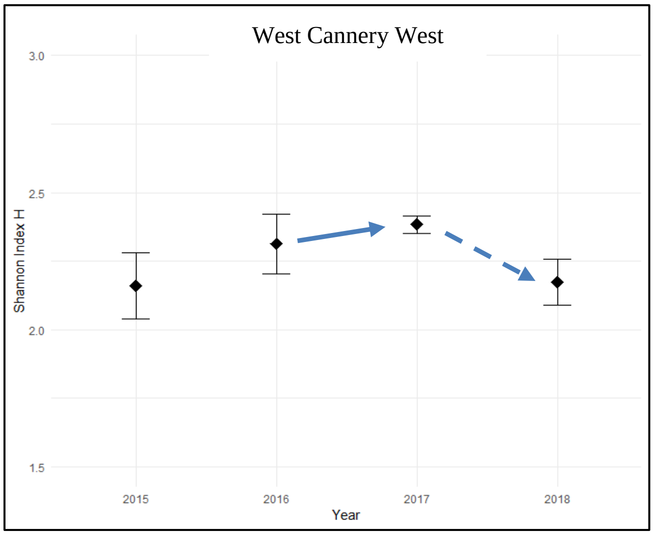
	2015			**2016**			**2017**			**2018**		
	Species	IV	*p*-value	Species	IV	*p*-value	Species	IV	*p*-value	Species	IV	*p*-value
West Cannery West	SPHY ELCA7	50.2 35.0	0.03 0.07	-	-	-	POPA14	53.4	0.04	FOAN2 MYSI	39.9 47.1	0.03 0.03
West Cannery East	-	-	-	TYLA	65.3	0.01	ELCA7	38.5	0.3	BARE METR3 SPHY	44.8 33.9 86.1	0.01 0.05 0.01
Eyak South	-	-	-	-	-	-	-	-	-	HIVU2	53.8	0.03
Wrong-way	PORI2 ELCA7	37.9 26.7	0.02 0.7	EQFL	45.5	0.04	-	-	-	FOAN2	33.9	0.01
Wooded	-	-	-	RATR ELCA7	39.8 27.4	0.04 0.6	ISOET POPUT3	90.2 67.6	0.01 0.05	-	-	-

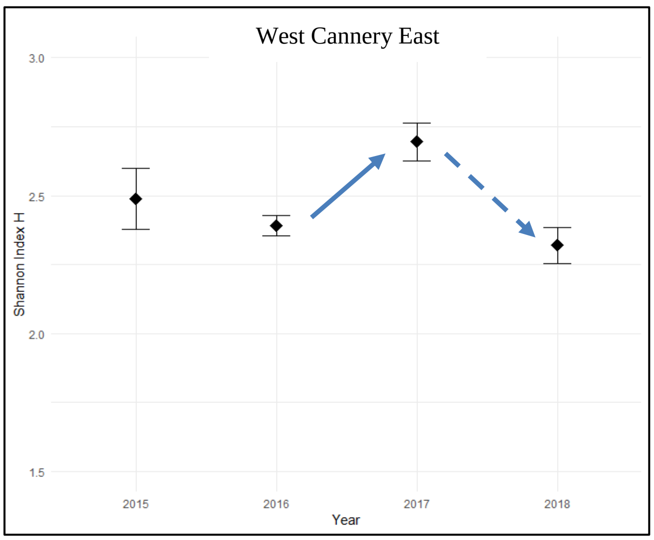
2.3.2 Question 2 Results: Temporal Diversity Analysis

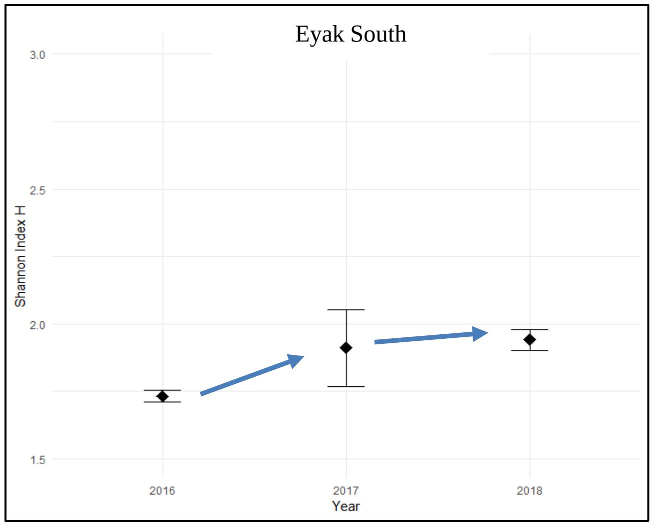
Shannon Diversity Index

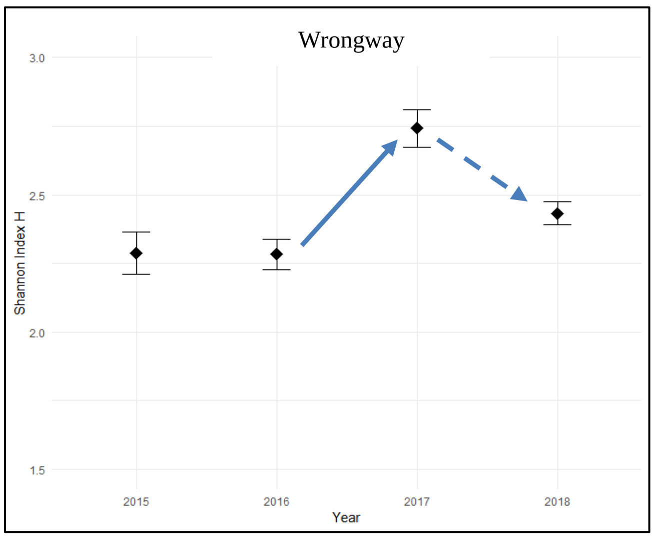
Computation of Shannon diversity index Hill values (H') revealed fluctuations in richness, abundance, and evenness of species over time. These values provided insight regarding how the overall abundance of species at the site was distributed among the species present at a given time point. The values can be viewed relative to one another at individual sites over time as the use of this index was not intended to make comparisons between sites for this study. The highest H' values were observed in sample year 3 (2017) for all sites except Eyak South pond where diversity was highest in 2018. There is a visible trend among all sites, with increasing H' values from 2016 to 2017, followed by a decrease in 2018 (Figure 2.5). The mechanism of the index formula is such that high H' values indicate that all or most species occur at a similar frequency, in other words when all community members have equitable stake in the sample. Hill values were calculated based on a data matrix separating species total mean abundance by month of each year.

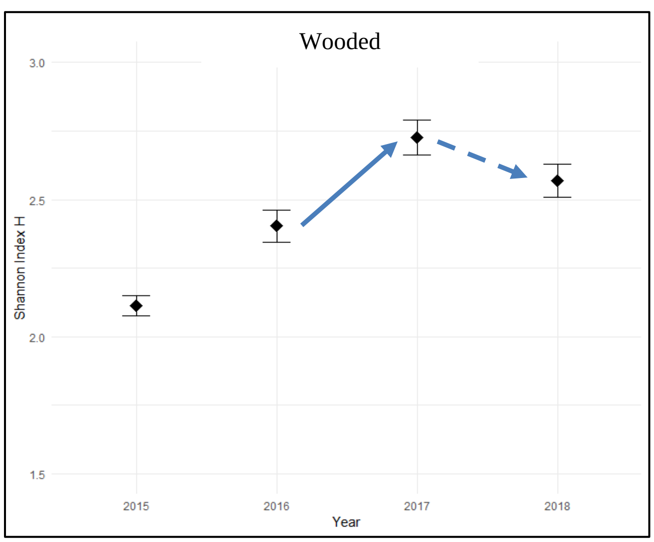
Figure 2.5 Change in Shannon Diversity Index, H', over time for West Cannery West, West Cannery East, Eyak South, Wrongway, and Wooded ponds. Arrows illustrate a pattern of rise (solid) and fall (dashed) of diversity from 2016 through 2018, with 2017 being the most diverse year in all ponds. Though there was variation among years, there was patterning in that variation indicating an effect of change in a common variable.






Eyak South
Shannon Index H
3.0
2.5
2.0
1.5
2016
2017
2018
Year


Wrongway
Shannon Index H
3.0
2.5
2.0
1.5
2015
2016
2017
2018
Year


Wooded
Shannon Index H
3.0
2.5
2.0
1.5
2015
2016
2017
2018
Year

Turnover

Replacement of species resulting from exotic infestation was investigated using an exploratory approach to document temporal dynamics of each site. Rather than comparing diversity measures of individual snapshots in time and comparing between years, temporal shifts in identity of species comprising richness and rank abundances of newly arrived (gained) and newly lost (lost) species were characterized. This turnover metric is calculated as the sum of species gained and species lost, divided by the total species observed between time points. Figure 2.6 shows highest species turnover occurring between the 2016-2017 year-pair. There were no other patterns common among all sites. However, certain ponds trend in total turnover mirrored on each other. West Cannery East, in the Eyak River site group changed in turnover with a similar slope as Wrongway pond in the Alaganik Slough site group; though, in an opposing direction. West Cannery West pond in the Eyak River site group changed in turnover with a similar slope as Wooded Pond in the Alaganik Slough site group; though, in an opposing direction. The relative contribution of appearances and disappearances to total turnover is reported in Table 2.8. Occurrence of species displacement may not take the form of all individuals in a species disappearing from the system, but rather in a trend of certain species reduction over time.

Figure 2.6 Total turnover considering all species from 2015 through 2018 measured as the sum of the number of species which appear and those which disappear between two years divided by the total number of species observed over the two time points represented as a proportion. Values for year 2015, not pictured on x-axis, are zero as it is the starting point. There was higher turnover in the Eyak sites in 2018 than in 2016, illustrated by the green and gold lines. There was a lower turnover in the Alaganik sites, illustrated by the purple and blue lines, over the same time period. The Eyak sites are less diverse overall; however, there is a figurative revolving door for species coming and going.

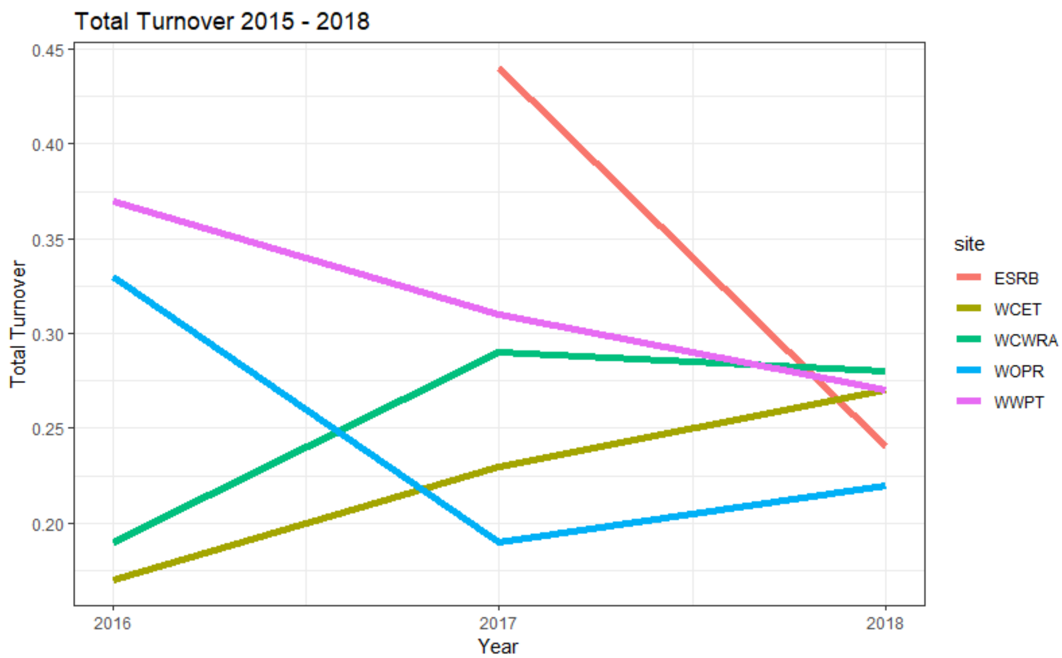


Table 2.8 Temporal diversity values by study pond.

	2015-2016				2016-2017				2017-2018				
Site	Total Turnover	Appearances	Disappearances	Mean Rank Shift	Total Turnover	Appearances	Disappearances	Mean Rank Shift	Total Turnover	Appearances	Disappearances	Mean Rank Shift	Rate of Change
W Cannery W	0.19	0.10	0.10	4.0	0.29	0.21	0.08	2.94	0.28	0.12	0.16	1.9	6.23
W Cannery E	0.17	0.09	0.09	4.9	0.23	0.19	0.04	3.4	0.27	0.04	0.23	2.21	8.02
Eyak South	-	-	-	-	0.44	0.28	0.17	1.3	0.24	0.12	0.12	1.3	0.50
Wrongway	0.37	0.11	0.26	4.12	0.31	0.31	0	3.37	0.27	0.03	0.23	3.0	1.86
Wooded	0.33	0.21	0.13	2.63	0.19	0.19	0	3.05	0.22	0.04	0.19	2.86	3.53

Species Relative Abundance

To investigate the contribution of individual species to turnover, Mean relative cover values of each species were compared over the study period to determine which species were most abundant in each year. Evidence of significance between yearly mean relative abundance values for an individual species was obtained by inspecting plots of 95% confidence intervals and looking for overlap in limits of CI bars. Figure 2.7a-e displays plots used for assessment of significant change. Species which were present in the first sample year and not present in the final sample year were considered to have significant change in relative abundance. Information regarding ratios of species present each year was supplemented by assessing the degree to which each species either increased or decreased in cover relative to other species. Year to year variation of species relative abundance was quantified by calculating percent change. Higher or lower degrees of change may be indicative of factors associated with certain years, or representative of variation within populations of individual species.

Inspection of these plots indicated significance increase of relative abundance between the first and last sample years in West Cannery West Pond for species *Myriophyllum sibiricum* between years 2016 and 2018. This pond also saw a significant fluctuation in relative abundance of *E. canadensis* as an increase was significant between 2015 and 2017, though change was not significant between the first and last sample years 2015 through 2018. *Chara* sp., an algae, also fluctuated significantly in relative abundance over the whole sample period but was only significantly different between 2016 and 2018, not between the first and last sample years.

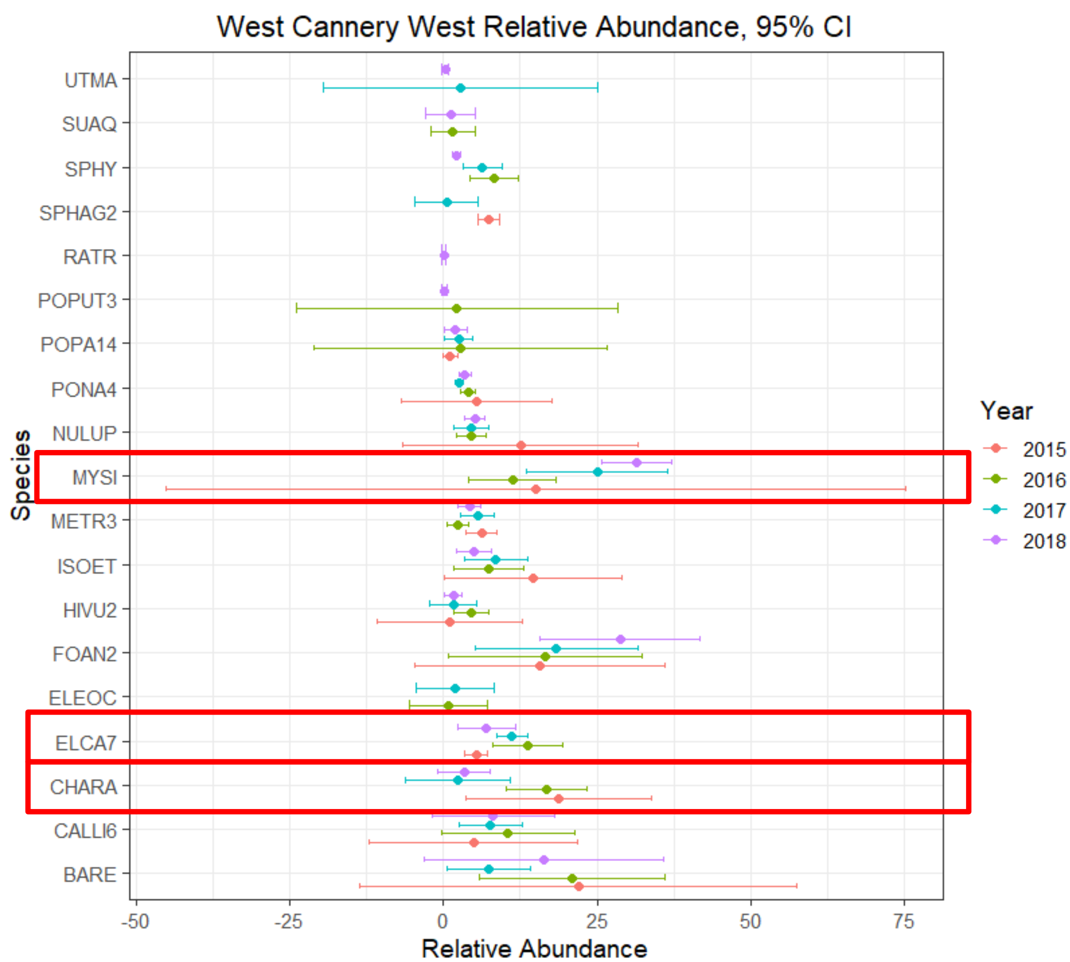
West Cannery East Pond experienced a drastic reduction in relative abundance of *Elodea canadensis* and *Equisetum fluviatile*; neither was captured in sample plots during any sample period in 2018. There was also a major increase in bare ground (noted as BARE in the species list) relative to overall plant cover between the first and last sample year. *Menyanthes trifoliata* also increased significantly between 2015 and 2018.

In Eyak South Pond, *Hippuris vulgaris* did not display a gap between confidence interval limits in different years; though, there was only slight overlap between the first and last sample years, 2016 and 2018. As stated previously, lack of separation in confidence limits does not imply lack of significance.

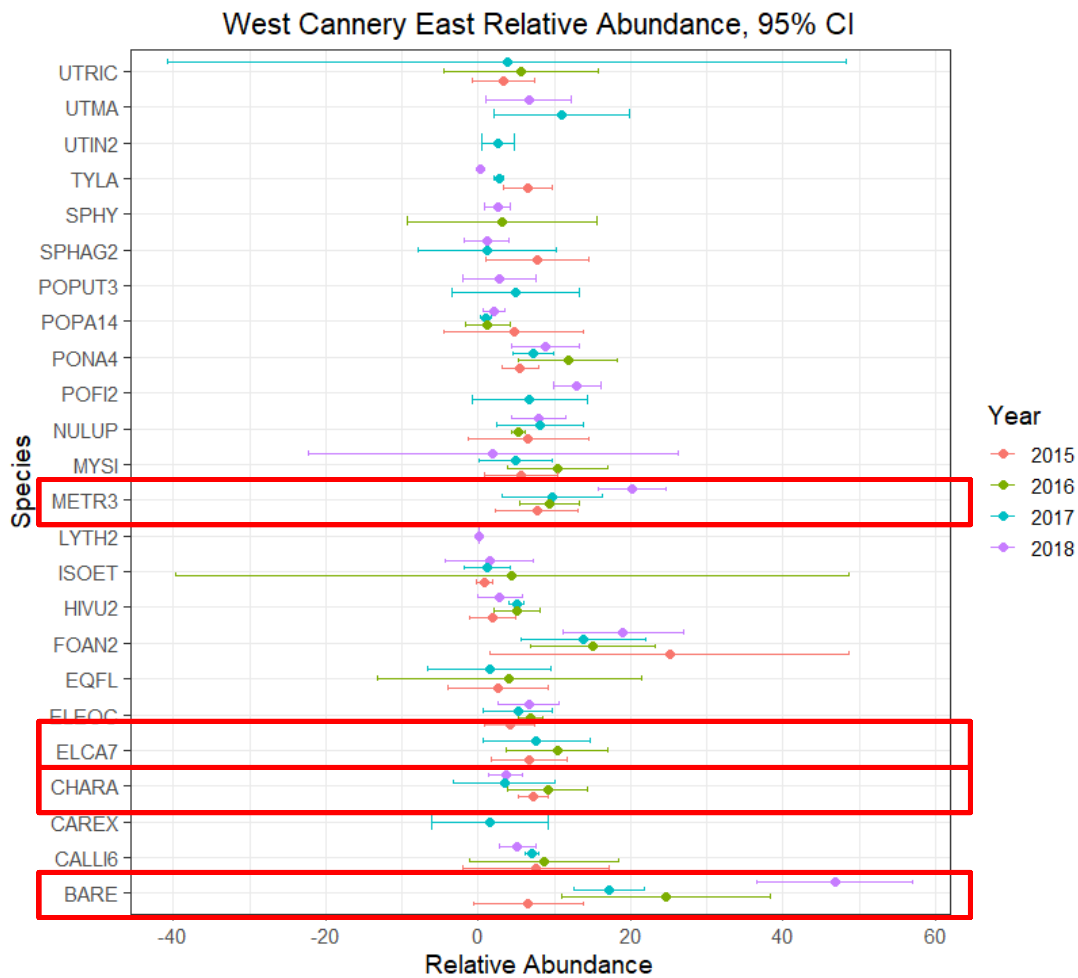
Wrongway Pond showed significant differences in relative abundance of *Isoetes* sp., increasing between year pairs 2015-2016 and 2015-2017; however, 2015 was not different than 2018. This is a low growing ground cover species and is often one of the first present at the beginning of a growing season. *Elodea canadensis* is among the dominant species in this pond; though it did not show significant changes in mean relative abundance over the four-year sample period. There was also a significant increase in bare ground cover between 2015 and 2018. No significance between species relative abundances were observed in Wooded Pond.

Figure 2.7a-e 95% Confidence Intervals bounding species relative abundance values used to infer statistical significance of abundance changes between years by observing overlap of CI bars. The different colors correspond to years and significant changes in abundance are represented by red boxes surrounding species values whose confidence limits do not overlap. Most of the species fluctuate in abundance from year to year but only a few to a substantial degree.

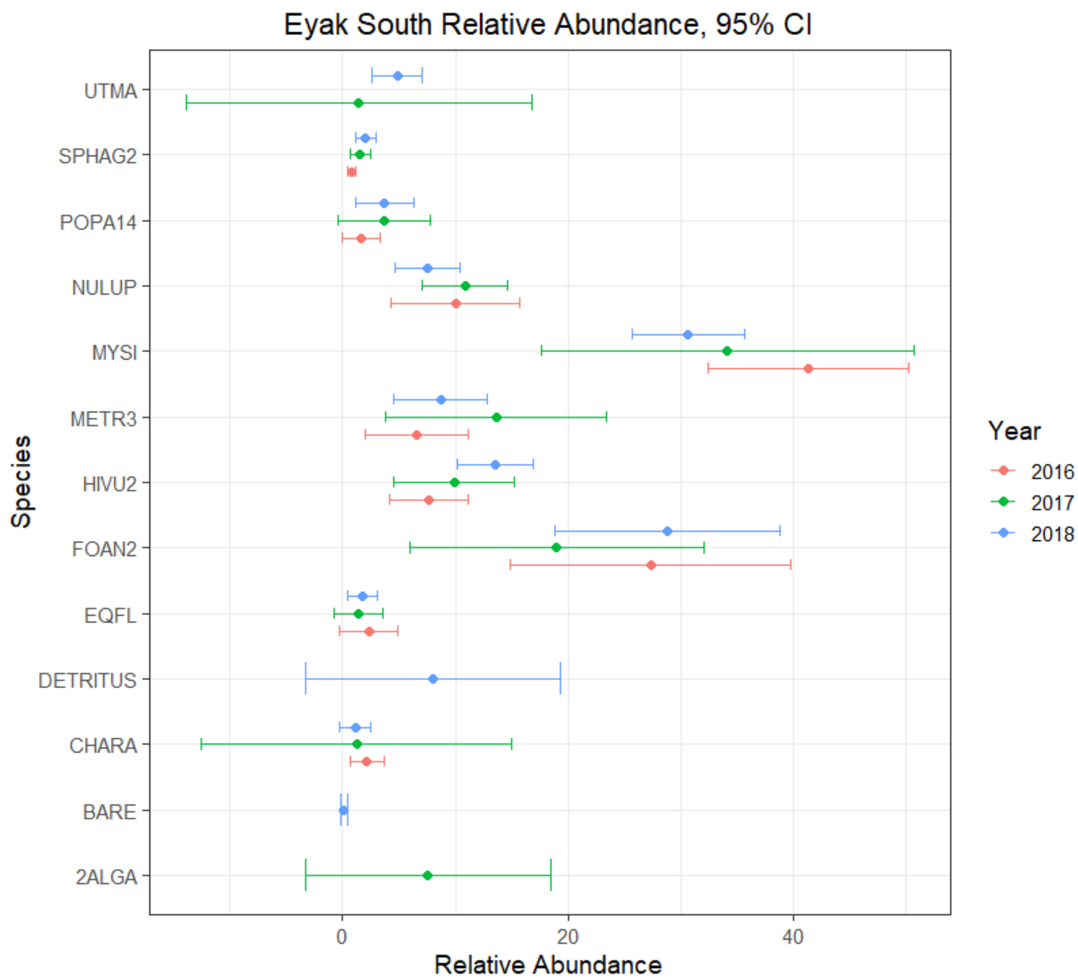
a)



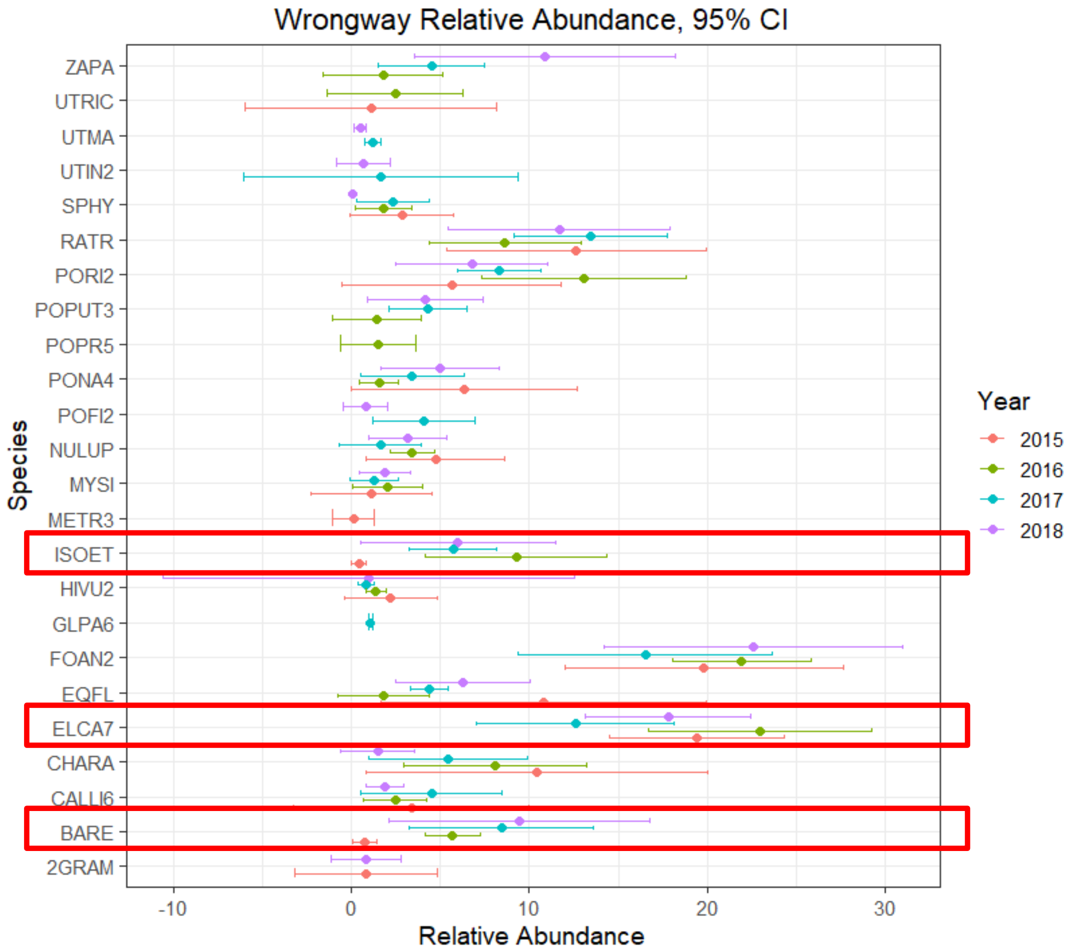
b)


West Cannery East Relative Abundance, 95% CI
UTRIC
UTMA
UTIN2
TYLA
SPHY
SPHAG2
POPUT3
POPA14
PONA4
POFI2
NULUP
MYSI
METR3
LYTH2
ISOET
HIVU2
FOAN2
EQFL
ELEOC
ELCA7
CHARA
CAREX
CALLI6
BARE
Species
-40
-20
0
20
40
60
Relative Abundance
Year
2015
2016
2017
2018

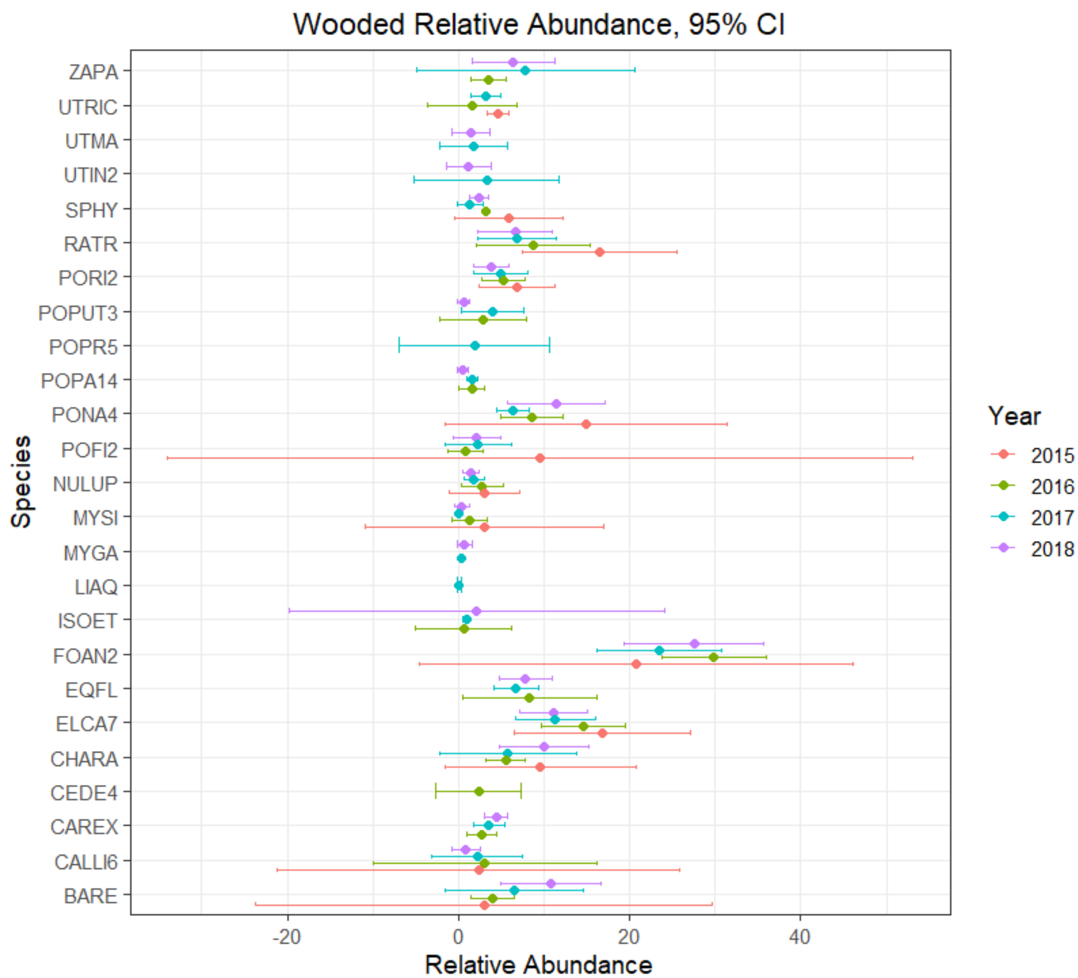
c)


Eyak South Relative Abundance, 95% CI
UTMA
SPHAG2
POPA14
NULUP
MYSI
METR3
HIVU2
FOAN2
EQFL
DETRITUS
CHARA
BARE
2ALGA
Species
0
20
40
Relative Abundance
Year
2016
2017
2018

d)

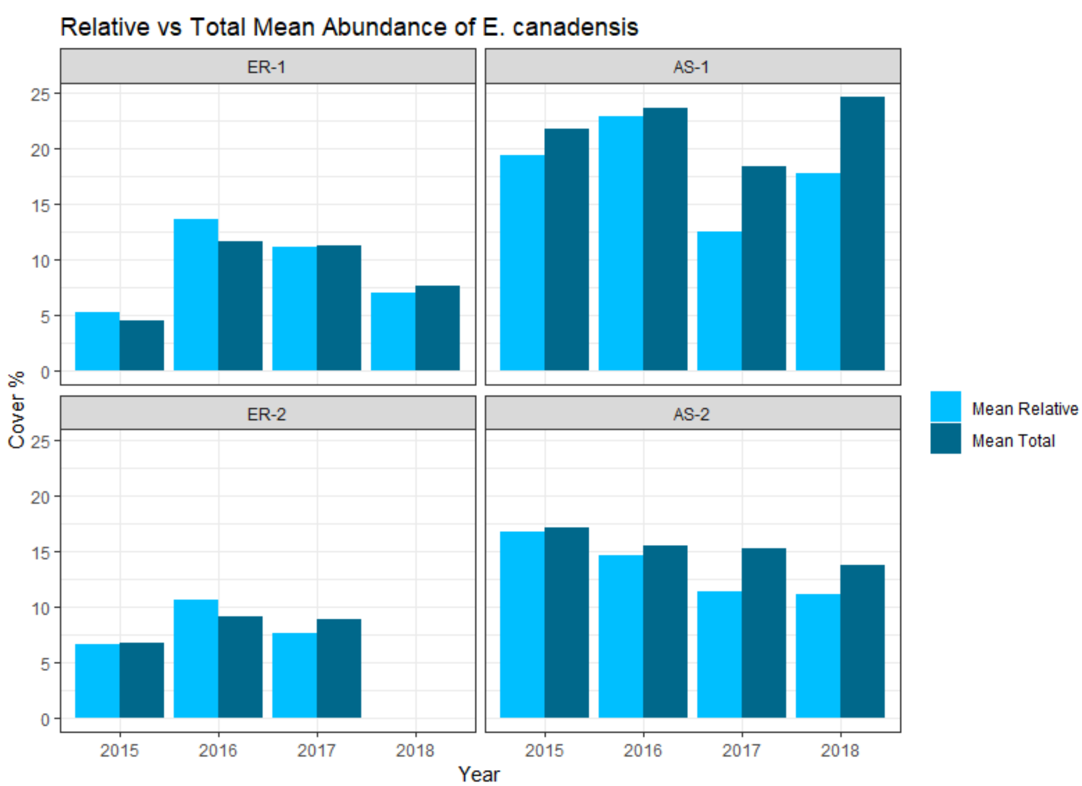

Wrongway Relative Abundance, 95% CI
ZAPA
UTRIC
UTMA
UTIN2
SPHY
RATR
PORI2
POPUT3
POPR5
PONA4
POFI2
NULUP
MYSI
METR3
ISOET
HIVU2
GLPA6
FOAN2
EQFL
ELCA7
CHARA
CALLI6
BARE
2GRAM
Species
-10
0
10
20
30
Relative Abundance
Year
2015
2016
2017
2018

e)



Though there is variation in the relative abundance of *E. canadensis* among years, there is no evidence of substantial change overall, disregarding the herbicide treated pond West Cannery West. Common among all ponds is a mean relative abundance of the focal species not exceeding 25% cover. The sample is representative of *E. canadensis* not contributing to more than 25% cover of all macrophyte species collectively. This is apparent even in the Alaganik group ponds where there is more macrophyte biomass present overall (Figure 2.8).

Figure 2.8 Mean relative and mean total abundance of *E. canadensis* throughout the study period. The dark blue bars show the mean total abundance, which are the raw values of percent cover from sample plots and are relative to everything in the plot including bare ground and other ground cover. This is representative of the % of the pond bottom covered by this species. The light blue bars show the mean abundance relative to other plants. It is representative of the proportion of total plant biomass in the pond which *Elodea* makes up. If *Elodea* was contributing greatly to the total abundance of all plants collectively, the light blue bars would be approaching 100%. Here, the limit in all sites is 25% yearly mean cover. *Elodea* is more abundance overall in the Alaganik group ponds.



Yearly Variation in Relative Abundance of Co-occurring Species

We saw above that relative abundance of species varies from year to year, though not always significantly. A simple sorting of species by yearly mean relative abundance revealed that dominance of a species is variable year to year which is displayed by the ranking of many species changing throughout the study period. To quantify the shifting of ranks in terms of individual relative abundance, percent change in relative abundance was calculated. Yearly mean relative abundance and percent change in mean relative abundance are reported in the left portions of tables 2.9a-e and display yearly variation, with inferred monthly variation provided by the standard deviation. The right portion of these tables is a summary of changes between he first and last sample year representing differences between endpoints.

The standard deviation of each yearly mean relative abundance is quite high in some cases which is indicative of a lot of monthly variation. For example, standard deviations associated with bare ground (BARE) values were quite high relative to its mean relative abundance value in all ponds in all years. This is to be expected as absence of vegetation co-varies with present of vegetation in a substantial way throughout the growing season as plant biomass accumulates and senesces. When relative dispersion is compared among all species in the form of unitless coefficient of variation, which puts all species' absolute squared variance (sd) on the same scale, certain species emerge as more variable over years. A dominant pattern among all ponds is that *E. canadensis* exhibits the least amount of variation from year to year relative to other dominant specie. This is expressed in Figure 2.9 by the relatively stable slope of the coefficient of variation *E. canadensis* over years.

Figure 2.9 Yearly coefficients of variation of dominant species representative of the degree to which the abundance of a species varies among the plots sampled. If a species trajectory sits low on the y-axis in a plot, this indicates low variability in abundance among plots sampled for that year. If a species trajectory takes the form of a straighter line, this indicates a consistency among years of a certain level of variation. In these scenarios, coverage of a species is irrelevant. Regardless of actual abundance, this indicates whether there is high or low variance in the abundance, and whether that variance in abundance is consistent over time. A common pattern in all of the plots is the black line, depicting *Elodea*. Its variance is rather low and remains low over time indicating high stability of this species.

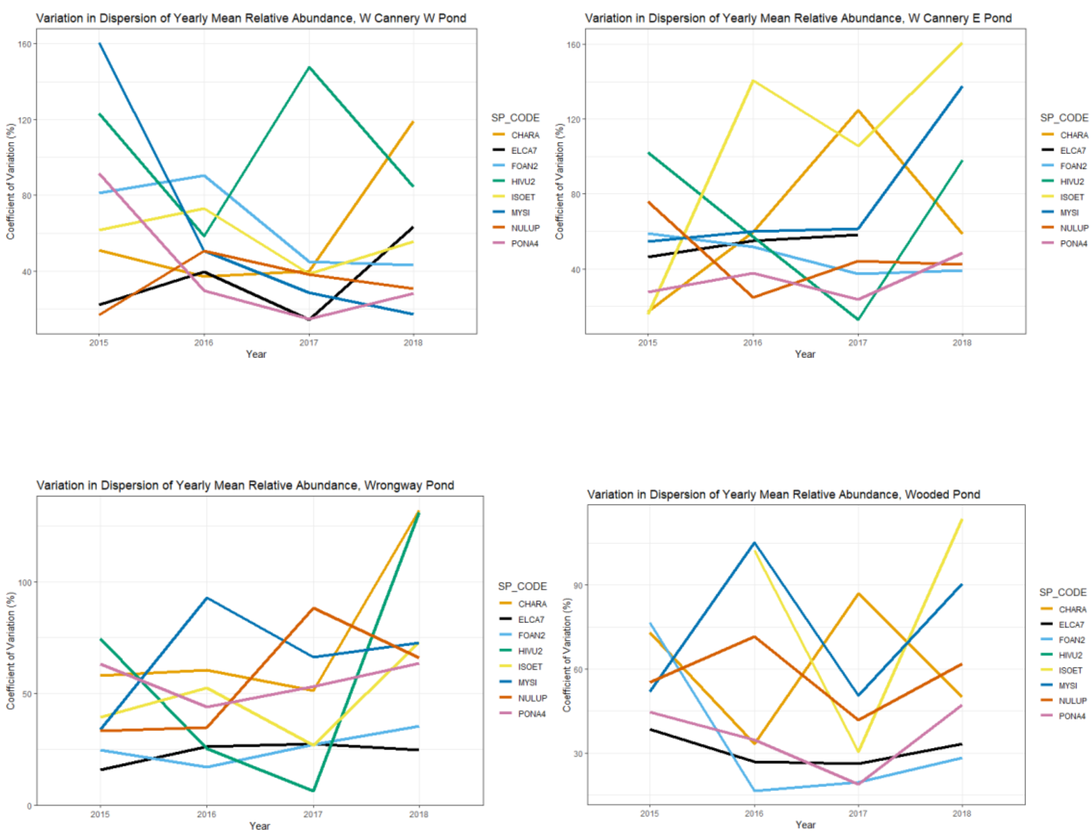


Table 2.9a-e. Summary of Variation in Species Abundance by Pond. Ranking indicates order of decreasing mean relative abundance and reflects dominance of species in a given year. For each year, Bare ground and *E. canadensis* are included along with the top 5 ranking other species. Percent change in yearly mean relative abundance is provided to reflect fluctuation in individual species abundance across years. The right portion of the table is a summary of overall differences between endpoints in sampling.

a)

West Cannery West Summary

	Species	**Rank**	**Mean Relative Abundance**	**% Δ Mean Relative Abundance**
2015	BARE	1	22.0 ± 22.4	-
	CHARA	2	18.7 ± 9.5	-
	FOAN2	3	15.8 ± 12.8	-
	MYSI	4	15.1 ± 24.2	-
	ISOET	5	14.7 ± 9.1	-
	NULUP	6	12.6 ± 2.1	-
	ELCA7	11	5.3 ± 1.2	-
2016	BARE	1	20.9 ± 14.3	-4.7
	CHARA	2	16.7 ± 6.2	-10.7
	FOAN2	3	16.6 ± 14.9	5
	ELCA7	4	13.7 ± 12.7	155.5
	MYSI	5	11.3 ± 5.7	-25.3
	CALLI6	6	10.5 ± 8.7	114.7
	SPHY	7	8.2 ± 3.7	315
2017	MYSI	1	25 ± 7.2	122.1
	FOAN2	2	18.4 ± 8.3	11.2
	ELCA7	3	11.2 ± 1.6	-18.5
	ISOET	4	8.6 ± 3.3	7.5
	CALLI6	5	7.6 ± 3.3	-27.2
	BARE	6	7.4 ± 4.2	-64.4
	SPHY	7	6.3 ± 2.0	-22.9
2018	MYSI	1	31.4 ± 5.4	25.6
	FOAN2	2	28.7 ± 12.4	56.3
	BARE	3	16.3 ± 18.5	118.9
	CALLI6	4	8.1 ± 6.3	5.5
	ELCA7	5	7.0 ± 4.5	-36.9
	NULUP	6	5.0 ± 1.6	11.7
	ISOET	7	5.0 ± 2.8	100.2

2015 v. 2018	
% Δ of Common Species	
Bare ground	↓ 25.8
Chara	↓ 82.2
Elodea canadensis	↑ 31.4
Fontinalis antipyretica	↑ 82.3
Hippuris vulgaris	↑ 53.7
Isoetes sp.	↓ 66
Myriophyllum sibiricum	↑108.4
Nuphar lutea polyselapa	↓ 59.6
Potamogeton natans	↓ 35.0
Avg Rank Shift (Re-ordering)	3.82
Total Turnover (Replacement)	0.26
Avg % Δ H’ (Diversity)	0.64

b)

West Cannery East Summary

Year	Species	Rank	Mean Relative Abundance	% Δ Mean Relative Abundance
2015	FOAN2	1	25.2 ± 14.8	-
	POFI2	2	11.5 ± 0	-
	METR3	3	7.7 ± 3.4	-
	SPHAG2	4	7.7 ± 2.7	-
	CALLI6	5	7.5 ± 6.0	-
	ELCA7	7	6.6 ± 3.1	-
	BARE	8	6.6 ± 5.0	-
2016	BARE	1	24.5 ± 5.9	272.4
	FOAN2	2	15.1 ± 7.8	-39.9
	ELCA7	3	10.7 ± 5.9	60.4
	PONA4	4	10.6 ± 4.0	92.7
	MYSI	5	10.6 ± 5.3	78.0
	CHARA	6	8.8 ± 7.9	22.0
	CALLI6	7	8.6 ± 2.9	14.2
2017	BARE	1	17.2 ± 2.9	-30.0
	FOAN2	2	13.8 ± 5.2	-8.5
	UTMA	3	11.0 ± 3.6	-
	METR3	4	9.7 ± 4.2	19.4
	NULUP	5	8.1 ± 3.6	34.1
	ELCA7	6	7.6 ± 4.4	-28.4
	PONA4	7	7.2 ± 1.7	-32.2
2018	BARE	1	46.8 ± 9.7	172.5
	METR3	2	20.2 ± 4.2	107.4
	FOAN2	3	19.0 ± 7.5	37.6
	POFI2	4	13.0 ± 3.0	91.8
	PONA4	5	8.8 ± 4.3	22.9
	NULUP	6	8.0 ± 3.4	-1.4
	ELCA7	-	-	-100

2015 v. 2018	
% Δ of Common Species	
Bare ground	↑ 610
Chara	↓ 50.4
Elodea canadensis	↑ 14.9
Fontinalis antipyretica	↓ 24.4
Hippuris vulgaris	↑ 49.5
Isoetes sp.	↑ 93.5
Myriophyllum sibiricum	↓ 64.9
Nuphar lutea polyselapa	↑ 21.5
Potamogeton natans	↑ 60.7
Avg Rank Shift (Re-ordering)	3.9
Total Turnover (Replacement)	0.36
Avg % Δ H’ (Diversity)	↓6.8

c)

Eyak South Summary

Year	Species	Rank	Mean Relative Abundance	% Δ Mean Relative Abundance
2016	MYSI	1	41.3 ± 7.1	-
2016	FOAN2	2	27.3 ± 10.0	-
2016	NULUP	3	10.0 ± 4.6	-
2016	HIVU2	4	7.7 ± 2.8	-
2016	METR3	5	6.5 ± 3.7	-
2016	BARE	6	2.85 ± 0	-
2016	EQFL	7	2.3 ± 2.1	-
2017	MYSI	1	34.2 ± 10.4	-17.4
2017	FOAN2	2	19.0 ± 8.2	-30.5
2017	METR3	3	13.6 ± 6.2	107.9
2017	NULUP	4	10.8 ± 2.4	8.5
2017	HIVU2	5	9.9 ± 3.4	29.1
2017	POPA14	6	3.7 ± 2.5	123.4
2017	UTIN2	7	2.4 ± 0	0
2018	MYSI	1	30.7 ± 4.8	-10.2
2018	FOAN2	2	28.8 ± 9.5	51.8
2018	HIVU2	3	13.6 ± 3.2	37.4
2018	METR3	4	8.7 ± 4.0	-36.2
2018	NULUP	5	7.5 ± 2.8	-31.1
2018	UTMA	6	4.8 ± 1.4	240
2018	POPA14	7	3.7 ± 2.1	1.8

2016 v. 2018	
% Δ of Common Species	
Bare ground	↓ 96.1
Chara	↓ 49.3
Elodea canadensis	-
Fontinalis antipyretica	↑ 5.5
Hippuris vulgaris	↑ 77.4
Isoetes sp.	0
Myriophyllum sibiricum	↓ 25.8
Nuphar lutea polyselapa	↓ 25.2
Potamogeton natans	↑ 532
Avg Rank Shift (Re-ordering)	1.6
Total Turnover (Replacement)	0.4
Avg % Δ H' (Diversity)	↑ 12.1

d)

Wrongway Summary

Year	Species	Rank	Mean Relative Abundance	% Δ Mean Relative Abundance
2015	FOAN2	1	19.8 ± 4.9	-
	ELCA7	2	19.4 ± 3.1	-
	RATR	3	12.6 ± 4.6	-
	EQFL	4	10.8 ± 5.7	-
	CHARA	5	10.4 ± 6.0	-
	PONA4	6	6.3 ± 4.0	-
	BARE	18	0.75 ± 0.4	-
2016	ELCA7	1	23.0 ± 6.0	18.4
	FOAN2	2	21.9 ± 3.7	10.7
	PORI2	3	13.1 ± 5.5	132
	ISOET	4	9.3 ± 4.9	2086.8
	RATR	5	8.6 ± 8.1	-31.6
	CHARA	6	8.1 ± 4.9	-22.1
	BARE	7	5.7 ± 1.5	662.2
2017	FOAN2	1	16.5 ± 4.5	-24.7
	RATR	2	13.4 ± 2.7	55.6
	ELCA7	3	12.6 ± 3.5	-45.2
	BARE	4	8.4 ± 3.2	48.9
	PORI2	5	8.3 ± 1.5	-36.5
	ISOET	6	5.7 ± 1.5	-38.5
	CHARA	7	5.5 ± 2.8	-32.7
2018	FOAN2	1	22.6 ± 8.0	36.8
	ELCA7	2	17.8 ± 4.4	41.5
	RATR	3	11.7 ± 5.9	-13.2
	ZAPA	4	10.9 ± 7.0	140.9
	BARE	5	9.4 ± 7.0	11.6
	PORI2	6	6.8 ± 4.1	-18.4
	EQFL	7	6.2 ± 3.6	43.1

2015 v. 2018	
% Δ of Common Species	
Bare ground	↑1166
Chara	↓ 85.6
Elodea canadensis	↓ 8.2
Fontinalis antipyretica	↑ 14.1
Hippuris vulgaris	↓ 56.0
Isoetes sp.	↑1314
Myriophyllum sibiricum	↑ 69.1
Nuphar lutea polyselapa	↓ 33.0
Potamogeton natans	↓ 20.7
Avg Rank Shift (Re-ordering)	3.3
Total Turnover (Replacement)	0.37
Avg % Δ H' (Diversity)	↑ 21.6

e)

Wooded Summary

Year	Species	Rank	Mean Relative Abundance	% Δ Mean Relative Abundance
2015	FOAN2	1	20.8 ± 15.9	-
	ELCA7	2	16.8 ± 6.5	-
	RATR	3	16.5 ± 5.6	-
	PONA4	4	14.9 ± 6.6	-
	CHARA	5	9.6 ± 7.0	-
	POFI2	6	9.6 ± 4.8	-
	BARE	13	3.0 ± 3.0	-
2016	FOAN2	1	29.9 ± 4.9	43.7
	ELCA7	2	14.7 ± 4.0	-12.8
	RATR	3	8.7 ± 2.4	-47.4
	PONA4	4	8.5 ± 3.0	-42.7
	EQFL	5	8.3 ± 6.3	4222
	CHARA	6	5.5 ± 1.8	-42.2
	BARE	8	4.0 ± 2.1	33.6
2017	FOAN2	1	23.4 ± 4.6	43.7
	ELCA7	2	11.3 ± 3.0	-22.7
	ZAPA	3	7.8 ± 5.1	121.5
	RATR	4	6.8 ± 2.9	-21.4
	EQFL	5	6.7 ± 1.7	-19.1
	BARE	6	6.5 ± 5.1	64.6
	PONA4	7	6.3 ± 1.2	
2018	FOAN2	1	27.5 ± 7.8	32.6
	PONA4	2	11.5 ± 5.4	81.3
	ELCA7	3	11.1 ± 3.7	11.1
	BARE	4	10.8 ± 5.6	65.5
	CHARA	5	9.9 ± 5.0	71.8
	EQFL	6	7.8 ± 3.0	16.6
	RATR	7	6.6 ± 4.2	6.6

2015 v. 2018	
% Δ of Common Species	
Bare ground	↑263.7
Chara	↑ 3.6
Elodea canadensis	↓ 33.9
Fontinalis antipyretica	↑ 32.6
Hippuris vulgaris	0
Isoetes sp.	↑658.9
Myriophyllum sibiricum	↓ 87.4
Nuphar lutea polyselapa	↓ 50.9
Potamogeton natans	↓ 23.0
Avg Rank Shift (Re-ordering)	2.9
Total Turnover (Replacement)	0.48
Avg % Δ H' (Diversity)	↑ 21.6

Rank Abundance

Ranking of species by their abundance, a way to depict both species richness and evenness, is often plotted in two dimensions where the slope of a line reflects species evenness or high similarity between abundance values among species. Rank clocks are another way to visualize the steep and shallow gradients presented by distributions of species abundances over time. The endpoints of a traditional trajectory are compressed in a chordal geometry allowed for better visualization of change in dominance between first and last sample years. Stability of species is highlighted by departure and return of a given species projection to and from the center of the plot. The magnitude of departure of abundance from the starting sample point to the endpoint is indicative of which species experience overall reordering in rank based on their abundance. Figure 2.10a-e shows rank abundance of each species per site over the four-year sample period, apart from the three-year period at Eyak South Pond. A trend emerged in West Cannery West Pond where two species rank abundance curves are steep indicating those species' contributions of abundance to a reduction of evenness. These species are *Myriophyllum sibiricum* and *Fontinalis antipyretica*. Stability of the community over the four-year period fluctuates slightly as is seen in migration and re-visiting of lines from the center point; however, it is overall rather stable aside from emergence of the dominant species.

West Cannery East Pond showed a dramatic steady shift to being dominated by bare ground in 2018. It is not clear whether this is reflective of the herbicide treatment which was accompanied by a lag time in mortality of *E. canadensis* first detectable in 2018. A steep gradient representing a reduction of abundance is displayed by *Fontinalis antipyretica*, an aquatic moss, and an increase in *Menyanthes trifoliata*, an emergent species. Interestingly, a strong treatment effect on *E. canadensis* is not overwhelmingly apparent in this plot as the exotic species was not overly dominant to begin with.

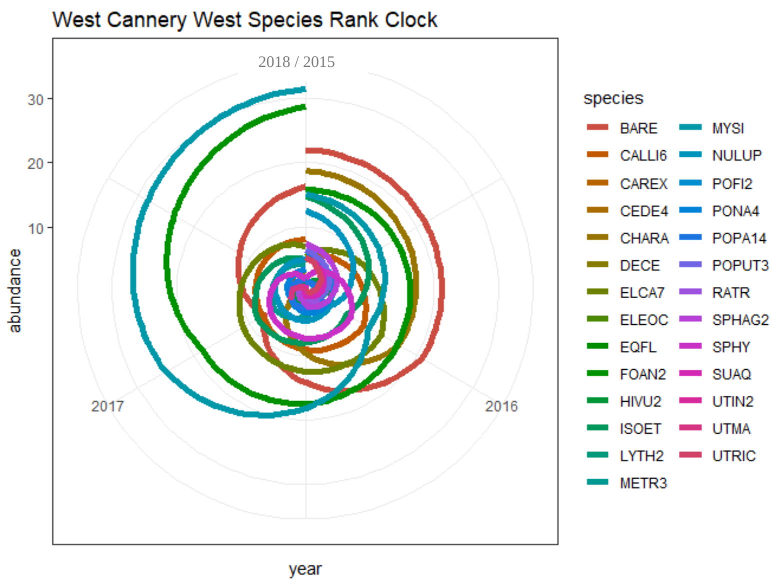
Eyak South Pond displayed the most stability of all ponds consistently dominated by *Myriophyllum sibiricum* and *Fontinalis antipyretica.* Wrongway Pond is dominated by *Fontinalis antipyretica* as well and *E. canadensis*, two species whose abundance has remained consistent over time, similar to patterns in abundance of *Ranunculus trichopyllus*. A similar pattern is reflected in Wooded pond, though with fewer species present and greater stability.

Overall changes in rank abundance between time points, mean rank shift (MRS) is reported in Table 2.8 and is depicted in Figure 2.11, which summarizes the shifting ranks or reordering of the species within the plant community at each site over time, as reflected in the slope of each line. Plateauing lines in the plot indicate a lack of reordering. The plot illustrates stability at Eyak South, Wrongway, and Wooded ponds, where West Cannery West and West Cannery East ponds do not reach a stable state with respect to reordering of species abundances. Stability is not necessarily and implicitly desired condition, as a site can exhibit “stability” in this sense even with a consistently high re-ordering of ranks representing species abundances over time.

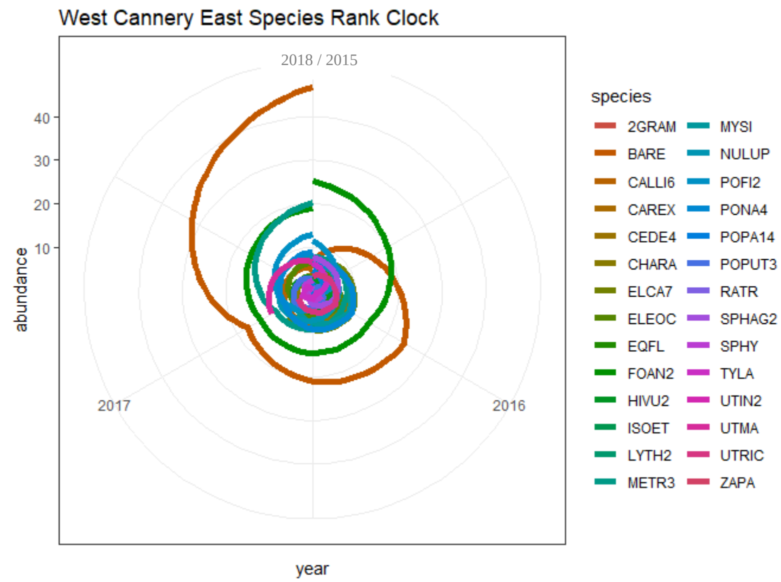
Another feature of importance in Figure 2.10 is the trend for the rank of many species to shift around over time. The trend in Wrongway indicates a decrease in re-ordering prior to stabilizing, where the trend in Wooded is an increase in re-ordering prior to stabilization. The negative slopes in West Cannery West and West Cannery East show a steady decrease in re-ordering of species over time.

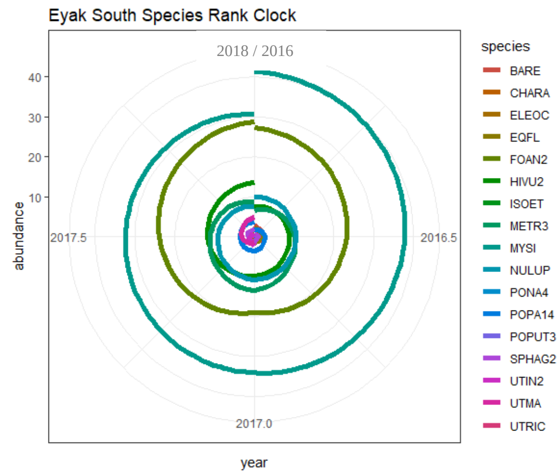
Figure 2.10a-e Rank Clocks of abundance of species over time. The plot converts a species trajectory into a cordal geometry where the consistancy of departure of each species' line from the origin as the plot progressed clockwise is indicative of the stability of that species cover over time. The disparity of species' lines at the 12 o'clock posotion allows for visualization of overall changes in abundance. A high overlap of species' trajectories deviating and returning to the origin over time represents a high re-ordering of species abundances as they change ranks from year to year.

a)

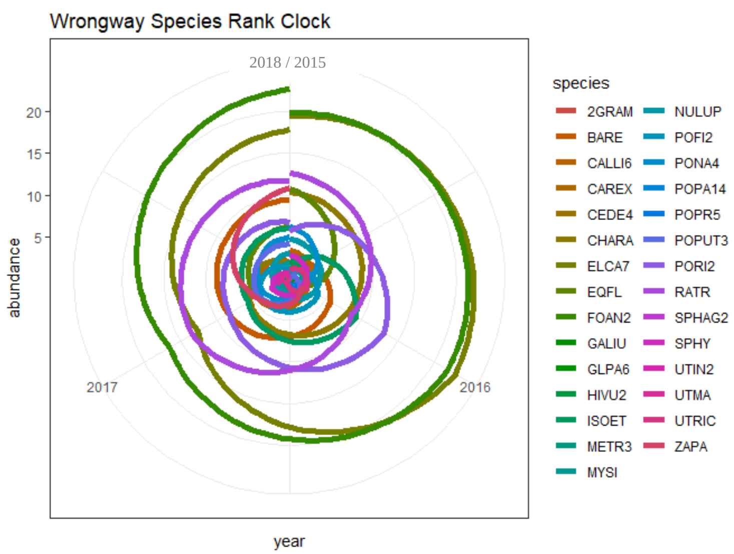


b)




Eyak South Species Rank Clock
2018 / 2016
2016.5
2017.0
2017.5
abundance
10
20
30
40
year
species
BARE
CHARA
ELEOC
EQFL
FOAN2
HIVU2
ISOET
METR3
MYSI
NULUP
PONA4
POPA14
POPUT3
SPHAG2
UTIN2
UTMA
UTRIC

c) d) e)


Wrongway Species Rank Clock
2018 / 2015
2016
2017
abundance
5
10
15
20
year
species
2GRAM
BARE
CALLI6
CAREX
CEDE4
CHARA
ELCA7
EQFL
FOAN2
GALIU
GLPA6
HIVU2
ISOET
METR3
MYSI
NULUP
POFI2
PONA4
POPA14
POPR5
POPUT3
PORI2
RATR
SPHAG2
SPHY
UTIN2
UTMA
UTRIC
ZAPA

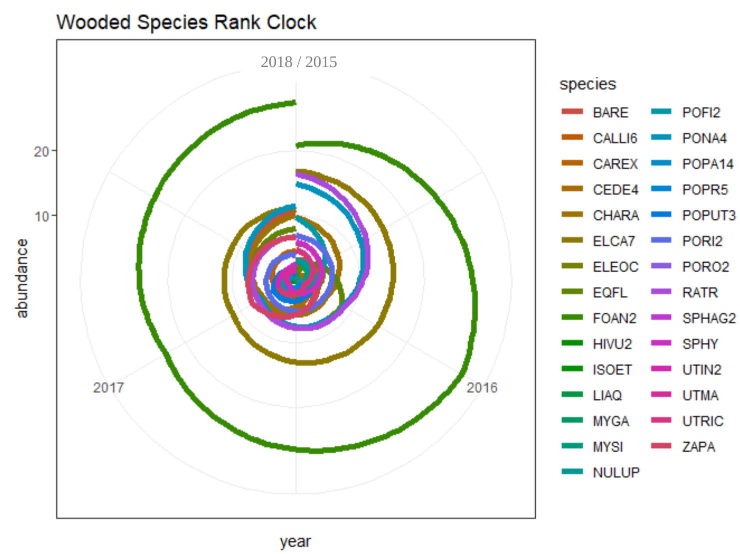
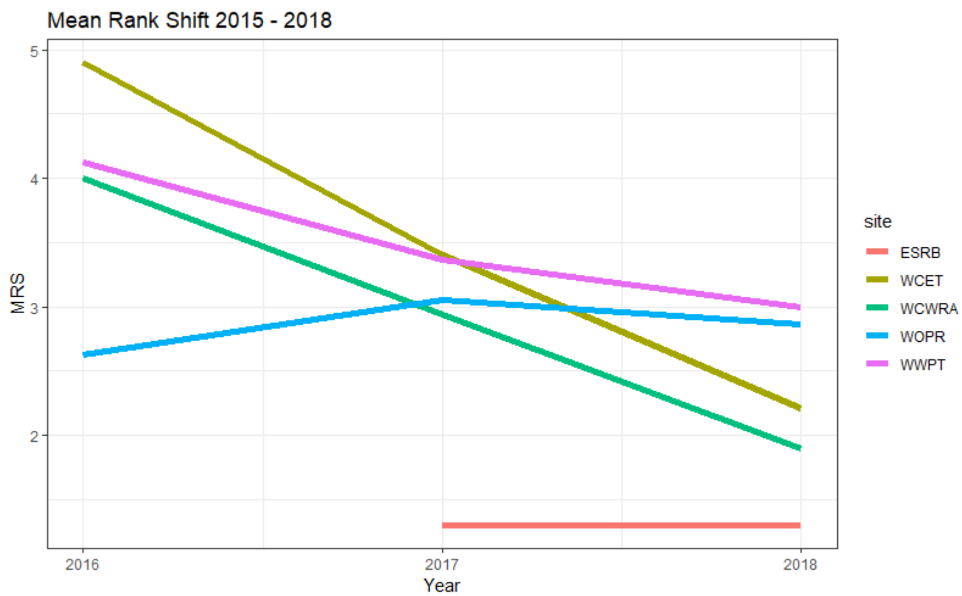

Wooded Species Rank Clock
2018 / 2015
2016
2017
abundance
10
20
year
species
BARE
CALLI6
CAREX
CEDE4
CHARA
ELCA7
ELEOC
EQFL
FOAN2
HIVU2
ISOET
LIAQ
MYGA
MYSI
NULUP
POFI2
PONA4
POPA14
POPR5
POPUT3
PORI2
PORO2
RATR
SPHAG2
SPHY
UTIN2
UTMA
UTRIC
ZAPA

Figure 2.11 Mean Rank Shift. Year labels along the x-axis indicate the endpoint of the two values of a year pair. The intercept of the lines represents the degree to which species re-order within the time period between subsequent year pairs based on a sorted list of ranked abundance. The highest re-ordering of species ranked abundance took place between 2015 and 2016 for all *Elodea* infested ponds and the least re-ordering took place between 2017 and 2018 indicating a trend toward stabilizing rankings of species' abundance.



2.3.3 Question 3 Results: Impact of Exotic Species Removal from Community Data

Non-metric Multidimensional Scaling

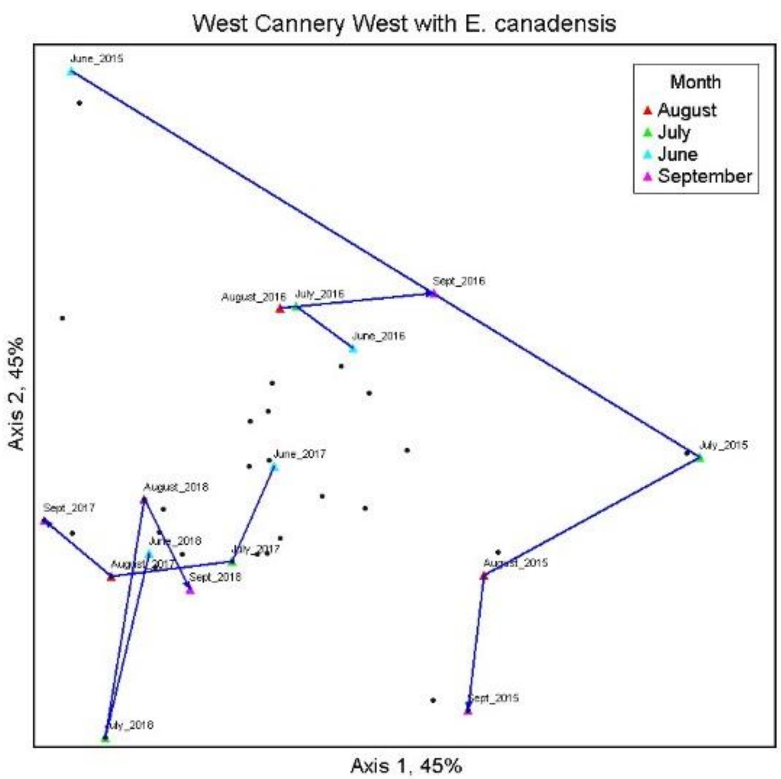
Paired NMS ordinations of sample units in both exotic-included and exotic-excluded species space illustrated the impact of *E. canadensis* based on its contribution to distances in the species matrix (Figure 2.12). Ordinations with and without the exotic in West Cannery West Pond produced two-dimensional solutions (Figure 2.12A). Final stress of 11.3 and 6.0 was reached after 57 and 39 iterations (p = 0.02) for ordination with and without, for the first and second ordinations respectively. For each ordination, the axis explained 90 % and 95% of the variation in the distance matrix (axis 1 = 45%, axis 2 = 45%; axis 1 = 36%, axis 2 = 51%). If *E. canadensis* had been a major dominant, its elimination would have resulted in a much more major alteration in the diagram and the axes would have explained much less of the variation in the distance matrix. Environmental variables were only weakly correlated with the axis at the Eyak River site, and no NMS ordination figure is included here. In Wrongway Pond, the paired NMS ordinations illustrating the impact of the exotic species based on its contribution to distances in the species matrix produced three-dimensional solutions (Figure 2.12B). Final stress of 6.3 and 5.9 was reached after 50 and 65 iterations (p = 0.02) for ordination with and without, for the first and second ordinations respectively. For each ordinations, the axis explained 93% and 94% of the variation in the distance matrix (axis 1 = 48%, axis 2 = 26%; axis 1 = 53%, axis 2 = 22%). Depth was the strongest environmental variable related to community structure of the Alaganik site (Wrongway Pond) ordinations as (r = 0.4, axis 2). Water temperature variables were only weakly correlated in these instances in both sites due to removal of early and late season sample periods, where drastic differences in temperature and GDD are observed, for purposes of sample effort congruency required of the Mantel Test. Neither of the sites were structured by abundance of *E. canadensis* when this was removed from the species matrix and inserted into the environmental matrix as a joint plot overlay vector. Successional arrows (Figure 2.12, shown in blue) show the trajectory of sample units through time. In this case, sample units consisting of quadrat-level species cover aggregated to total mean abundance are migrated through months in the same patterns when ordinated in combined native and exotic species space versus only native species space.

Mantel Test

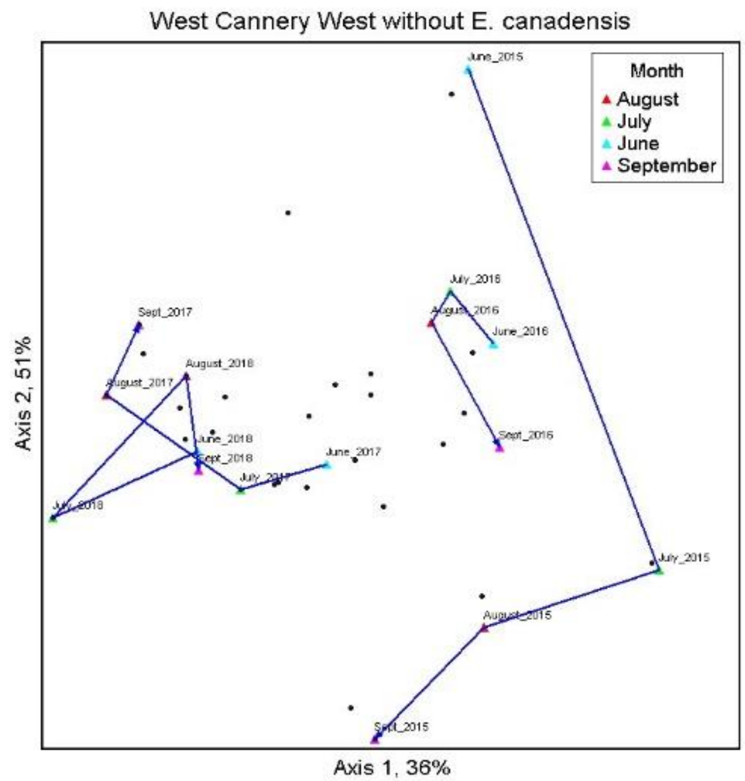
The Mantel Test results for the comparison between community configuration with *E. canadensis* included versus without yielded almost perfect correlation (r = 0.99, p = 0.001) in West Cannery West Pond. This high correlation is reflected in the NMS plots which project the distances between sample units in a reduced space. Wrongway pond also yielded distance matrices configurations almost perfectly correlated (r = 0.97, p = 0.001). The NMS and Mantel Test were not repeated for Wooded Pond as *E. canadensis* was even less dominant at that site, and Eyak South pond was free of the exotic species.

Figure 2.12 NMS ordination plots illustrating high correspondence indicated from Mantel Tests by comparing migration of sample units through time in species space included (A1, B1) and excluding *E. canadensis* (A2, B2). The left figures depict community structure with *Elodea* present in the dataset, the right depicts structure without *Elodea*. The triangles represent sample units whose orientation in the space is based on the dissimilarity in their species composition. Direction of arrows connect sample units belonging to the same sample year by month and represent chronology and length of vectors represents magnitude of change among months. Over the 2015 growing season, the composition in the sample units migrated around the ordination space in a distinct trajectory accounting for *Elodea* in the species composition. After removing *Elodea* from the composition, the trajectory did not change indicating little influence on the variability of structure and composition within a growing season. If *Elodea* were exerting strong pressure on the system, these configuration of these arrows would be wildly different in their direction and magnitude between the actual dataset and the simulated dataset.

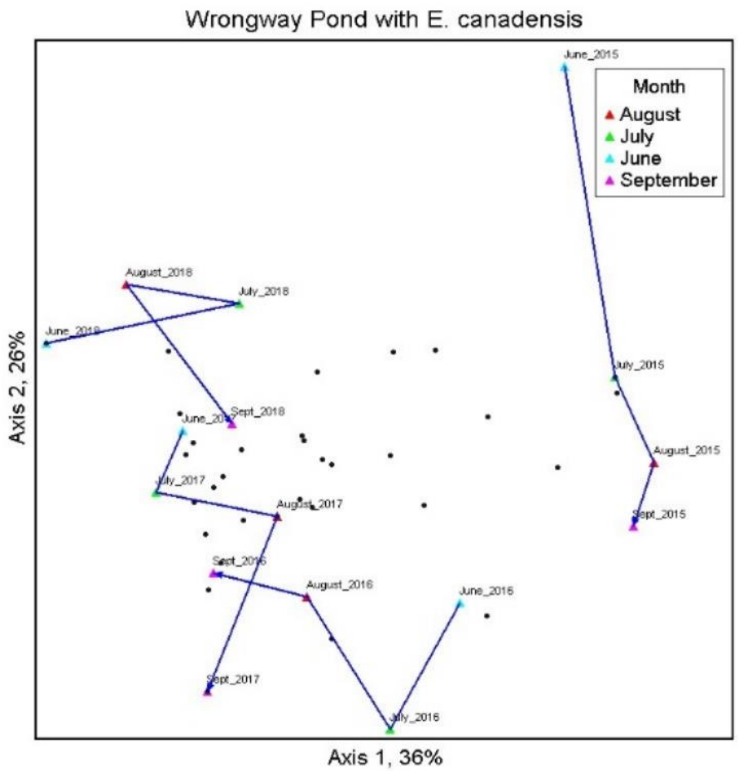
A1)


West Cannery West with E. canadensis
Month
August
July
June
September
June_2015
August_2016
July_2016
Sept_2016
June_2016
June_2017
July_2015
August_2018
Sept_2017
June_2018
July_2017
August_2017
Sept_2018
August_2015
Sept_2015
July_2018
Axis 2, 45%
Axis 1, 45%

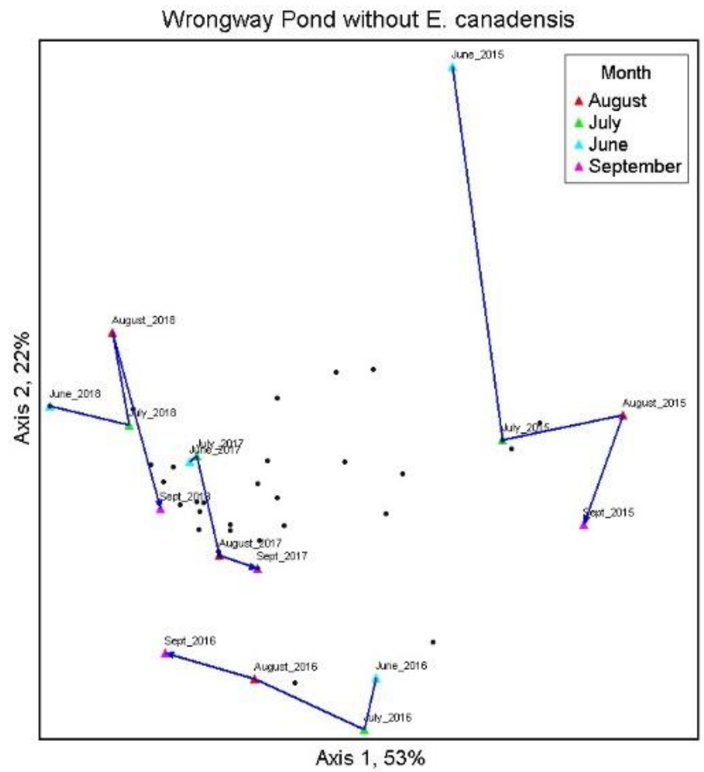
B1)


West Cannery West without E. canadensis
Month
August
July
June
September
June_2015
July_2016
August_2016
June_2016
Sept_2017
August_2018
August_2017
June_2018
Sept_2018
June_2017
Sept_2016
July_2018
July_2015
August_2015
Sept_2015
Axis 2, 51%
Axis 1, 36%

A2)


Wrongway Pond with E. canadensis
Month
August
July
June
September
June_2015
July_2015
August_2015
Sept_2015
August_2018
July_2018
June_2018
Sept_2018
July_2017
August_2017
Sept_2017
Sept_2016
August_2016
June_2016
July_2016
Axis 2, 26%
Axis 1, 36%

B2)


Wrongway Pond without E. canadensis
Month
August
July
June
September
June_2015
July_2015
August_2015
Sept_2015
August_2018
June_2018
July_2018
Sept_2018
July_2017
June_2017
August_2017
Sept_2017
Sept_2016
August_2016
June_2016
July_2016
Axis 2, 22%
Axis 1, 53%

2.4 Discussion

Of utmost interest to the overall story of invasion by *E. canadensis* is the contrast between first and last sample years as change between the two timepoints covers the breadth of our assessment and parameterizes the window, or snapshot, from which we can gain insights into various storylines within the invasion timeline. By taking a pattern analysis approach and assessing the study ponds on a case-by-case basis at a yearly timestep, trends have emerged which apply to all ponds. Through questioning mechanisms of these trends, inherent differences among the ponds were unveiled which we can discuss using the data, but which require further investigation to characterize fully using a study design catered toward statistical comparison. The current dataset does not have the capacity to support statistically based inferences comparing differences in effects between ponds due to lack of power born from a small sample size and lack of replication as it often the case in ecological field studies.

Multivariate tests and ordination techniques operating on data reduction methods allowed for informative comparisons to be made over time beyond simple descriptions of species dominance based on abundance and which extended into more complex components of diversity such as community organization. When measures of dissimilarity (distance) of composition and organization among sample units in individual ponds were compared, ponds displayed congruency of community structure over the course of their study period. The Mantel Test revealed a pattern of consistency between 2016 and 2018 which extended to all ponds. West Cannery West, Wrongway, and Wooded ponds displayed a more moderate correlation between the first year of sampling fixed plots and the last. When years 2017 and 2018 were tested against each other to get a sense of the progression of change, Wrongway and Wooded ponds both displayed a stronger correlation over the one-year time period. The pond which never contained *E. canadensis*, Eyak South, demonstrated a very strong correspondence between the first and last sample years; however, this is not necessarily an indication that lack of change is due to the absence of the exotic plant, as West Cannery East, the pond which contained the exotic that was then removed, also displayed a strong correlation indicating a lack of change in community structure. While the degree to which some community structures in ponds correlated among the years varies, all correlation coefficients were significant. The Mantel Test only considers data from fixed transect plots, and these fixed plots do not always account for rare species or those with more disperse growing habits. These rare and dispersed species may have been more effectively captured in randomly placed plots. However, the fixed nature of these plots increases the precision needed for accurately capturing change over time as there is less contribution of random change present in the test.

An assessment of species compositional changes using the blocked multi-response permutation procedure (MRPB) yielded high agreeance, or homogeneity of species, between sample units in the first and last year of sampling for all sites except for Eyak South. The Eyak South pond is a site where the dominant species tend to occupy the entirety of the plot when sampled. The effect of this is reflected in MRPB where the test statistic indicated low levels of homogeny for sample units among years, regardless of the static nature of the community, since each sample unit may be occupied by only one species and thus would be 100% not homogenous with another sample unit occupied by another species. This effect is also seen in the Indicator Species Analysis for the same reason; the same species have approximately equal likelihood of membership to each year group resulting in no one species emerging as an indicator. *E. canadensis* did not emerge as a significant indicator of any year group for any of the ponds. In 2018, *Myriophyllum sibiricum* was indicative of West Cannery West which matches very well with anecdotal field observations. Another noteworthy result of ISA was the significantly high indicator value for bare ground in West Cannery East pond in 2018, which may be interpreted as a result of the herbicide treatment. While the herbicide treatment undoubtedly reduced abundance of *E. canadensis*, the overall structure and composition of the community was not significantly affected according to the tests. Bare ground emerging as an indicator could represent an overall reduction in cover of all species such that more substrate is visible when estimating cover from above, though it is unclear and cannot be inferred to be due to a reduction in *E. canadensis.*

The Mantel Test was used again to evaluate how community structure may shift with the hypothetical absence of the exotic focal species. As this was a simulation executed by the simple deletion of *E. canadensis* abundance data from the species matrix, which was then compared to the original matrix including *E. canadensis*, it did not account for real lagged effects the species may have had on the community prior to the sampling period. From the previous Mantel Test and MRPB procedure, we observed that there was little structural and compositional change over the three-year period, so this simulated test only provided information regarding subtle variation in change over time with and without *E. canadensis* such as magnitude and direction of change represented by successional arrows in ordination space (Figure 2.12). If there had been overall structural and compositional changes observed from the first two tests, we could use this third test to draw a conclusion of the association of *E. canadensis* to that change. However, causal inference would still not be appropriate given the statistical setting.

Regarding species displacement, not only is it of interest to note the year pairs displaying high and low values of total turnover, but the overall fluctuation of species richness inherent in the systems. These fluctuations are often driven by rare species and their response to abiotic and biotic factors during any given growing season. In the case of species displacement, totals of species appearance and disappearance from the system is informative, but trends in reduction of abundance at the species level may also provide evidence of individuals in a species population being displaced over time. It may not be obvious that a phenomenon such as this is due to the presence of a particular species such as an exotic.

West Cannery East Pond experienced a reduction in relative abundance of *Equisetum fluviatile* where it was not captured in randomly distributed samples during any sample period in 2018. There was also a drastic increase in bare ground relative to overall plant cover between the first and last sample year. It is unclear whether this is due to the herbicide treatment effective in 2018 as bare ground values were also high at points in 2016 immediately after the first herbicide application and prior to an observable effect on plant biomass.

Ranking abundance is an effective way of qualifying differences in abundance of each species with relation to all other species (relative abundance) by describing the order of things. Over time, ranking of each species changes and reordering of the community takes place. The level of reordering is indicative of overall stability as reordering is affected by turnover in species richness (coming and going) and the rate at which these events take place. When rank abundance was viewed through a lens of chordal geometry (rank clock), it was revealed that Eyak South Pond is the most stable of all ponds consistently dominated by *Myriophyllum sibiricum* and *Fontinalis antipyretica.* Interestingly, this stability was not reflected in the Shannon Index H' value as the distribution of abundance is spread over a few dominants lowering the evenness component of the site's H' calculation. However, the stability was reflected in the computed rate of change value remaining small. A very steady departure of a species trajectory from the center of the rank clock represents a steep slope over time indicating that species contribution of abundance to a reduction of evenness. At West Cannery West pond, *Myriophyllum sibiricum* and *Fontinalis antipyretica* became dominant over time.

While no simple test is available to determine whether changes in diversity and indications of species displacement are due to an effect of *E. canadensis*, the collection of information resulting from investigation of components of diversity can provide evidence toward a conclusion. The Mantel Test is one statistical technique available to assess whether overall changes are due to the exotic; however, since there is no data for pre-infestation conditions comparisons, a hypothetical deletion of *E. canadensis* was tested. This deletion does not account for any subtle effects the exotic may have had on the resident community which may have manifested over a longer time period. Results indicated significant departure from the original configuration and was demonstrated in NMS ordination by only slight migration of sample units in species space for the two ponds where *E. canadensis* was most dominant. Mantel Test results showed no significant change even in the community structure of West Cannery East Pond over the sampling period, despite the successful removal of *E. canadensis* from the system effective in 2018. These results indicate that *E. canadensis* was not a dominant species in this pond by illustrating that the actual removal, as opposed to hypothetical, of the exotic species did not impact measures of dissimilarity among sample units. Results from the MRPB procedure showed high agreement reflecting homogeneity among sample units between the first and last sample year in this pond despite presence of the exotic species from 2015 to 2017, and eradication by herbicide effective in 2018. This further emphasizes the lack of dominance and lack of influence of this species on community composition in this pond.

Due the complex nature of the communities and variation in structural characteristics of each pond, an in-depth pattern analysis was required to determine trend among ponds while not directly comparing these entities. The community analysis including multiple tests and exploratory techniques for similar questions in order to view change over time from many angles. Comparing results of these tests provided somewhat of an agreeance regarding the presence and extent of change in each pond and in the overall sample. There has not been a sweepingly significant change in community characteristics over the four-year sample period, however, there is still variability observed over the course of the study. This variability is the key to understanding how the native community responds to *E. canadensis*. Further investigation was conducted into the mechanisms influencing the variability and response of dominant species to the overarching factor of temperature.

2.5 Conclusion

There is heterogeneity in response of native flora to non-native species establishment and invaders are not uniformly detrimental where they may facilitate desirable native species dynamics by engineering the ecosystem (Rodriguez, 2006). They may not affect, temporarily affect, or permanently change ecosystem function for associated fauna (Rybicki & Landwehr, 2007). It is also important to note that levels of influence of a non-native species on native species abundance and thus community dynamics may change over time and timelines needed for accurate evaluation of impacts may exceed those of management objectives.

Through a pattern analysis approach taken to evaluate all sites considered separately, common trends emerged. Rather than determine effects by evaluating differences in infested versus un-infested ponds, this approach took data from a sample design with limited statistical power and sought out what was common throughout sites with varying geomorphological and hydrologic properties, and community characteristics. This process illuminated trends which were common throughout the scope and timeline of the study:

- No significant differences in community structure or composition were observed over the four-year study period for any of the ponds; four containing

E. canadensis and one containing only native species, despite herbicide treatment to one pond.

- There was no evidence of species displacement from the first sample year to the last (2015 to 2018); however, fluctuation in diversity was detected between some years.

- Actual removal of *E. canadensis* from the treatment pond did not influence community structure. Influence of the exotic species on community structure in non-treatment ponds was also investigated statistically by testing matrices with and without the species. This comparison indicated low impact of the exotic species.

In conclusion, there is evidence indicating that the study ponds are variable in diversity throughout the four-year study period, but this variability is not great enough to promote significantly different community characteristics. The variation that does exist among years, and between the first and last sample year, is not influenced heavily by *Elodea canadensis* at the level of abundance it has maintained over the sample period. Displacement of native species has not been demonstrated at the its current levels of relative abundance. Mechanisms influencing the magnitude and direction of change in species abundances needs further investigation as they are important in mediating species interactions which shape communities.

This research can be viewed as a case study investigating the trajectory of invasiveness of *E. canadensis* and invasability of the native aquatic plant community in a sample of freshwater ponds on the CRD. What was found was a lack of evidence of the non-native plant following hallmark invasion characteristics after successful establishment of populations in the study sites. This is not the first example of this species infesting waterbodies yet not displaying invasive characteristics. A recent study performed by Kolada & Kutyla (2016) of approximately 130 Polish lowland lakes infested with *E. canadensis* reported findings of similar patterns of lack of substantial increases in abundance over two 4-year periods of time and concluded that this species was a non-aggressive addition to the collective flora.

Regardless of rigorous study on the topic, mechanisms behind successful invasion are still quite vague (Levine et al., 2003) because it is not often that we can predict an invasion far enough ahead of time to study the biotic and abiotic conditions prior to the invasion, nor is it true that certain traits of invasive species favor invasiveness across all habitats (Alpert et al., 2000). We are left to study the outcome for clues regarding invasion mechanisms. In the event of a non-native species introduction, success of establishment and colonization depends largely upon habitat characteristics (Knapton & Petrie, 1999; Parker et al., 1999; Ali & Soltan, 2006) which include physiochemical conditions and resources as well as potential inter-specific competition between species for resources. However, specific traits may have differing influence on the invasiveness of an aquatic macrophyte to other macrophytes and organisms of other trophic levels (Schultz & Dibble, 2012). Species invasion occurs in stages which may extend over a much longer timeline than a scientific study allows. Since we cannot know the exact position of these sites on their invasion timelines and do not have information prior to infestation, predictions regarding changes in beta diversity and probabilistic rankings of susceptibility based on physiochemical characteristics of waterbodies on the delta are not implicit. For these reasons, there is value in examining a four-year snapshot in the invasion timeline in greater detail at the monthly time step.

It is a challenge in ecological field studies to find replicate sites for control purposes for a statistically robust study design. Caution should be exercised when extrapolating results of his study to answer the question of whether infestation of *Elodea canadensis* is changing aquatic plant communities delta-wide because the study design could not include a large enough sample size to serve as replicates and/or reference areas for purposes of statistical inference.

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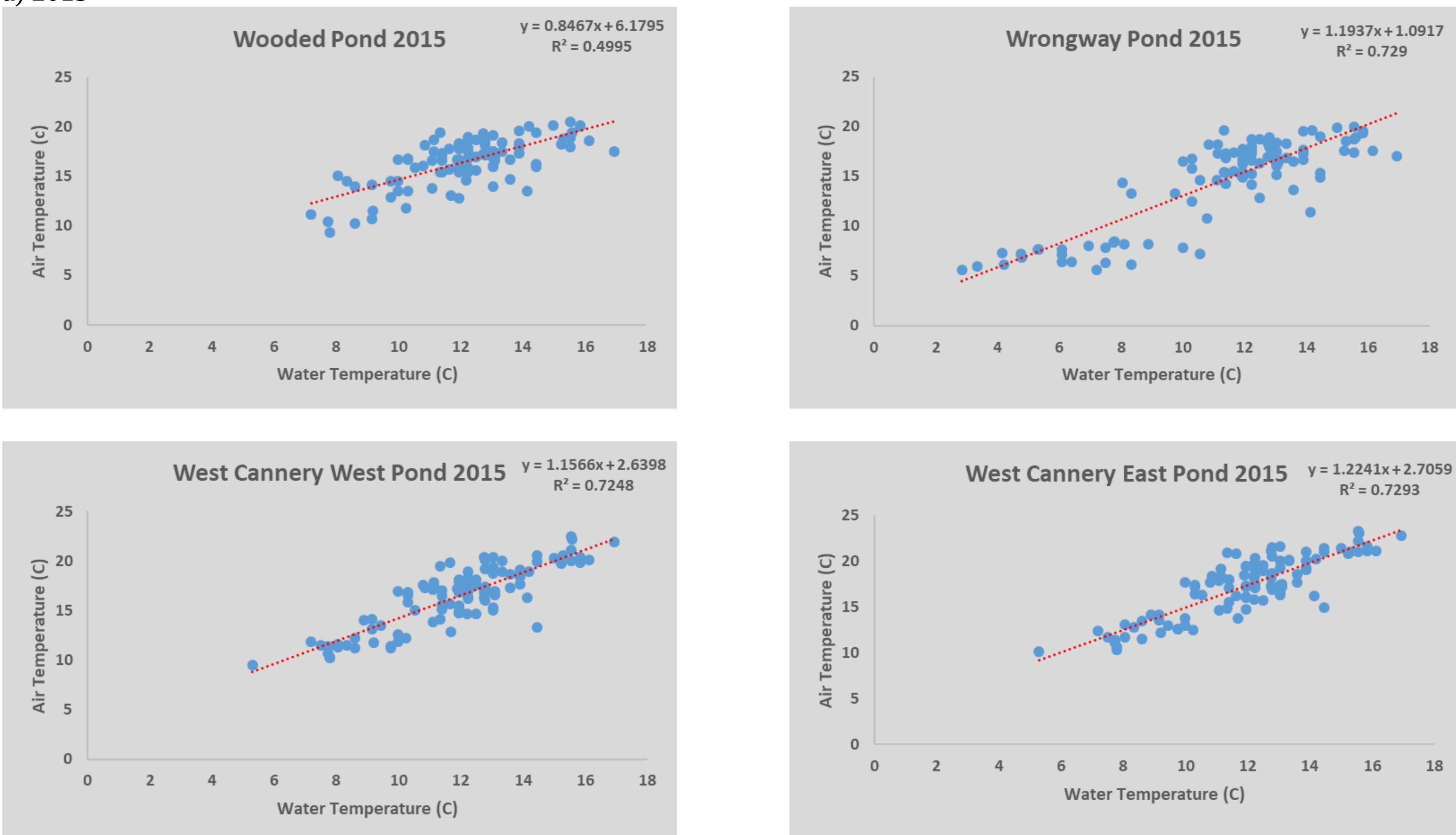
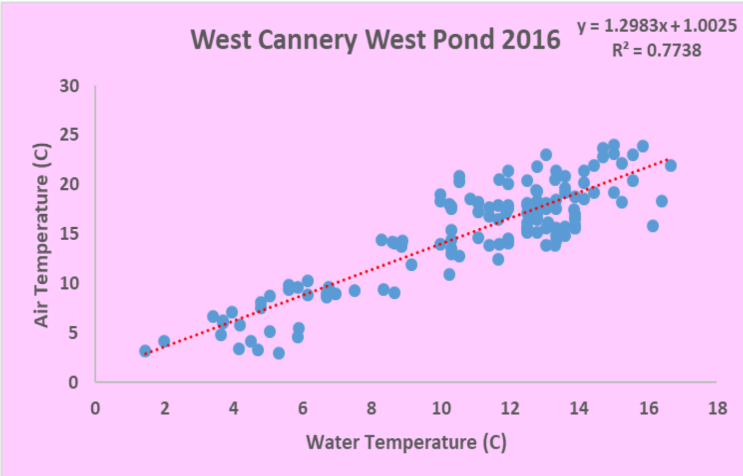
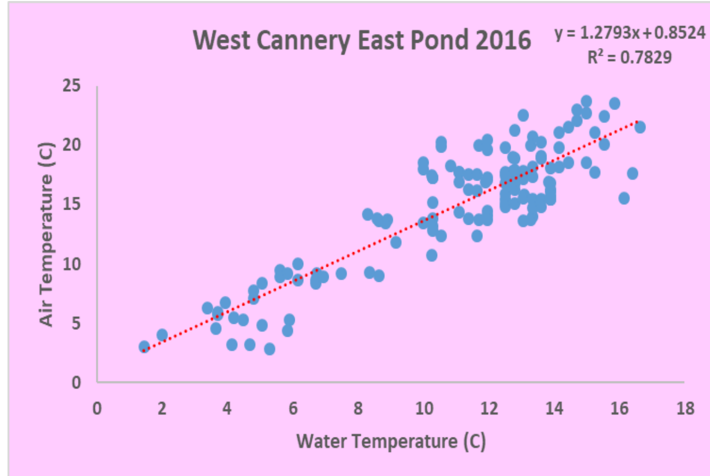
Appendix A. Oversized Figures

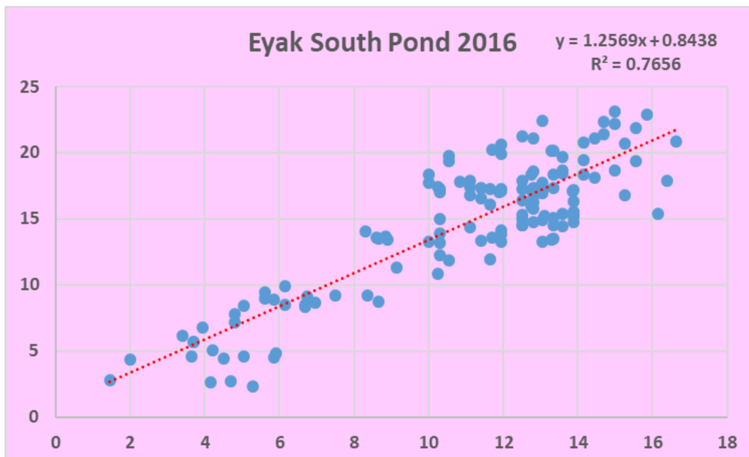
Figure A.1a-d Air and Water Temperature Relationships
a) 2015

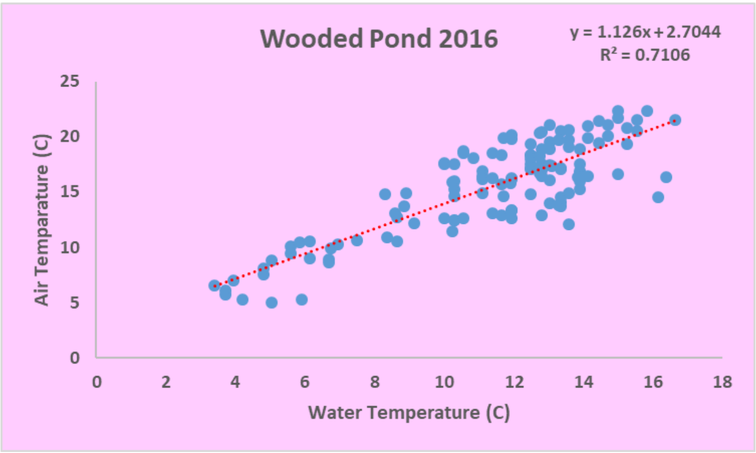


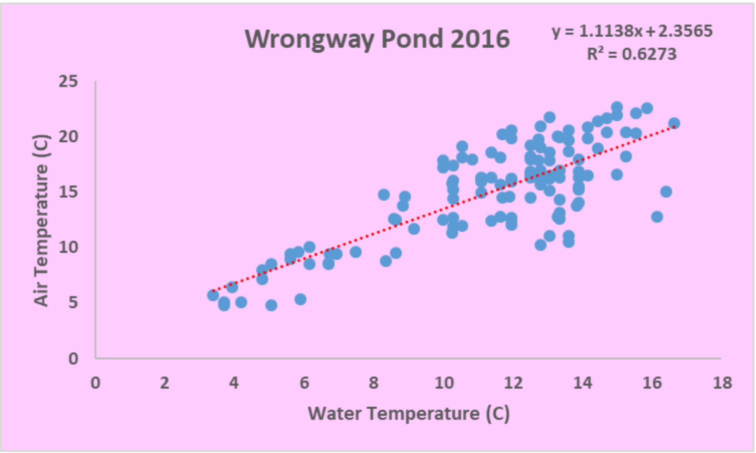
b) 2016


West Cannery West Pond 2016
y = 1.2983x + 1.0025
R² = 0.7738
Air Temperature (C)
Water Temperature (C)
0
5
10
15
20
25
30
0
2
4
6
8
10
12
14
16
18

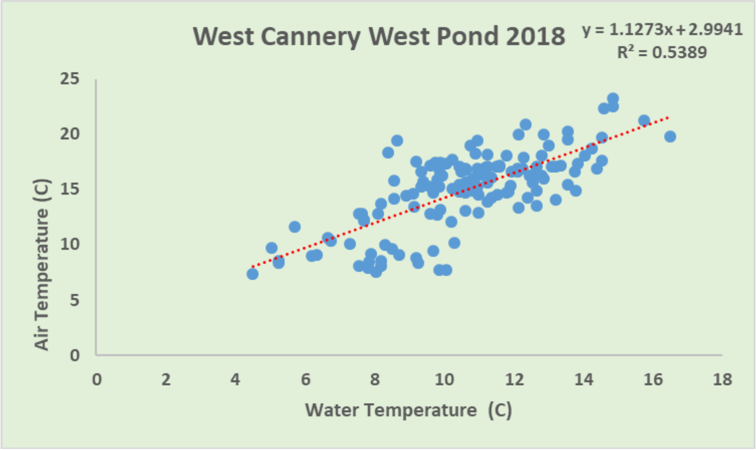

West Cannery East Pond 2016
y = 1.2793x + 0.8524
R² = 0.7829
Air Temperature (C)
Water Temperature (C)
0
5
10
15
20
25
0
2
4
6
8
10
12
14
16
18

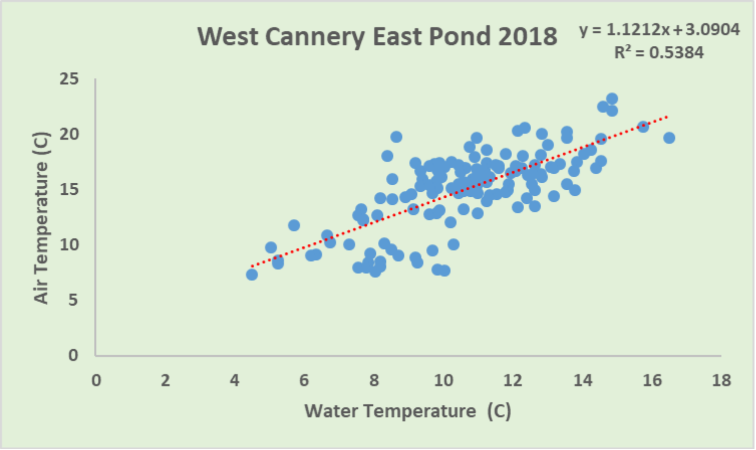

Eyak South Pond 2016
y = 1.2569x + 0.8438
R² = 0.7656
0
5
10
15
20
25
0
2
4
6
8
10
12
14
16
18

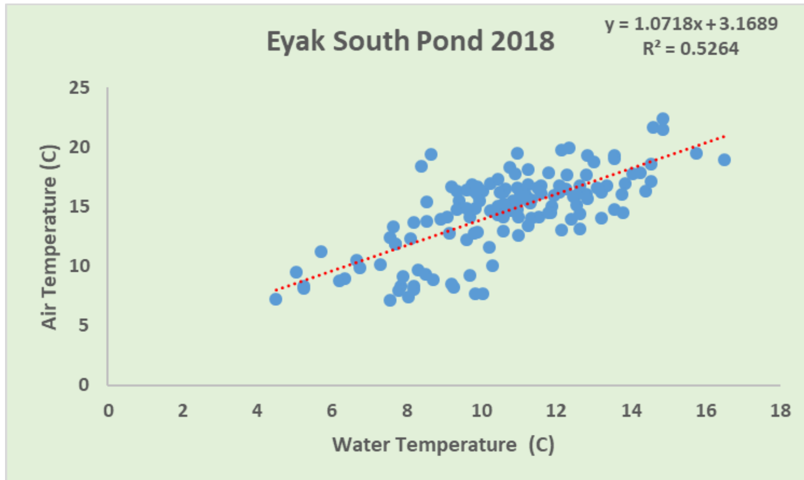


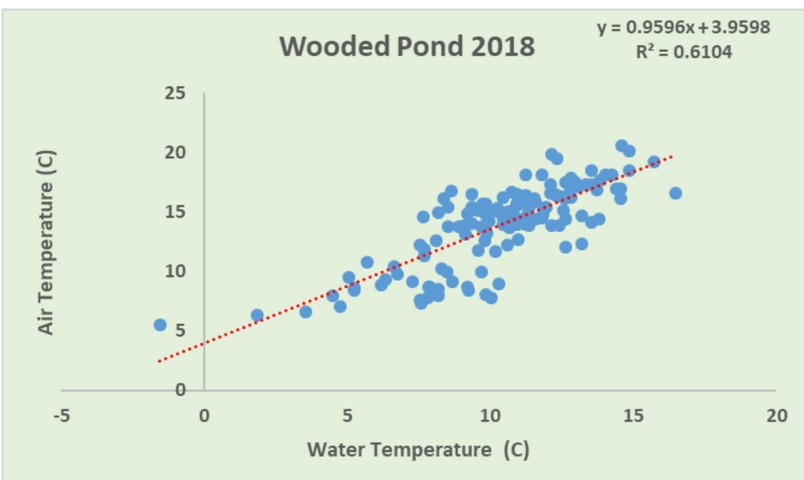


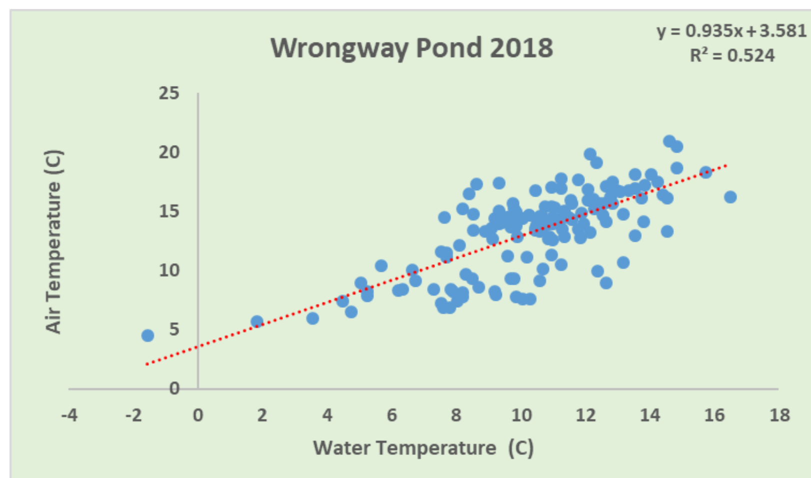
c) Air and Water Temperature Relationships 2018



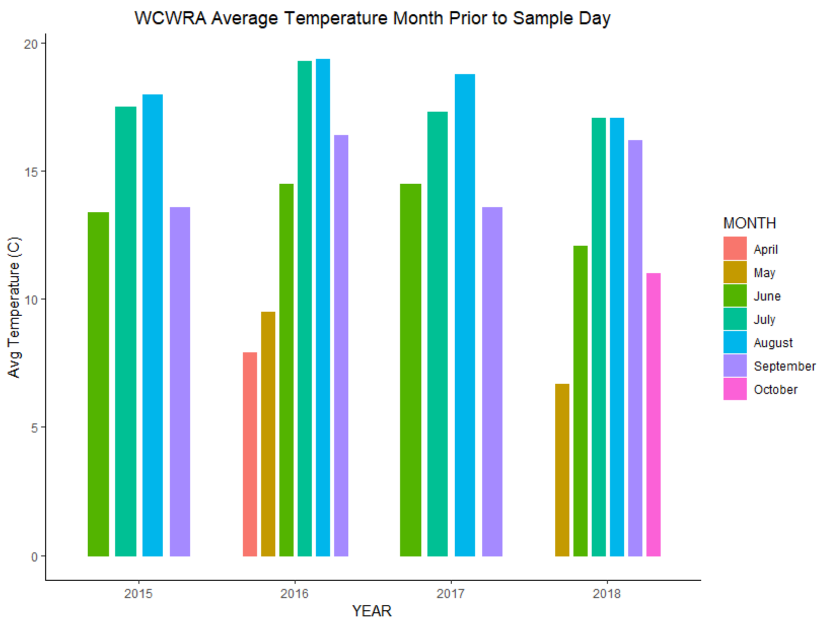


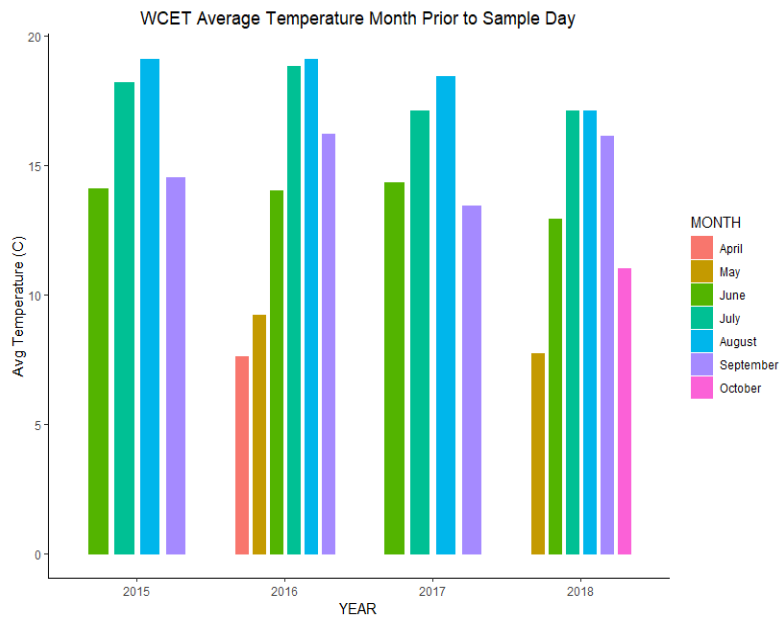

Eyak South Pond 2018
y = 1.0718x + 3.1689
R² = 0.5264
Air Temperature (C)
Water Temperature (C)
0
2
4
6
8
10
12
14
16
18
0
5
10
15
20
25

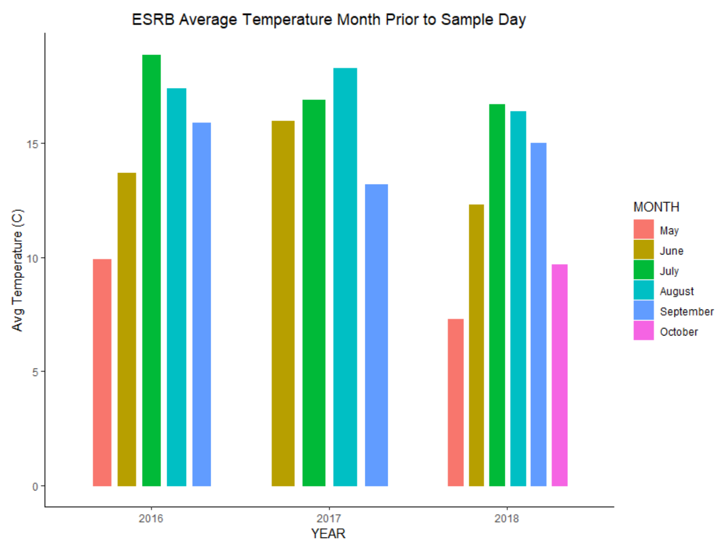

Wooded Pond 2018
y = 0.9596x + 3.9598
R² = 0.6104
Air Temperature (C)
Water Temperature (C)
-5
0
5
10
15
20
0
5
10
15
20
25

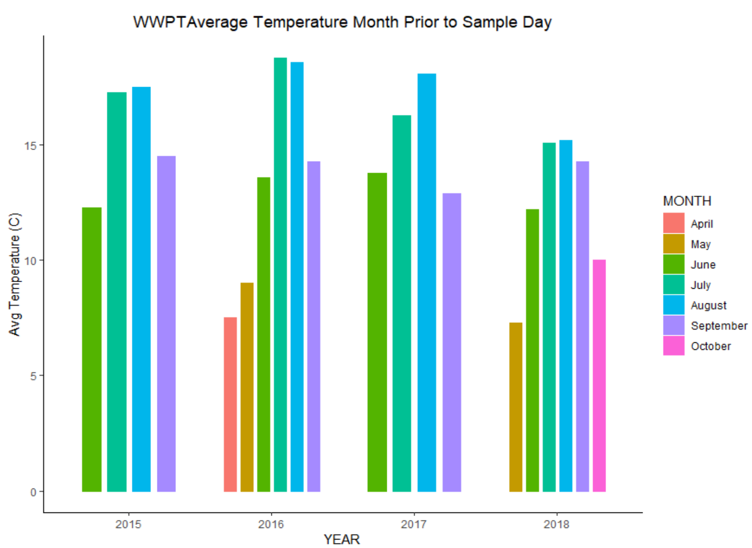

Wrongway Pond 2018
y = 0.935x + 3.581
R² = 0.524
Air Temperature (C)
Water Temperature (C)
-4
-2
0
2
4
6
8
10
12
14
16
18
0
5
10
15
20
25

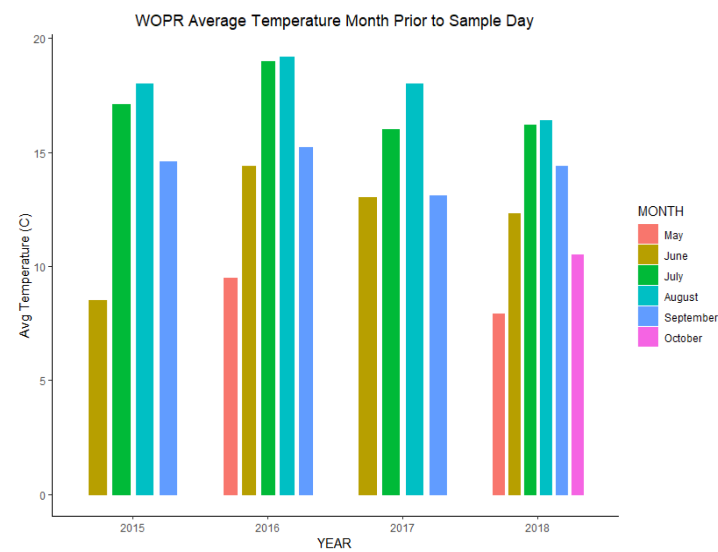
A.2a-d Physiochemical Parameter: Mean monthly water temperatures for 30-day period prior to each vegetation sampling date. The seasonal cycle of heating and cooling is not substantially different among sites. All sites were consistent in the expected cycling of heating and cooling over the growing season





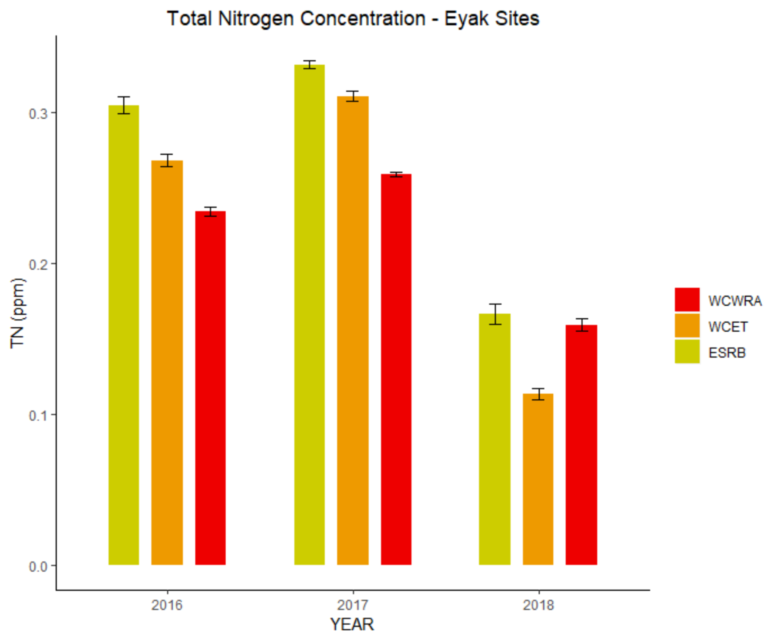

ESRB Average Temperature Month Prior to Sample Day
Avg Temperature (C)
0
5
10
15
2016
2017
2018
YEAR
MONTH
May
June
July
August
September
October


WWPTAverage Temperature Month Prior to Sample Day
Avg Temperature (C)
0
5
10
15
2015
2016
2017
2018
YEAR
MONTH
April
May
June
July
August
September
October

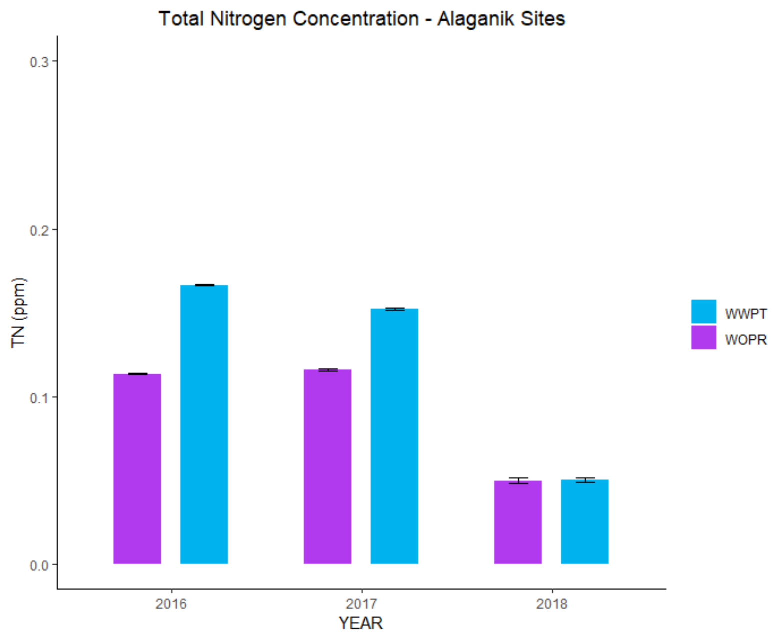

WOPR Average Temperature Month Prior to Sample Day
Avg Temperature (C)
0
5
10
15
20
2015
2016
2017
2018
YEAR
MONTH
May
June
July
August
September
October

A.3a-b Physiochemical Parameter: Mean monthly total nitrogen (TN), which includes all forms of the nutrient and is not limited to Reactive nitrogen forms which are readily available to support plant growth, primarily nitrate, nitrite, ammonium, and organic N. In terms of comparative concentrations, the Alaganik sites are more nutrient poor overall.

a)



b)



A.4a-b Physiochemical Parameter: Mean monthly pH. Both pond groupings can be considered slightly acidic. The average yearly pH of the Eyak ponds approaches 6 which is considered less basic, where the average yearly pH of the Alaganik ponds exceeds 6, which is considered more basic. For context, a bog is highly acidic and has a pH of 4 or below.

a)

b)