

Climate Change, Phenological Shifts, and Species Interactions:  
Case Studies in Subalpine Plant and Migratory Fish Populations

by

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Dissertation submitted in partial fulfillment of  
the requirements for the degree of Doctor  
of Philosophy in the University Program in Ecology  
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2019

ABSTRACT

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## Abstract

Phenology, the timing of biological events across the year, is shifting in response to climate change. Not all species within a community are responding to the same environmental cues by shifting their phenology to the same degree. As a consequence, the strength and direction of species' interactions are also undergoing rapid changes. In this dissertation, I used observations, experiments, and demographic modeling to explore the relationship between climate, phenology, and species interactions in one terrestrial and one aquatic field system. With these two systems, I attempted to answer the central question, "What are the environmental drivers and ecological consequences of phenological shifts?"

In chapter two, I examined how co-flowering subalpine spring ephemerals (*Claytonia lanceolata*, *Mertensia brevistyla*, and *Mertensia fusiformis*) in the Colorado Rocky Mountains, USA compete with and facilitate one another for biotic and abiotic resources. These flowering species were the first to emerge and flower shortly after snowmelt. As a result of phenological shifts, these species showed greater temporal overlap under early snowmelt conditions. Using field experiments, I found that these species did not facilitate one another or compete for pollinator resources, but they did affect each other's vital rates in two years.

In chapter three, I simulated how the presence of neighbors, including all heterospecific neighbors, affected population growth of *Claytonia* and *Mertensia* under future predictions of spring snowmelt date. I used data from field experiments to parameterize integral projection models and forecast population growth into the future. I found that neighbors significantly influenced population growth rate under average snowmelt conditions, but not under early snowmelt conditions. Under future predictions of early snowmelt, populations declined rapidly regardless of neighbor presence.

In chapter four, I worked with the Northeast Climate Adaptation Science Center to determine the environmental drivers of alewife (*Alosa pseudoharengus*) migration in Massachusetts. First, I used field-collected daily fish counts to assess how the timing of migration has changed. I found that some of the streams showed significant advances in run timing, while others did not. Second, I combined migration timing metrics with publicly available climate data. I found that shorter, wetter winters and mild spring temperatures were correlated with earlier run initiation dates.

Collectively, my research from subalpine meadows and coastal streams revealed three significant conclusions. First, the temporal variability in the strength and direction of species interactions may be important for predicting future coexistence. Second, unequal phenological shifts between members of a community may not only impede coexistence, but could facilitate coexistence in the future through positive effects on

population growth. Finally, experiments mechanistically linking phenology and species interactions are necessary for understanding implications of phenology on coexistence.

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# 1. Introduction

Over the past few decades, warming and other climatic changes have led to shifts in phenology in plants and animals (Parmesan, 2006, Walther *et al.*, 2002). Changes in phenology may have fitness consequences, because organisms rely on environmental cues to time physiological processes and activities critical for growth, reproduction, and survival (Miller-Rushing *et al.*, 2010, Rasmussen & Rudolf, 2015). Furthermore, shifts in phenology affect how species interact with one another, potentially affecting the ability of species to coexist (Tylianakis *et al.*, 2008, Valladares *et al.*, 2015, Yang & Rudolf, 2010).

*The goal of my dissertation was to assess the relationship between climate, phenology, and species interactions using a combination of observations, field experiments, and demographic models in one terrestrial and one aquatic study system.*

Although I do not forge the full chain of links between climate, phenology, and species interactions in a single system, studying two organisms has given me the opportunity to learn how researchers across fields approach phenology. Therefore, in this introduction, I will briefly 1) review the methods and challenges to evaluating phenological shifts in plants and animals, and 2) provide an outline of my dissertation.

## **1.1 Approaches and challenges to studying phenology in terrestrial and marine organisms**

Phenological shifts of sessile organisms are well characterized in temperate, terrestrial ecosystems (Parmesan & Yohe, 2003, Thackeray *et al.*, 2010). Monitoring phenology in immotile terrestrial organisms, such as herbaceous plants and trees, is relatively straightforward. A variety of methods exist to track phenophases of individuals, populations, and whole communities. Frequent censusing of the same individuals, employing camera traps, and analyzing satellite imagery are methods often used to monitor phenology in plants and trees. Given the availability of approaches, tracking phenological events across the life cycle of a single organism is possible in these systems.

Detecting phenological shifts in mobile and cryptic organisms is more challenging than in most plant systems. Animal studies rely on mark-recapture, camera traps, and frequent censusing to assess phenology. While these data may be more difficult to gather and encompass greater uncertainty, there is a great need for these types of data. By coupling phenological events of plants and animals within the same ecosystem, we can start making better predictions about the ecological and evolutionary consequences of phenological shifts.

## **1.2 Outline of dissertation:**

For chapters two and three, I worked at the Rocky Mountain Biological Laboratory in Colorado, USA. In chapter two, I assessed whether two subalpine plant

taxa compete with each other for soil resources and pollinators. Under early snowmelt, temporal overlap between *Claytonia lanceolata* (Montiaceae), *Mertensia brevistyla*, and *Mertensia fusiformis* (Boraginaceae) was higher, suggesting the potential for increased overlap under future climate change. First, I used a neighbor removal experiment and found that the effects of *Claytonia* on *Mertensia* and *Mertensia* on *Claytonia* vital rates varied between years. Secondly, although these species flower at the same time and have been documented to share pollinators, visitation rates to *Claytonia* and *Mertensia* were not affected by each other's local floral density. Combined, these results suggest that competition and facilitation between these species for multiple shared resources are complex and vary temporally.

For chapter three, I coupled a neighbor removal and supplemental water experiment to a population model to determine how the presence of neighbors affected population growth rate in *Claytonia* and *Mertensia*. I assessed how climate influenced the effects of neighbors on deterministic population growth ( $\lambda$ ) by capitalizing on variation in weather between years, as snowmelt date and snowpack were average in 2017 and early and low in 2018. First, I found that neighbor presence positively and negatively affected vital rates in *Claytonia* and *Mertensia* in both years. Second, neighbor effects on vital rates resulted in differences in deterministic population growth rate. Third,  $\lambda$  was significantly lower under early snowmelt conditions relative to the average snowmelt conditions. Fourth, in an early snowmelt year, the neighbor effects on vital rates did not

result in significant differences in  $\lambda$  between most neighbor removal treatments in either species. Finally, under future climate predictions of snowmelt date, all simulated populations of both *Claytonia* and *Mertensia* in neighbor removals declined. In conclusion, neighbors did not strongly mitigate or intensify the detrimental effects of early and low snowpack.

For my fourth and final chapter, I worked collaboratively with researchers at the Northeast Climate Adaptation Science Center (NECASC), which is a consortium of seven research institutions from across the Northeast and Midwest United States (funded by NSF Graduate Research Internship Program, GRIP). Co-authors of this chapter are Adrian Jordaan (University of Massachusetts Amherst, NE CSAC), Jack T. Finn (University of Massachusetts Amherst), John S. Sheppard (Massachusetts Division of Marine Fisheries), and Michelle Staudinger (University of Massachusetts Amherst, NECSAC). We determined the extent of phenological shifts in the timing of adult migration in anadromous alewife (*Alosa pseudoharengus*) in 12 coastal streams along coastal Massachusetts. Anadromous fishes are particularly susceptible to phenological shifts, as they are subject to strong seasonal cycles when transitioning between marine and freshwater habitats to spawn. We evaluated migration timing across coastal streams relative to regional-scale seasonal environmental predictors including spring and fall transition dates, winter duration, sea surface temperature (SST), as well as the North Atlantic Oscillation (NAO) and Gulf Stream indices. The direction and magnitude of

phenological shifts were variable among streams, with some systems showing significant shifts and others showing no detectable changes over time. Overall, there was a trend towards earlier initiation dates, and because shifts in run end dates did not change, this resulted in longer run duration. We found that higher spring minimum SST, more positive winter NAO (representing warmer ocean surface conditions and increased regional precipitation in New England), and later fall transition dates (indicative of shorter winters) best predict run initiation. Our results suggest shorter, wetter-winters and milder winter and spring temperatures result in earlier adult migration. Future analyses focusing on population and site-specific influences of migration are still needed to understand how climate change is affecting and interacting with other anthropogenic drivers of change (e.g., restoration, barriers to passage).

## **2. Competition and facilitation for abiotic and biotic resources in two subalpine spring ephemerals**

### **2.1 Introduction**

Climate change is causing shifts in phenology or the timing of biological events across a year (Parmesan, 2006, Thackeray *et al.*, 2016, Walther *et al.*, 2002). Species are responding differently to the same environmental cues, resulting in unequal phenological shifts and temporal mismatches between interacting community members (Kharouba *et al.*, 2018, Thackeray *et al.*, 2016, Thackeray *et al.*, 2010). Such changes in synchrony between interacting species are likely to have fitness consequences (Johansson *et al.*, 2015, Miller-Rushing *et al.*, 2010, Rafferty *et al.*, 2015).

To improve predictions about phenological shifts and species coexistence under climate change, we have to evaluate how co-occurring species compete with or facilitate one another for the acquisition of shared resources. For example, if climate-induced phenological shifts cause two species with differing competitive abilities to have higher niche overlap, fitness differences may cause the exclusion of the weaker competitor (Chesson, 2000, Valladares *et al.*, 2015). By contrast, if these species facilitate one another through mechanisms such as stress amelioration or protection from harsh abiotic conditions, coexistence may be feasible when previously impossible (Valladares *et al.*, 2015).

Species may exert a combination of positive and negative effects on one another for different resources (Callaway & Walker, 1997, Hart & Marshall, 2013). Interspecific

interactions for biotic resources (e.g., pollinators and seed dispersers) and abiotic resources (e.g. sunlight, nutrients, and water) are not often studied concurrently, yet both may induce changes in vital rates in novel climates (Amarasekare, 2002, Ashman *et al.*, 2004). Shifts in flowering phenology may result in access to a different community of pollinators, potentially resulting in reduced pollinator visitation frequency (Hegland *et al.*, 2009, Memmott *et al.*, 2007). Such changes in visitation rates may affect fecundity and subsequently population growth (Ashman *et al.*, 2004). If two species compete for pollinator services, an increase in flowering overlap may lead to more competition. At the same time, if these species facilitate one another through protection from frost, then an increase in overlap may be beneficial (Brooker *et al.*, 2008, Callaway, 1995).

I determined the degree to which two subalpine early-spring plant taxa compete for or facilitate one another for shared abiotic and biotic resources in two years by asking the following questions: 1) Is temporal overlap between *Claytonia* and *Mertensia* correlated to climate and early snowmelt?, 2) How do neighbors affect growth, reproduction, and survival in average and early snowmelt years?, and 3) Do these species compete with or facilitate one another for pollinator visitation?

## **2.2 Materials and methods:**

### **2.2.1 Study system**

I conducted this study in three subalpine meadows near the Rocky Mountain Biological Laboratory (RMBL) in Gothic, CO from 2016 to 2018 (Marriage Meadow

(MM): 38°57'59.6"N 106°59'26.4"W; Avery Campground (AC): 38°58'58.6"N 107°00'06.2"W; Kebler Pass (KP): 38°51'08.8"N 107°05'50.0"W).

The growing season at the RMBL typically begins in mid-May or early-June when the snow melts (average date: May 19, Table 1). From 1974 to 2018, the RMBL received an average of  $1072.14 \pm 42.49$  cm (mean  $\pm$  S.E.) of snow during the winter (barr, 2019) (Table 1). In one year of this study (2017 - 2018), snowfall was the second lowest on record since 1975 (barr, 2019). Spring snowmelt date was earlier in 2018 compared to other years of this study (Table 1, Figure 1) (barr, 2019). Although the three subalpine meadows where I conducted this study were similar in elevation (MM: 3000m, AC: 2950m, KP: 3015 m), they melted out sequentially over a period of two weeks (MM earliest, then AC, then KP).

**Table 1. Total snowfall (cm), snow water equivalent (cm), and snowmelt date (Julian date) in three years of this study at the Rocky Mountain Biological Laboratory, CO, USA. Mean  $\pm$  S.E. are in the last row. Data are from barr (2019).**

Years	Total snowfall (cm)	Snow water equivalent (cm)	Snowmelt date (Julian date)
2015 - 2016	837	53.6	139
2016 - 2017	990	78.5	144
2017 - 2018	490	42.4	125
1975 - 2018 (mean $\pm$ S.E.)	$1072 \pm 43$	$69.45 \pm 2.87$	$139.70 \pm 2.04$

Spring ephemerals at the RMBL emerge shortly after snowmelt and senesce before the monsoon season in July. Average ambient precipitation at the RMBL during the growing season of spring ephemerals in this study (May until the end of June) from

2000 – 2017 was  $5.78 \pm 0.33$  cm (NADP, 2019). In 2016 precipitation during the growing season was slightly above average (6.80 cm) and slightly below average in 2017 (4.19 cm) (NADP, 2019).

*Claytonia lanceolata* (Montiaceae), *Mertensia fusiformis* (Boraginaceae), and *M. brevistyla* (Boraginaceae) are herbaceous perennials that flower shortly after snowmelt (Inouye, 2008, Price & Waser, 1998). *Claytonia* produces small, white and pink, obligately outcrossing flowers (Davis, 1966, Mistretta & Liston, 1992), and *Mertensia fusiformis* and *M. brevistyla* produce blue self-incompatible campanulate flowers (Lin & Forrest, 2017). Although *M. fusiformis* and *M. brevistyla* species differ slightly in floral morphology, they are comparable in size and have very similar pollinator assemblages at the RMBL (Lin & Forrest, 2017). *Mertensia fusiformis* was present at sites MM and AC. *Mertensia brevistyla* was the dominant early-season *Mertensia* at KP, although *M. fusiformis* was present in an adjacent field (Lin & Forrest, 2017). Throughout this paper, I will refer to both *M. brevistyla* and *M. fusiformis* as *Mertensia* and will treat the two species as being equivalent.

*Claytonia* and *Mertensia* were ideal species to study competition and facilitation for multiple shared resources several reasons. First, at the RMBL, onset, median, and end of flowering dates in both *Claytonia* and *Mertensia* have been occurring earlier in the season in response to early spring snowmelt; however, the magnitudes of these shifts are different for each species (CaraDonna *et al.*, 2014, deKeyzer *et al.*, 2016, Gezon *et al.*,

2016, Price & Waser, 1998). These unequal shifts in flowering phenology may result in changes in temporal overlap with one another. Secondly, these species tend to grow right next to one another and have a shared pollinator community, which includes small solitary bees, *Lasioglossum rudiosense* (Halictidae), *L. sedi*, and *L. inconditum*, and occasionally queen *Bombus flavifrons* (Apidae) (Forrest *et al.*, 2011, Gezon *et al.*, 2016, Irwin *et al.*, 2018). Finally, pollen may be a limiting resource in some years, as *Claytonia* and *Mertensia* experienced pollen-limitation in the early season in two previous studies (Forrest & Thomson, 2010, Gezon *et al.*, 2016).

## 2.2.2 Temporal overlap calculations

Flowering data: Since 1974, David Inouye and colleagues have recorded daily flower counts of all species in 2 x 2 m<sup>2</sup> permanent plots around the RMBL (n = 105 species). I selected a subset of these plots that occur in subalpine meadows and aspen forest (“Rocky Meadow plots”), which are most similar to the habitat type of my experimental sites. I omitted years of data when onset of *Claytonia* was not observed (n = 9 years). Data collection in these years did not begin early enough in the season to capture some flowering days of the earliest individuals, and therefore would severely bias analyses. I used daily flower count to estimate floral overlap between *Claytonia* and *Mertensia*. Although these data do not determine vegetative overlap, date of vegetative emergence was strongly correlated to date of first flowering in both *Claytonia* and

*Mertensia* in 2017 (Pearson's product moment correlation; *Claytonia*:  $r = 0.96$ ,  $t = 49.6$ ,  $df = 157$ ,  $p < 0.001$ ; *Mertensia*:  $r = 0.86$ ,  $t = 18.8$ ,  $df = 117$ ,  $p < 0.002$ ) (Dalton, unpublished data).

Snowmelt data: Snowmelt date, which is the first day of year that a permanent 5 x 5 m<sup>2</sup> plot is free of snow, was recorded at the RMBL from 1975 to 2017 (barr, 2019).

Analysis: Similar to an analysis conducted by Forrest *et al.* (2010), I calculated a symmetric overlap index,  $S_{cm}$ , for *Claytonia* (species  $c$ ) and *Mertensia* (species  $m$ ) for each plot following Schoener (1970):

$$S_{cm} = 1 - 0.5 \sum_{k=1}^n |p_{ck} - p_{mk}| \quad (\text{Eq. 1})$$

where  $p_{ck}$  is the proportion of all of *Claytonia*'s flowers for that year that are open on day  $k$ ,  $p_{mk}$  is the proportion of *Mertensia* on day  $k$ , and  $n$  is the total number of days in the season. Values of  $S_{cm}$  close to zero indicate little temporal overlap between species, while values closer to one indicate higher overlap. Next, I determined the relationship between snowmelt date and year using a simple linear regression. I then used a mixed-effects linear model (LMM) to assess the relationship between the average overlap indices and snowmelt date and included plot as a random effect. I log-transformed overlap indices to meet assumptions of mixed effects models. For all linear regressions, I used the function `lmer()` in the "lme4" package (Bates *et al.*, 2014) in R version 3.5.1 (R Core Team, 2018).

While others have previously assessed overlap among these taxa using a similar approach (e.g., CaraDonna *et al.* (2014)), my methods differed in several ways. First,

rather than using all long-term flowering data, I used a subset of plots that were most similar to the plots where I performed my experiments. The long-term flowering phenology plots span a variety of habitat types, from willow seeps to drier meadows. I selected the subset of plots that were most similar to the habitat types of my study sites. Second, I used a different overlap index at the plot level (Schoener's index) instead of an asymmetric index across all plots. Since I designed experiments to assess shared abiotic and biotic resources at small spatial scales, understanding species overlap at the plot scale is critical. However, overlap indices presented in CaraDonna *et al.* (2014) may be more important for pollinator-mediated species interactions, as they incorporate species interactions over larger spatial scales.

### **2.2.3 Neighbor removal and supplemental water experiment**

Field methods: Neighbor density and habitat quality may be positively correlated, obscuring the effects of neighbor density on performance in observational data. I therefore used a neighbor removal experiment in which I randomly assigned density treatments to break any such correlation. To assess how vital rates in *Claytonia* and *Mertensia* are impacted by one another, I selected focal individuals of *Claytonia* and *Mertensia* at sites AC and KP in 2016 (n = 90 *Claytonia* and 89 *Mertensia*). I selected 4 focal individuals within 2 x 2m<sup>2</sup> plots along 40 m long transects at each site (5 transects at site AC, 6 at KP). I then randomly assigned each focal plants in these plots to either a control or a "competitor" removal treatment, *Mertensia* (for *Claytonia* focal plants) or *Claytonia*

(for *Mertensia* focal plants). Prior to neighbor removal, I measured plant size (total number of leaves  $\times$  length of largest leaf), flower number, and fruit number of all focal plants. Plant size was positively correlated to aboveground biomass in both species (Pearson's product-moment correlation; *Claytonia*:  $r = 0.96$ ,  $p < 0.001$ , *Mertensia*:  $r = 0.89$ ,  $p < 0.001$ ) (Dalton, unpublished data). When there were at least two consecutive dry days in the forecast, I clipped aboveground biomass of relevant neighbors in a 30 cm radius and painted the cut stems with Roundup® Weed and Grass Killer (Glyphosate) to inhibit regrowth and kill roots. In 2017 and 2018, I scored survival, vegetative size, flower number, and fruit number of focal plants. I also scored percent cover of the neighborhood and computed Schoener's overlap index (Eq.1) between *Claytonia* and *Mertensia* in each plot.

After finding evidence for positive interactions between *Claytonia* and *Mertensia* in the neighbor removal experiment in 2017 (see 2.3.2 Neighbor removal and supplemental water experiment), I designed an experiment to test a possible mechanism underlying these interactions, amelioration of water stress by neighboring plants. I hypothesized that if neighbors were reducing water stress, supplemental watering should reduce the benefit of neighbors. In 2018, I randomly selected half of the plots in the neighbor removal experiment for a water addition treatment. To reduce the flow of water between plots, I trenched around the perimeter of all plots to a depth of 15 cm following methods presented in Gallagher and Campbell (2017). Every two to three

days over the growing season, I hand watered each plot with 9.4L of water, which is approximately double the average precipitation every 2 days from May until July during 2000 – 2017 at the RMBL (NADP, 2019). Before watering the plots each day, I measured volumetric water content (VWC) by inserting a 12 cm Campbell Scientific Hydrosense Soil Water Measurement System® into the center of each plot.

Analysis: First, I determined the efficacy of the neighbor removal experiment by determining how treatments affected percent cover around the focal plants. I used LMs with fixed effects of neighbor removal treatment and site. Next, I assessed how plant performance (survival, reproduction, and growth) was affected by neighbor removal treatment using LMs and generalized linear fixed effects models (GLMs) for each species in each year. I used a GLM with a binomial error distribution to assess the probability of survival and fruit set, and a LM for growth models. For metrics of plant performance measured in 2017, I began with a full model which included fixed effects of neighbor removal treatment, plant size (in 2016 or 2017), an interaction term (size x neighbor removal treatment), and site. For plant performance quantified in 2018, I constructed the same models, but I added an additional fixed effect of water treatment and the interaction term (water x neighbor removal treatment and water x size). I calculated and compared Akaike Information Criterion (AIC) score for candidate models using the *AICtab()* function in the “bbmle”. I selected the best-fit models with at minimum the following fixed effects: size, neighbor removal treatment, and site. I used the *emmeans()*

function in the package “emmeans” to calculate least squares means and standard error (Lenth, 2018).

#### **2.2.4 Pollinator observations and experiment**

Observations: I assessed how the density and presence of *Claytonia* and *Mertensia* affected one another’s pollinator visitation rate. At each field site from 2016 to 2017, I conducted 20-minute pollinator observations on 2 x 2 m<sup>2</sup> plots during rain-free periods (n = 166 observations, 680 pollinator visits to focal species). Prior to each observation, I recorded floral abundance of all species within the plot, cloud cover (full sun, partly cloudy, overcast), and time of day. I documented insect visitation (when insects touched reproductive parts i.e. anthers, stigmas) to every flower over the observation period as well as the sequence of each insect visitor in the plot. To determine transect-level floral abundance estimates, I recorded the total number of open flowers of all species in transects established for the neighbor removal experiment every two to three days. To account for differences in the number of transects between sites, I calculated an average transect level flowering abundance. I began recording flower number on the first day of bare ground until early July, when *Claytonia* and *Mertensia* had senesced.

Experiment: To assess interspecific competition for pollinators in *Claytonia*, I manipulated the floral abundance of *Mertensia* in 2 x 2 m<sup>2</sup> plots in 2017. I either removed or systematically added cut *Mertensia* flowers in florist water picks to plots with *Claytonia*. Prior to each observation, I recorded floral abundance of all species within

plots, cloud cover, and time of day. I conducted 20-minute pollinator observations during rain-free periods and observed visitation rate and pollinator constancy to unmanipulated and manipulated plots (n = 46 observations, 316 visits to *Claytonia* and *Mertensia*).

Analysis: To control for differences in the abiotic environment during observation periods, I downloaded the average temperature and wind speed from the RMBL weather station (NADP, 2019). I used LMMs to assess the relationship between visitation rate (number of visits/flower/hour) and plot floral abundance, transect floral abundance, presence/absence of focal species, cloud cover, wind speed, temperature, time of day, and Julian date. I included random effects of site, year, and observer. I used a similar approach when analyzing the results from the experiment, except I ran separate models for each manipulation (*Mertensia* addition or *Mertensia* removal) and the only random effects in these models were site and observer. I selected the best fit models based on AIC scores.

## **2.3 Results**

### **2.3.1 Temporal overlap**

Summary: Early snowmelt was correlated with higher temporal overlap between *Claytonia* and *Mertensia*.

Snowmelt has advanced by  $0.29 \pm 0.16$  days per year since 1975 at the RMBL (LM:  $F_{1,42} = 3.54$ ,  $p = 0.07$ , Figure 1A). Plot level temporal overlap between *Claytonia* and

*Mertensia* was correlated with snowmelt date (LMM:  $\chi^2 = 9.13$ ,  $p = 0.003$ , Figure 1B).

However, site-level overlap was not significantly affected by snowmelt date (LM:  $F_{1,32} = 0.004$ ,  $p = 0.95$ ).

At my experimental sites, average Schoener's overlap index between *Claytonia* and *Mertensia* at the plot level (in control plots) varied between years (LMM:  $\chi^2 = 95.2$ ,  $p < 0.001$ ). In 2018, when snowmelt was the seventh earliest year on recorded since 1975, overlap was significantly higher in experimental plots than in 2017 (least squares mean  $\pm$  S.E.; 2017:  $0.57 \pm 0.02$ , 2018:  $0.72 \pm 0.02$ ).

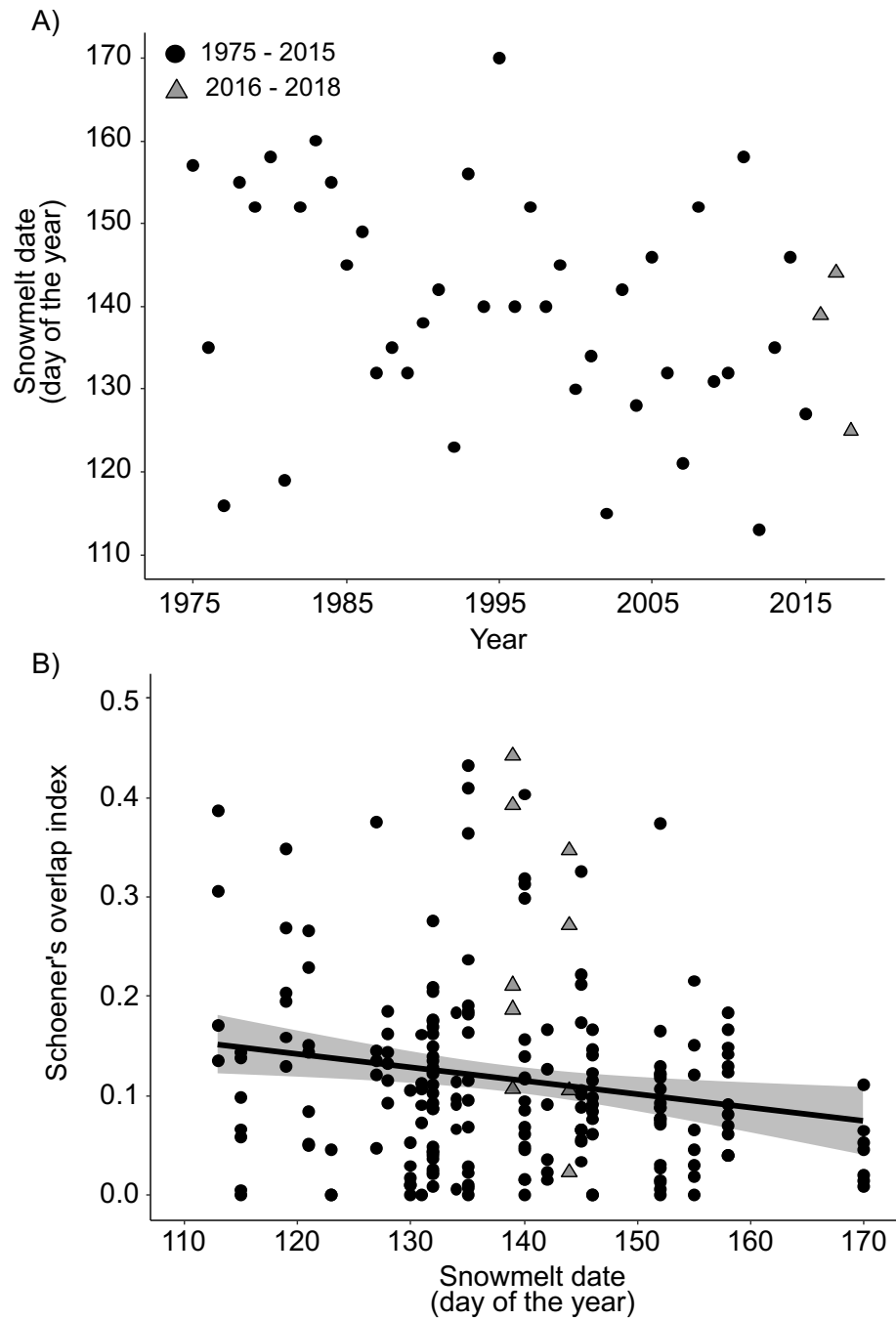


Figure 1. A) Snowmelt date (day of the year of bare ground) over time at the Rocky Mountain Biological Laboratory. B) Schoener's overlap index between flowers of *Claytonia* and *Mertensia* versus snowmelt date. Data recorded before this study began are in black circles (1975 – 2015), while data collected during the time of this study are in gray triangles (2016 – 2018)

### 2.3.2 Neighbor removal and supplemental water experiment

Summary: Reproduction in *Claytonia* and survival, growth, and reproduction in *Mertensia* were affected by neighbor removal treatments. The effects of neighbor removal treatments varied between 2017 and 2018 (Table 2, Table 3, and Table 4).

Competitor neighbor removals (removing *Mertensia* neighbors from *Claytonia* focal plants and vice versa) resulted in a 10.0% ( $t = 1.26$ ,  $p = 0.21$ ) and 15.3% ( $t = 2.34$ ,  $p = 0.02$ ) reduction in neighborhood percent cover, respectively.

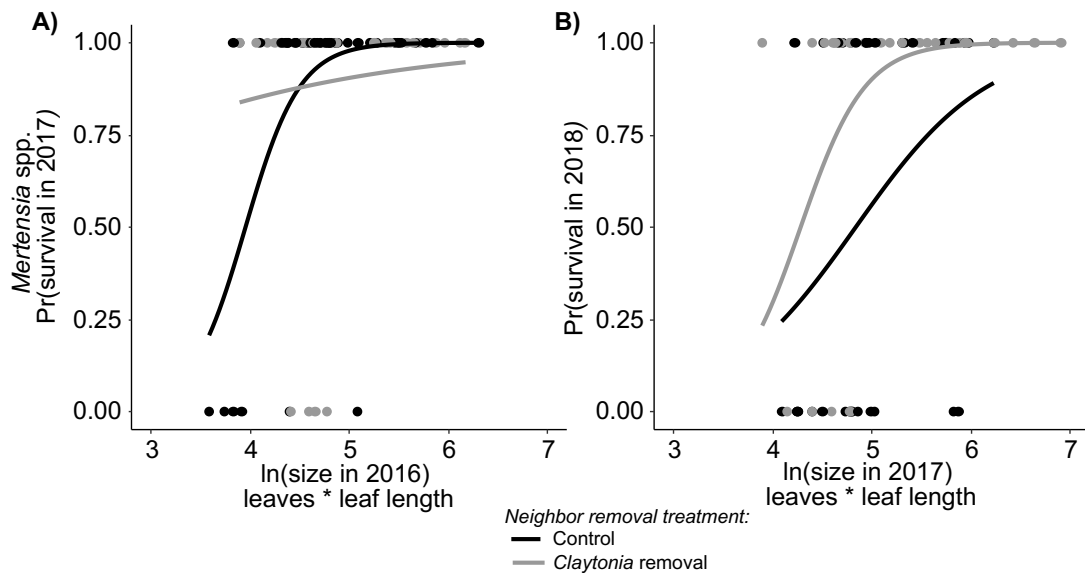
Volumetric water content was slightly higher in supplemental water plots compared to control plots two to three days post watering, although this difference was not statistically significant (least squares mean VWC  $\pm$  S.E.;  $16.1 \pm 0.2$  water vs.  $15.0 \pm 2.3$  control) (LMM:  $\chi^2 = 2.14$ ,  $p = 0.14$ ).

*Survival*: Probability of survival for *Claytonia* was unaffected by neighbor removal treatments in 2017 and 2018 (Table 3).

In 2017, the probability of survival of small *Mertensia* plants in the *Claytonia* removal was higher than controls, and the probability of survival of larger plants was unaffected by neighbor removals (Table 4, Figure 2B). This may be a result of a low sample size of small plants in the *Claytonia* neighbor removal treatment. In 2018, survival of *Mertensia* plants in *Claytonia* removal treatments was higher than control plants (Figure 2B).

**Table 2. Summary table of results from the neighbor removal experiment. Positive effects of *Mertensia* on *Claytonia* and *Claytonia* on *Mertensia* are indicated by "+", negative effects by "-", and no effect "0."**

Vital rate	<i>Mertensia</i> effect on <i>Claytonia</i>		<i>Claytonia</i> effect on <i>Mertensia</i>	
	2017	2018	2017	2018
Growth	0	0	0	-
Fruit set	+	-	Small: -, Large: +	0
Survival	0	0	Small: -, Large: 0	-



**Figure 2. Probability of survival in year  $t+1$  as a function of plant size year  $t$  of *Mertensia* in control (black) and *Claytonia* neighbor removal treatments (gray) in A) 2017 and B) 2018.**

Growth: *Claytonia* neighbor removal significantly affected growth in *Mertensia* in 2017 (Table 4). There was no effect of *Mertensia* removal on *Claytonia* growth.

Reproduction: In 2017, *Claytonia* fruit set (mean number of fruits per flower) was significantly lower in *Mertensia* neighbor removal treatments relative to control (least

squares mean  $\pm$  S.E; control:  $0.66 \pm 0.07$ , *Mertensia* removal:  $0.43 \pm 0.08$ ) (Figure 3).

Conversely, in 2018, *Claytonia* fruit set was reduced in the control treatment relative to the *Mertensia* neighbor removal treatment (least squares mean  $\pm$  S.E; control:  $0.44 \pm 0.05$ , conspecific removal:  $0.36 \pm 0.05$ , *Mertensia* removal:  $0.27 \pm 0.05$ ) (Figure 3).

Reproductive success in *Mertensia* was affected by the interaction between size and *Claytonia* removal treatment in 2017 (Table 4, Figure 4). Smaller *Mertensia* plants had higher fruit set when *Claytonia* neighbors were removed. However, larger plants in *Claytonia* neighbor removals produced fewer fruits than control plants (Figure 4).

*Mertensia* reproductive success in 2018 was unaffected by *Claytonia* removal. Although neighbor removal treatment did not affect *Mertensia* reproduction in 2018, supplemental water did (Table 4). For a plant at the median size, fruit set was 13.5% higher in plants that received supplemental water relative to control plants (least squares mean  $\pm$  S.E.; control:  $0.74 \pm 0.02$ , water treatment:  $0.64 \pm 0.03$ ) (Appendix A, Figure 18).

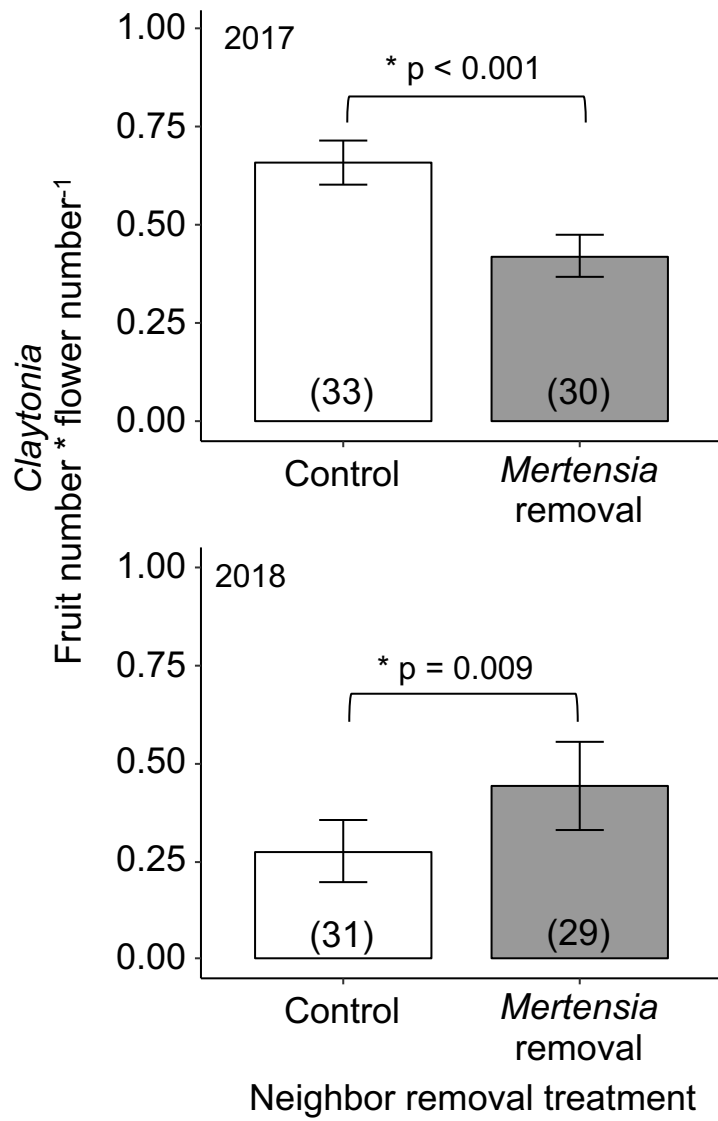


Figure 3. Fruit set in *Claytonia* (fruit number x flower number<sup>-1</sup>, least squares mean  $\pm$  S.E.) between control (white) and *Mertensia* removal treatments (gray) in 2017 and 2018. Asterisks indicate significant differences between the control and competitor removal ( $p \leq 0.05$ ). Sample sizes are in parentheses.

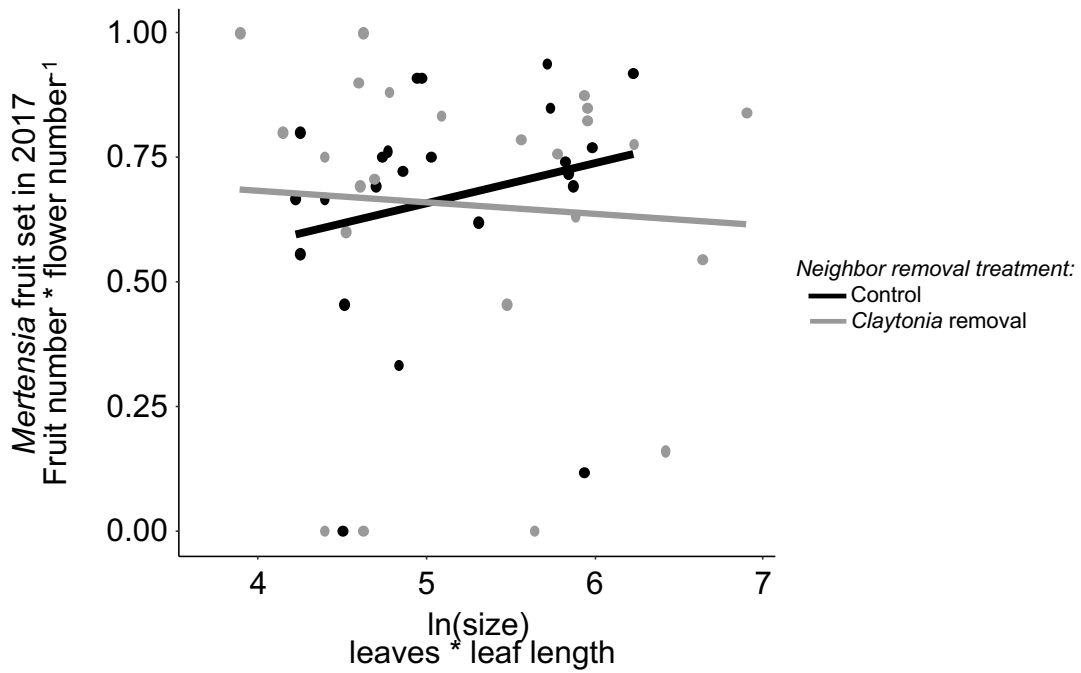


Figure 4. Fruit set (fruit number/flower number, least squares means  $\pm$  S.E.) of *Mertensia* in control (black) and *Claytonia* removal treatments (gray) in 2017 as a function of plant size.

**Table 3. Summary table of linear models for *Claytonia* neighbor removal and water supplement experiment in 2017 and 2018. Significant p-values are bolded.**

Year	Fixed effects	Survival: Pr(survival)				Growth: Size in year $t+1$				Reproduction: Pr(fruit flower)			
		Estimate $\pm$ S.E.	t	p	AIC	Estimate $\pm$ S.E.	t	p	AIC	Estimate $\pm$ S.E.	t	p	AIC
2017	Intercept	2.21 $\pm$ 3.31	0.7	0.504	32.2	<b>3.91 <math>\pm</math> 0.39</b>	<b>9.9</b>	<b>&lt;0.001</b>	123.5	0.12 $\pm$ 0.69	0.2	0.857	357.3
	Size in 2016	0.37 $\pm$ 0.91	0.4	0.686		-0.001 $\pm$ 0.11	0.0	0.994					
	Size in 2017									0.23 $\pm$ 0.16	1.4	0.158	
	<i>Mertensia</i> removal	0.58 $\pm$ 1.27	0.5	0.647		-0.04 $\pm$ 0.13	-0.3	0.773		<b>-0.97 <math>\pm</math> 0.15</b>	<b>-6.4</b>	<b>&lt;0.001</b>	
	<i>Mert.</i> removal x size												
	Site	-1.12 $\pm$ 1.28	-0.9	0.383		<b>0.32 <math>\pm</math> 0.14</b>	<b>2.3</b>	<b>0.025</b>		<b>-0.80 <math>\pm</math> 0.17</b>	<b>-4.6</b>	<b>&lt;0.001</b>	
2018	Intercept	-1.99 $\pm$ 2.32	-0.9	0.388	72.0	2.38 $\pm$ 0.51	4.7	<0.001	102.6	<b>-2.62 <math>\pm</math> 0.88</b>	<b>-3.0</b>	<b>0.003</b>	170.5
	Size in 2017	1.10 $\pm$ 0.62	1.8	0.079		0.16 $\pm$ 0.13	1.2	0.220					
	Size in 2018									0.44 $\pm$ 0.26	1.7	0.084	
	<i>Mertensia</i> removal	-0.64 $\pm$ 0.66	-1.0	0.332		0.07 $\pm$ 0.14	0.5	0.625		<b>0.73 <math>\pm</math> 0.28</b>	<b>2.6</b>	<b>0.009</b>	
	Water									0.55 $\pm$ 0.29	1.9	0.060	
	Site	-0.86 $\pm$ 0.66	-1.3	0.188		<b>0.38 <math>\pm</math> 0.14</b>	<b>2.6</b>	<b>0.011</b>		-0.27 $\pm$ 0.30	-0.9	0.360	

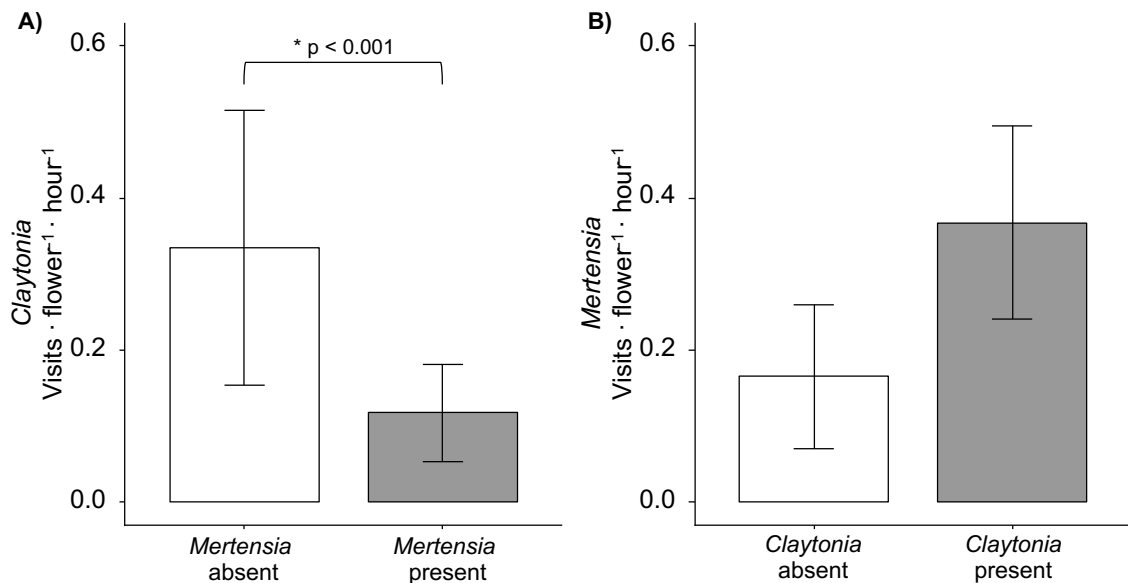
**Table 4. Summary table of linear models for *Mertensia* neighbor removal and water supplement experiment in 2017 and 2018. Significant p-values are bolded.**

Year	Fixed effects	Survival: Pr(survival)				Growth: Size in year $t+1$				Reproduction: Pr(fruit flower)			
		Estimate $\pm$ S.E.	t	p	AIC	Estimate $\pm$ S.E.	t	p	AIC	Estimate $\pm$ S.E.	t	p	AIC
2017	Intercept	<b>-14.51 <math>\pm</math> 6.00</b>	<b>-2.4</b>	<b>0.016</b>	58.6	<b>2.36 <math>\pm</math> 0.77</b>	<b>3.0</b>	<b>0.003</b>	108.6	-1.65 $\pm$ 1.00	-1.6	0.099	349.8
	Size in 2016	<b>3.68 <math>\pm</math> 1.41</b>	<b>2.6</b>	<b>0.009</b>		<b>0.49 <math>\pm</math> 0.16</b>	<b>3.0</b>	<b>0.004</b>					
	Size in 2017									<b>0.50 <math>\pm</math> 0.19</b>	<b>2.6</b>	<b>0.010</b>	
	<i>Claytonia</i> removal	<b>15.76 <math>\pm</math> 6.75</b>	<b>2.3</b>	<b>0.019</b>		<b>2.53 <math>\pm</math> 0.92</b>	<b>2.8</b>	<b>0.008</b>		<b>3.46 <math>\pm</math> 1.24</b>	<b>2.8</b>	<b>0.005</b>	
	<i>Clay.</i> removal x size	<b>-3.47 <math>\pm</math> 1.54</b>	<b>-2.2</b>	<b>0.025</b>		<b>-0.47 <math>\pm</math> 0.19</b>	<b>-2.5</b>	<b>0.017</b>		<b>-0.65 <math>\pm</math> 0.22</b>	<b>-3.0</b>	<b>0.003</b>	
	Site	-0.15 $\pm$ 0.84	-0.2	0.859		<b>0.65 <math>\pm</math> 0.14</b>	<b>4.8</b>	<b>&lt;0.001</b>		0.04 $\pm$ 0.21	0.2	0.852	
2018	Intercept	<b>-11.20 <math>\pm</math> 3.63</b>	<b>-3.1</b>	<b>0.002</b>	70.5	0.81 $\pm$ 1.11	0.7	0.472	93.2	-0.58 $\pm$ 0.66	-0.9	0.383	229.2
	Size in 2017	<b>2.37 <math>\pm</math> 0.77</b>	<b>3.1</b>	<b>0.002</b>		<b>0.64 <math>\pm</math> 0.22</b>	<b>2.9</b>	<b>0.006</b>					
	Size in 2018									<b>0.33 <math>\pm</math> 0.13</b>	<b>2.5</b>	<b>0.012</b>	
	<i>Claytonia</i> removal	<b>1.43 <math>\pm</math> 0.66</b>	<b>2.2</b>	<b>0.030</b>		2.3 $\pm$ 1.3	1.8	0.083		0.08 $\pm$ 0.20	0.4	0.687	
	Water									<b>-0.47 <math>\pm</math> 0.19</b>	<b>-2.5</b>	<b>0.012</b>	
	<i>Clay.</i> removal x size					-0.43 $\pm$ 0.24	-1.7	0.090					
Site	-0.81 $\pm$ 0.79	-1.0	0.303		<b>0.84 <math>\pm</math> 0.21</b>	<b>3.9</b>	<b>&lt;0.001</b>		-0.03 $\pm$ 0.27	-0.1	0.898		

### 2.3.3 Pollinator observations and experiment

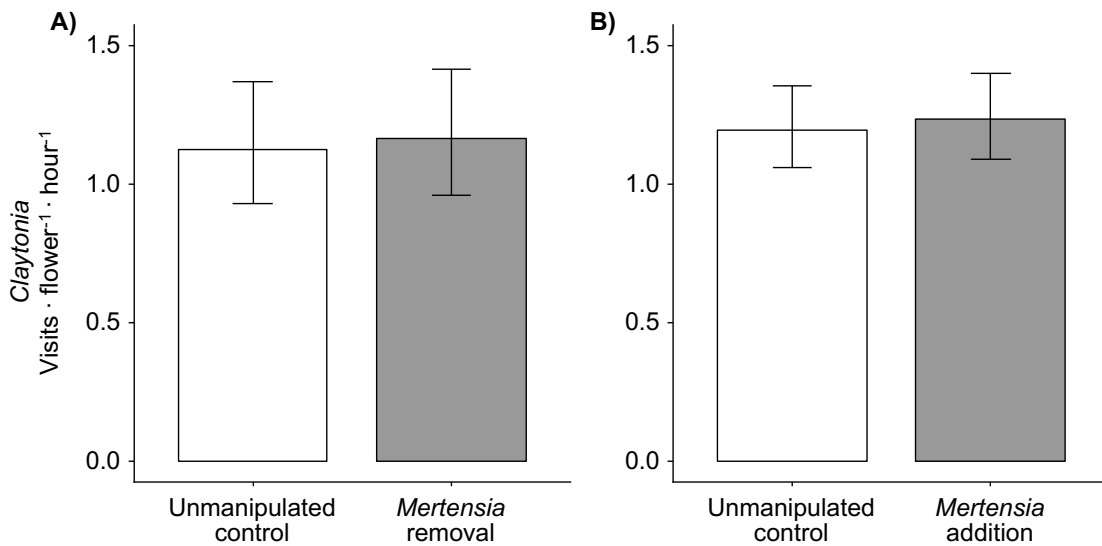
*Claytonia* and *Mertensia* do not compete for or facilitate one another for pollinator resources at the scale of this study.

Visitation rate to *Claytonia* was reduced when *Mertensia* was present in the plot (LMM:  $\chi^2 = 11.8$ ,  $p < 0.001$ ) (Figure 5A). While the presence of *Mertensia* in the plot reduced visitation rate to *Claytonia*, plot and transect-level floral abundances of *Mertensia* did not (plot *Mertensia* abundance: LMM:  $\chi^2 = 2.99$ ,  $p = 0.08$ , transect *Mertensia* abundance: LMM:  $\chi^2 = 1.15$ ). *Mertensia* was unaffected by the presence of *Claytonia* (LMM:  $\chi^2 = 3.55$ ,  $p = 0.28$ ) (Figure 5B).



**Figure 5. Pollinator visitation rate (visits x flower<sup>-1</sup> x hour<sup>-1</sup>, least squares means ± S.E.) to A) *Claytonia* and B) *Mertensia* in natural density plots from 2016 – 2017 in the absence and presence of focal competitor species. Asterisks indicate significant differences ( $p \leq 0.05$ ) between observation groups.**

Although observational data suggested that the presence of *Mertensia* reduced visitation to *Claytonia* at small spatial scales, the results from the experiment did not corroborate this trend. In the experiment, I manipulated the presence of *Mertensia* in plots of *Claytonia* by adding or removing *Mertensia* in 2017. When I added *Mertensia* to plots with only *Claytonia*, visitation to *Claytonia* was unaffected (total *Mertensia* flowers added, mean  $\pm$  S.E.: 41.53  $\pm$  8.14 flowers; LMM:  $\chi^2 = 0.14$ ,  $p = 0.71$ ) (Figure 6A). Similarly, when I removed *Mertensia* from plots, visitation rate to *Claytonia* was unaffected (total *Mertensia* flowers removed, mean  $\pm$  S.E.: 43.51  $\pm$  9.31 flowers; LMM:  $\chi^2 = 0.18$ ,  $p = 0.67$ ) (Figure 6B).



**Figure 6. Pollinator visitation rate (visits x flower<sup>-1</sup> x hour<sup>-1</sup>, least squares means  $\pm$  S.E.) to *Claytonia* in unmanipulated control and experimental plots in 2017. A) Visitation rate to *Claytonia* is unaffected by *Mertensia* removal. B) Visitation rate to *Claytonia* is unaffected by the addition of *Mertensia* to a plot.**

During the pollinator experiment in 2017, I recorded few cases when a pollinator visited both *Claytonia* and *Mertensia* during a single foraging bout. Pollinators showed high constancy in the plot, as only 14.1% of pollinators visiting two or more flowers visited two or more different species. Most pollinators that visited *Claytonia* came from another *Claytonia* flower (96.6% of visitors to *Claytonia* flowers). Similarly, most pollinators visiting *Mertensia* had previously visited *Mertensia* (95.6% visitors to *Mertensia* flowers).

## **2.4. Discussion**

To better understand how climate-induced phenological shifts will affect species coexistence, I used observational and experimental data to assess how two subalpine early-season plant taxa compete for or facilitate one another for abiotic and biotic resources. Though interspecific interactions for shared abiotic and biotic resources may operate at different spatial and temporal scales, both may be important for fitness and population growth. For example, neighboring con- and heterospecific nurse plants may facilitate survival in harsh environmental conditions by increasing microhabitat water retention (Callaway, 2007, Maestre *et al.*, 2001). At the same time, both nearby nurse plants and other distant neighbors may compete for pollinators, potentially leading to an overall reduction in reproductive success (Rathcke, 1983). Thus, interactions for pollinators may not match the scale at which plants may influence each other's uptake of

water or other abiotic resources (Gathmann & Tschardtke, 2002, Schwinning & Weiner, 1998, Zurbuchen *et al.*, 2010).

In this study, I determined the degree to which *Claytonia* and *Mertensia* compete for and facilitate one another for abiotic and biotic resources. These two species were well-suited for this study, as floral temporal overlap between *Claytonia* and *Mertensia* was positively correlated with snowmelt. This trend suggested that under future spring warming and early snowmelt conditions, these species may continue to increase in overlap. Although intuitive to think increased temporal overlap may result in increased competition for resources, the effects of neighbors on fitness in *Claytonia* and *Mertensia* were complex and varied between years.

I found evidence of positive interactions between *Claytonia* and *Mertensia* in this study. In an average snowmelt year (2017), *Claytonia* and large *Mertensia* plants had lower reproductive success when neighbors were removed. Potential mechanisms of facilitation could include water-stress amelioration, increase in pollination success, and/or protection from frost-damage (Callaway, 1995). This study tested two of these mechanisms (water-stress amelioration and pollination success). First, if facilitation between neighbors was due to water stress amelioration, I would have expected to find a reduction in the positive effects of neighbors in plots with supplemental water. I did not find evidence that water supplementation reduced the positive effects of neighbors on *Claytonia* reproductive success in the following year, and therefore water-stress

amelioration may not be a mechanism of facilitation. Secondly, in an experiment, the addition of *Mertensia* to a plot did not result in higher visitation rates to *Claytonia*. A mechanism of facilitation that I did not test, protection from frost damage, may potentially affect *Claytonia*. At the RMBL, frost-damaged early-flowering species at the RMBL have lower reproductive success than plants that do not experience frost (Gezon *et al.*, 2016, Inouye, 2000, Pardee *et al.*, 2017). Therefore, neighbors may have protected *Claytonia* from frost.

In addition to positive interactions between species, I found the presence of neighbors also decreased plant performance. In the second and more abiotically stressful year of this study, *Claytonia* reproductive success was higher in the *Mertensia* neighbor removal treatment, and both growth and the probability of survival in *Mertensia* were higher in *Claytonia* neighbor removal treatments. These results suggested that under early snowmelt conditions, these species may compete with one another for limited resources.

In an observational study, the presence of *Mertensia* reduced pollinator visitation rate to *Claytonia*. However, this pattern did not hold when I experimentally manipulated *Mertensia* floral density at small spatial scales. *Claytonia* and *Mertensia* have been documented to share pollinators and exhibit some evidence of pollen limitation (Forrest & Thomson, 2010, Gezon *et al.*, 2016, Irwin *et al.*, 2018). However, I found that these species do not appear to compete for pollinators at small spatial scales. Pollinator

constancy was extremely high in this study. Most insect pollinators are generalist foragers and can switch between plant species during a foraging bout (Waser *et al.*, 1996). Nevertheless, pollinator generalization is predicted when floral rewards are similar across species, travel is costly, and behavioral and morphological constraints are minor (Waser *et al.*, 1996). First, *Claytonia* produces more dilute nectar than *Mertensia fusiformis* (Roy, 1993), indicating that these two plants may not provide equal resources for pollinators. Secondly, most insect-pollinators forage for flowers at larger spatial scales than the scale of this study, potentially up to 1 km for solitary bees and 2 – 3 km for bumblebees (Gathmann & Tschardt, 2002, Greenleaf *et al.*, 2007, Zurbuchen *et al.*, 2010). Third, some of the shared pollinators may have a difficult time accessing resources in both flowers. For example, *Bombus flavifrons* queens are often too large to forage on *Claytonia* and seem to only visit *Claytonia* when other resources are low (Dalton, personal observation). Therefore, pollinators may be acting as specialists at the plot level but generalists at larger spatial scales (Brosi, 2016), which my flower density manipulations did not capture.

Predicting which species will coexist under future climate change becomes especially challenging when species compete for and facilitate one another for multiple shared resources (Chesson, 2000, Valladares *et al.*, 2015). If temporal niche partitioning facilitates coexistence, then climate change may affect how species coexist in the future. It is important to note that temporal overlap alone does not necessarily correlate to the

magnitude of competition or facilitation (Freckleton, 2009). I did not directly manipulate phenology. Nonetheless, in an average snowmelt year, when phenological overlap was lower, *Mertensia* neighbors provided a benefit to *Claytonia*. In an early snowmelt year when floral overlap was higher, the presence of neighbors reduced plant performance in both *Claytonia* and *Mertensia*.

Although results from this study indicated that increased temporal overlap may be detrimental to future coexistence between *Claytonia* and *Mertensia*, there are caveats to this study. First, I did not directly manipulate timing of snowmelt (and phenological overlap between these species) and instead relied on the natural variation between years. Therefore, I did not control for other differences in the abiotic and biotic environment as a result of early snowmelt. For example, rainfall between the period of snowmelt and the onset of monsoon rains was below average at the RMBL in 2018, potentially compounding the negative effects of early snowmelt. Secondly, I only assessed competition and facilitation for pollinator resources in 2017, which was abiotically less stressful than 2018. Therefore, these species may actually compete for or facilitate one another for pollen resources, but not at the temporal or spatial scale that I conducted this study.

In conclusion, an increase in temporal overlap as a result of climate change between species sharing resources or growing next to one another might reduce coexistence if competitive interactions outweigh facilitative ones. However, climate

change may paradoxically facilitate coexistence if increased overlap results in species benefiting one another. Furthermore, incorporating information about phenological events other than flowering, such as vegetative emergence, will be important for predicting coexistence as competition and facilitation is occurring over longer time periods than just flowering.

## ***2.5 Data accessibility***

Long-term flowering phenology data from the RMBL can be requested at <https://www.bio.fsu.edu/~nunderwood/homepage/RMBLphenologyproject.html>. RMBL weather data can be requested at <https://weatherstations.rmbll.org>. Snowmelt and precipitation data are available at <http://www.gothicwx.org/-data.html>. All field-collected data will be deposited in Dryad Repository upon submission to a scientific journal.

## **3. Early snowmelt and neighbors interact to influence population growth of two subalpine spring ephemerals**

### **3.1 Introduction**

One of the greatest challenges in ecology is predicting how species will persist under climate change (Gilman *et al.*, 2010). One approach is to assess how changes in environmental drivers directly affect demographic responses of populations or species (direct effects of climate). However, this approach overlooks species interactions and perhaps more importantly, it ignores the indirect effects of climate change on the strength of those interactions (indirect effects of climate) (Gilman *et al.*, 2010, Tylianakis *et al.*, 2008, Wisz *et al.*, 2013). Indirect effects of climate may be more important than direct effects for species coexistence (Gilman *et al.*, 2010, Suttle *et al.*, 2007), either causing species that now coexist to no longer do so or facilitating coexistence where previously impossible.

Climate may affect how strongly species interact with one another through shifts in phenology (Gilman *et al.*, 2010, Parmesan, 2006). For example, in subalpine ecosystems, warmer spring temperatures and early snowmelt are causing some plant species to emerge and flower earlier in the season (Dunne *et al.*, 2003). If one of these species begins growing too early, its competitive ability could be reduced. A reduction in competitive ability of one species may thereby free another from competition, even if the second species is not directly affected by climate. Therefore, combining indirect and

direct effects of climate when predicting population growth rate into the future will allow us to understand how species are going to respond to climate change.

Positive and negative species interactions, both of which are critical for the maintenance of biodiversity in alpine plant communities, are sensitive to the abiotic environment (Callaway, 1998). For example, neighboring nurse plants may facilitate survival in harsh environmental conditions by increasing microhabitat water retention (Callaway, 2007, Maestre *et al.*, 2001), providing frost protection from frost-damage, and/or increasing pollination success (Callaway, 1995, Stachowicz, 2001). However, under a different set of environmental conditions, these same plants may compete with one another for access to soil and light resources (stress gradient hypothesis; (Bertness & Callaway, 1994, He *et al.*, 2013).

In this study, I evaluated how early snowmelt and neighbors affect population growth of two co-flowering plant species. I used a neighbor removal and water addition experiment coupled with a population model to simulate future population growth under predictions of early snowmelt. I asked the following questions: 1) How does the presence of neighbors affect vital rates in average and early snowmelt conditions?; 2) Does neighbor presence and snowmelt date affect deterministic population growth rate?; and 3) Under future climate change, will neighbors reduce the negative effects of early snowmelt?

## **3.2. Materials and methods**

### **3.2.1 Study system**

I conducted this study in two subalpine meadows near the Rocky Mountain Biological Laboratory (RMBL) in Gothic, CO from 2016 to 2018 (Avery Campground: 38°58'58.6"N 107°00'06.2"W, 2950m; Kebler Pass: 38°51'08.8"N 107°05'50.0"W; 3015m). The growing season begins in May or June shortly after spring snowmelt, and the time when early spring plants emerge and flower is largely driven by snowmelt date (Dunne *et al.*, 2003, Inouye *et al.*, 2002, Lambert *et al.*, 2010).

Climate models disagree on how precipitation is expected to shift under different greenhouse gas emissions scenarios in the Rocky Mountains. However, spring warming and changes in the timing of precipitation are projected to lead significant reductions in snowpack and earlier snowmelt date in the Colorado River Basin (Clow, 2010, Pachauri & Reisinger, 2008, Ray *et al.*, 2008, Stewart *et al.*, 2004). Under future climate change scenarios, snowpack is predicted to decrease by 30% of current snow water equivalent (SWE), or the amount of water contained within the snowpack, by the year 2070. In addition to the decrease in snowpack, warmer spring temperatures are expected to lead to significant changes in the timing of snowmelt. Under the “business as usual” emissions scenario, snowmelt is expected to advance by 15 – 25 days before 2099 in the region near the RMBL (Stewart *et al.*, 2004).

At the RMBL, snowmelt date is highly correlated to annual SWE (Pearson's product-moment correlation:  $t = 12.06$ ,  $df = 41$ ,  $p < 0.001$ ,  $r = 0.88$ ) (Figure 19). Total snowfall (cm), annual SWE (cm), and snowmelt date (day of the year) differed between years of this study (Table 1) (barr, 2019). In 2017, SWE and snowmelt date were close to the average, while snowmelt date was early and snowpack was low in 2018. I used this natural variation in snowmelt date between years to ask how early snowmelt (and early phenology) influences the effects of neighbors on vital rates.

*Claytonia lanceolata* (Montiaceae), *Mertensia brevistyla* (Boraginaceae), and *Mertensia fusiformis* are perennial spring ephemerals that emerge shortly after snowmelt and senesce before the monsoon season in July (Inouye *et al.*, 2000, Price & Waser, 1998). *Claytonia* produces self-compatible, but largely outcrossing protandrous flowers and *M. brevistyla* and *M. fusiformis* produce self-incompatible flowers (Davis, 1966, Lin & Forrest, 2017, Mistretta & Liston, 1992). These species are well-suited for demographic studies as asexual reproduction is negligible in *Claytonia* (Stewart & Wiens, 1971), and *M. brevistyla* and *M. fusiformis* are rhizomatous and individuals are generally compact and easy to distinguish in the field (Pelton, 1961). *Mertensia fusiformis* was the only early-flowering *Mertensia* species at Avery Campground, while *M. brevistyla* was the dominant early-flowering *Mertensia* species at Kebler Pass. The meadows around Kebler Pass were a hybrid zone between *M. brevistyla* and *M. fusiformis* (Lin & Forrest, 2017). In this study, I treated these species as equivalent (hereafter *Mertensia*). In addition to *Claytonia*

and *Mertensia*, other herbaceous flowering plants, grasses, and sedges dominated these subalpine rocky meadows during the growing season. Common herbaceous species that grew in the early season are *Erythronium grandiflorum* (Liliaceae), *Hydrophyllum capitatum* (Hydrophyllaceae), *Delphinium nuttallianum* (Ranunculaceae), *Fragaria virginiana* (Rosaceae), *Ranunculus inamoenus* (Ranunculaceae), *Taraxacum officinale* (Asteraceae), *Potentilla pulcherrima* (Rosaceae), *Viola praemorsa* (Violaceae), and *V. adunca* (Violaceae).

### **3.2.2 Experimental design:**

I used the same experimental approach described in Section 2.2.3 Neighbor removal and supplemental water experiment. In this chapter, I added additional neighbor removal treatments for a total of four neighbor removal treatments and a control. I removed (1) *Mertensia* (for *Claytonia* focal plants) or *Claytonia* (for *Mertensia* focal plants) as presented in chapter two, (2) conspecific neighbors, (3) heterospecific neighbors, or (4) all neighbors (conspecifics and heterospecific neighbors) (n = 228 *Claytonia* and 238 *Mertensia*).

### **3.2.3 Analyses:**

Vital rate regressions: I used R version 3.5.1 for all statistical analyses (R Core Team, 2018). First, I quantified plant performance (survival, reproduction, and growth) in neighbor removal treatments in an average (2017) and an early snowmelt (2018) year. I used the functions *glmer()* and *lmer()* in the “lme4” package (Bates *et al.*, 2014) to run generalized linear mixed effects models (GLMMs) and linear mixed effects models

(GLMMs). I ran separate GLMMs and LMMs for each species for each one-year transition. For vital rates in 2017, I began with a full model which included fixed effects of neighbor removal treatment, plant size in 2016, a neighbor removal treatment  $\times$  size interaction, and a random effect of site. For vital rates quantified in 2018, I constructed the same models as described above for the neighbor removal experiment in 2017, but I added an additional fixed effect of watering treatment and interaction terms (water treatment  $\times$  neighbor removal treatment and water  $\times$  size). I selected best fit models based on Akaike's Information Criterion (*AICtab()* in "MuMIn" package) (Barton & Barton, 2018).

I used GLMMs with a binomial error distribution to fit probability of survival. I removed all individuals from the survival analysis that did not survive to 2017 as a result of *Thomomys talpoides* (Northern pocket gopher) activity (n = 32 of 466 plants). *Thomomys talpoides* activity was extremely low in winter 2017 – 2018 and did not noticeably reduce survival. I used GLMMs with a binomial error distribution to assess the probability of flowering and fruiting and GLMMs with a Poisson error distribution to determine how the fixed effects influenced the total number of flowers produced. I used LMMs to predict size in year  $t+1$  based on size in year  $t$ . Finally, I regressed the squared residuals from the regression of size in year  $t+1$  on size in year  $t$  and all fixed effects. To calculate least squares means of plant performance metrics and Tukey pairwise comparisons, I used the package "emmeans" (Lenth, 2018).

Integral projection model: I assessed how snowmelt date, neighbor removal, and water addition treatments affected population growth rate by constructing deterministic integral projection models (IPMs) (Easterling *et al.*, 2000, Merow *et al.*, 2014). I used the best-fit regressions of each demographic response variable to construct deterministic IPMs for each species in an average and an early snowmelt year. I combined vital rate regressions to create a kernel,  $K$ , that described how the size distribution ( $m$ ) changes from year  $t$  to year  $t+1$ :

$$n_{t+1}(m') = \int_L^U K(m', m) n_t(m) dm \quad (\text{Eq. 2})$$

where  $m'$  is size in year  $t+1$ , and  $m$  is size in year  $t$ ,  $U$  and  $L$  are the upper and lower limits of plant size, respectively. The kernel was comprised of a growth/survival kernel ( $P$ ) and a fecundity/recruitment kernel ( $F$ )

$$K(m', m) = P(m', m) + F(m', m) \quad (\text{Eq. 3}).$$

$$K(m', m) = P(m', m) + F(m', m) \quad (\text{Eq. 3})$$

The growth/survival kernel,  $P$ , was a function of growth,  $g$ , and survival,  $s$ . Growth and survival depended on plant size, neighbor removal treatment ( $r$ ), and when applicable, water treatment ( $w$ )

$$P(m', m) = g(m' | m, r, w) s(m, r, w) \quad (\text{Eq. 4}).$$

$$P(m', m) = g(m' | m, r, w) s(m, r, w) \quad (\text{Eq. 4})$$

The fecundity kernel,  $F$ , was determined by the probability of flowering ( $p_{\text{flower}}$ ), total number of flowers produced ( $f_{\text{flower number}}$ ), the probability of producing a fruit given

flowering ( $p_{fruit|flower}$ ), recruitment rate ( $b$ ), the size distribution of recruits ( $f_{recruitsize}$ )

$$F(m', m) = p_{flower}(m, r, w) * f_{flower\ number}(m, r, w) * p_{fruit|flower}(m, r, w) * b f_{recruitsize}(m') \quad (\text{Eq. 5}).$$

$$F(m', m) = p_{flower}(m, r, w) * f_{flower\ number}(m, r, w) * p_{fruit|flower}(m, r, w) * b f_{recruitsize}(m') \quad (\text{Eq. 5})$$

As recruitment rate ( $b$ ) in the field was difficult to estimate, I used a constant  $b$  for each year, neighbor removal, and water treatments. I first recorded whether a new seedling established in 2017 within the 30cm neighborhood of each focal plant. I then multiplied the average probability of a new seedling establishing by a constant to achieve a median deterministic growth rate of 1 for control plants in the average snowmelt year, 2017. The underlying assumption was that populations are at least at replacement rate in control plants under average snowmelt conditions.

I next calculated the asymptotic population growth rate ( $\lambda$ ), or the growth rate to which a population will converge if the environment and demographic transitions do not change. I used a numerical integration method (mid-point rule) to discretize  $K$  at 100 mesh points. I calculated the dominant eigenvalue of  $K$  to estimate  $\lambda$ . To incorporate parameter uncertainty into these estimates, I generated 5000 bootstrap replicates of parameter values for the fixed effects in the vital rate regressions. Specifically, I sampled from the multivariate normal distribution of the coefficients in each regression defined by the best-fit estimates of the coefficients and the variance-covariance matrix of the estimates. For each replicate, I calculated the difference in  $\lambda$  between control and

neighbor removal treatments. I used the 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles of the bootstrap values as the 95% confidence limits for these differences.

Projections of population growth under early snowmelt conditions: I next simulated how projected early snowmelt conditions will affect future stochastic population growth rate ( $\lambda_s$ ) of *Claytonia* and *Mertensia* in neighbor removal treatments. I used snowmelt date projections under the “business as usual” emissions scenario from 2020 to 2099 for west-central Colorado (Stewart *et al.*, 2004). Under this scenario, snowmelt date is expected to occur 0 - 5 days earlier from 2000 to 2020, 5 – 15 days earlier from 2040 to 2060, and 15 – 25 days earlier from 2080 to 2099 relative to the average from 1950 to 1980 (Stewart *et al.*, 2004). I incorporated the trend in snowmelt date predictions by running an LM with the lowest value of each prediction (0 days earlier for 2000 - 2020, 5 days for 2040 – 2060, and 15 days for 2080 – 2099). I then used the parameter estimates from the LM and the average snowmelt date at the RMBL from 1975 to 1999 to predict the expected snowmelt date for each year between 2020 and 2099. For each simulated future year, I randomly selected a snowmelt date from a normal distribution with mean given by the expected trend and a standard deviation of 12.13 days, which is the standard deviation of snowmelt date at the RMBL from 1975 to 2018 (barr, 2019). I projected population growth forward over time using the  $K$  matrices estimated from average snowmelt and early snowmelt year field data (starting population size,  $N = 500$ ). If the randomly selected snowmelt date was later than the

2018 snowmelt date (Julian day 125), I used a  $K$  matrix from 2017 (the average snowmelt year) and if the date was earlier, I used a  $K$  matrix from 2018 to project the population forward one year. I drew 1000 bootstrap samples of the parameter estimates (one for each year for each vital rate), and for each bootstrap replicate, I simulated 100 trajectories of population growth until the year 2099. I estimated  $\lambda_s$  for each treatment in each bootstrap replicate by calculating the geometric mean of  $\lambda$  over the time series. I computed the 2.5<sup>th</sup>, 50<sup>th</sup>, and 97.5<sup>th</sup> percentiles of  $\lambda_s$ . I additionally examined how total population size,  $N$  (the sum of the discretized version of the population structure), changed over time by calculating the 2.5<sup>th</sup>, 50<sup>th</sup>, and 97.5<sup>th</sup> percentiles of  $N$  each year.

### **3.3 Results**

Efficacy of neighbor removal and supplemental water treatments: Neighbor removal treatments resulted in a significant decrease in percent cover around focal plants in heterospecific and all neighbor removal treatments. I reduced percent cover around *Claytonia* focal plants by 10.0% in *Mertensia* removals, 8.7% in conspecific removals, 35.7% in heterospecific removals, and 55.6% in all neighbor removals (Figure 20A). The only significant differences in percent cover between the control and neighbor removal treatments were in the heterospecific and all neighbor removal treatments (Tukey's HSD: control vs. heterospecific:  $t = -4.36$ ,  $p < 0.001$ , control vs. all neighbor removal:  $t = -6.90$ ,  $p < 0.001$ ). I reduced neighborhood percent cover around *Mertensia* focal plants by 15.3% in *Claytonia* removals, 16.4%, in conspecific removals, 32.2% in

heterospecific removals, and 52.8% in all neighbor removals (Figure 20B). These differences were only statistically significant between the control and the heterospecific and all neighbor removals (Tukey's HSD: control vs. heterospecific:  $t = -5.40$ ,  $p < 0.001$ , control vs. all neighbor removal:  $t = -8.31$ ,  $p < 0.001$ ).

On average, supplemental water plots had a slightly higher VWC compared to control plots after two to three days post water, although this difference was not statistically significant (see 2.3.2 Neighbor removal and supplemental water experiment). Additionally, supplemental water did not result in any changes to vegetative percent cover around focal plants for either *Claytonia* or *Mertensia* (Table 9).

Neighbor removal and supplemental water affected *Claytonia* and *Mertensia* vital rates. The difference between focal plants in the control treatment and all four neighbor removal treatments are summarized in Appendix B (Table 10 and Table 11).

Survival in *Claytonia*: The probability of survival in *Claytonia* was unaffected by neighbor removal and water treatments (Table 5).

Growth in *Claytonia*: In 2018, larger *Claytonia* plants in the all neighbor removal treatment tended to grow more than controls (size x neighbor removal interaction) (Table 5).

Reproductive success in *Claytonia*: In 2017, control plants set more fruits than those in *Mertensia* and conspecific neighbor removals. Fruit set in *Claytonia* was 20.9% and 10.4% lower in *Mertensia* and conspecific neighbor removal treatments, respectively,

relative to the control (least squares mean  $\pm$  S.E.: control:  $0.67 \pm 0.04$ ; *Mertensia* removal:  $0.54 \pm 0.06$ ; conspecific removal:  $0.60 \pm 0.06$ ) (Figure 7). In 2018, *Claytonia* plants in the control set fewer fruits relative to all four neighbor removal treatments (Figure 7). However, this difference was greatest in the all neighbor removal treatment (least squares mean  $\pm$  S.E.; control:  $0.28 \pm 0.08$ , all neighbor removal:  $0.49 \pm 0.08$ ).

Survival in *Mertensia*: In 2017, the probability of survival in *Mertensia* was significantly higher in controls relative to all neighbor removal (probability of survival least squares mean  $\pm$  S.E.; control:  $0.96 \pm 0.07$ , all neighbor removal:  $0.57 \pm 0.18$ ). *Mertensia* survival in 2018 was affected by the interaction between size in 2017 and neighbor removal treatment (Table 5). Small *Mertensia* plants in the conspecific and heterospecific neighbor removals were more likely to survive relative to control plants; while larger plants in the conspecific removals were less likely to survive relative to control plants (Figure 8). Furthermore, the effect of neighbor removal was not affected by supplemental water (Table 5).

Growth in *Mertensia*: *Mertensia* growth was unaffected by neighbor removal and supplemental water treatment in 2017 and 2018 (Table 5).

Reproductive success in *Mertensia*: In 2017, *Mertensia* plants in the conspecific neighbor removals set more fruits than control plants (least squares mean  $\pm$  S.E.: control:  $0.71 \pm 0.03$ ; conspecific removal:  $0.78 \pm 0.02$ ). In *Claytonia* removals, small plants had higher fruit set than controls, while larger plants suffered from reduced fruit set. In 2018,

*Mertensia* plants at the median size in heterospecific neighbor removals had lower fruit set than control plants (least squares mean  $\pm$  S.E.: control:  $0.71 \pm 0.03$ ; heterospecific removal:  $0.63 \pm 0.03$ ). Finally, plants at the median size across all treatments produced fewer fruits in supplemental water treatments relative to control plants (Figure 18).

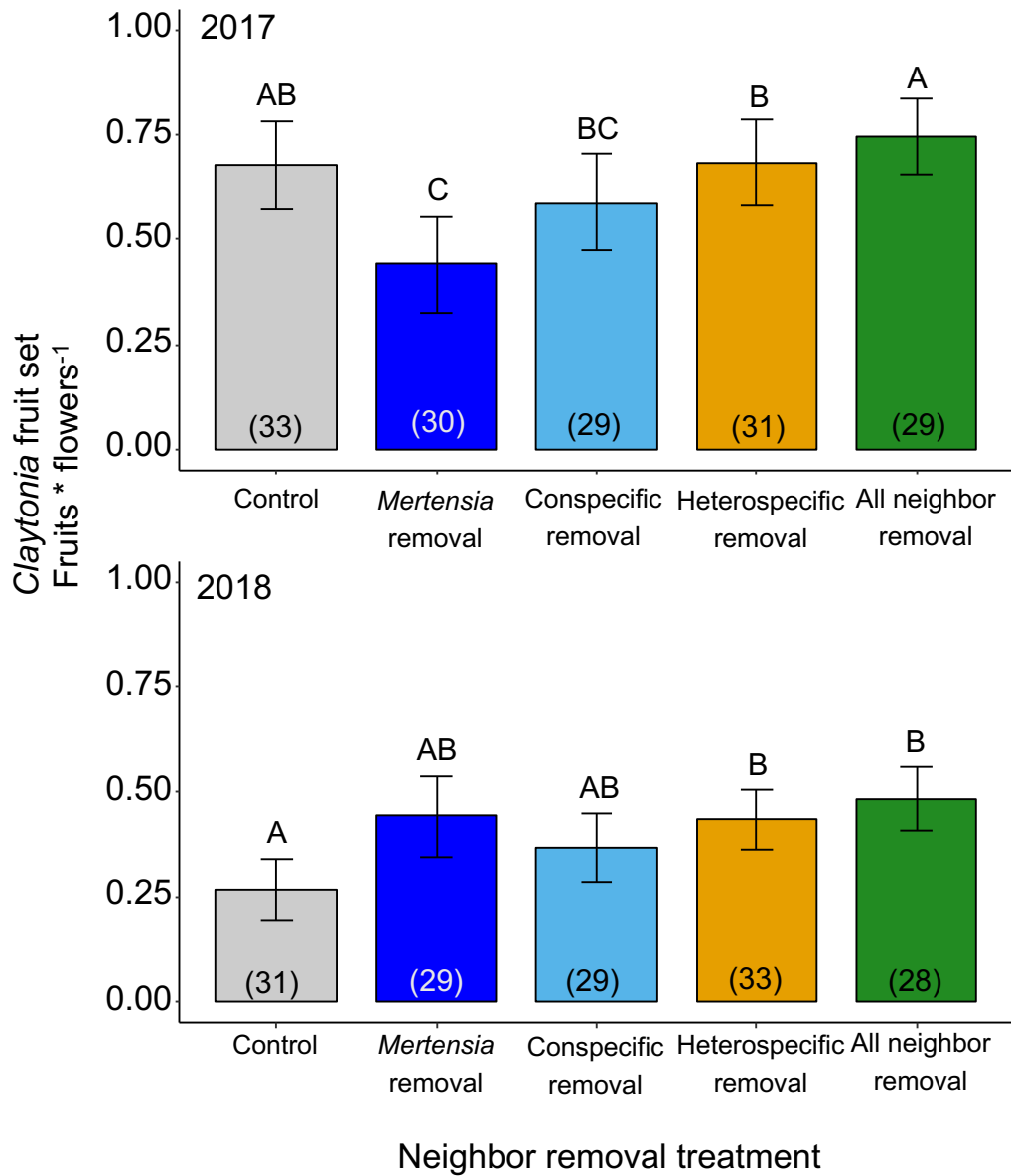


Figure 7. Fruit set (fruits x flowers<sup>-1</sup>) in *Claytonia* (least squares mean ± S.E.) in neighbor removal treatments in 2017 and 2018. Letters indicate significant differences between neighbor removal treatments (Tukey's HSD, p ≤ 0.05). Sample sizes are in parentheses.

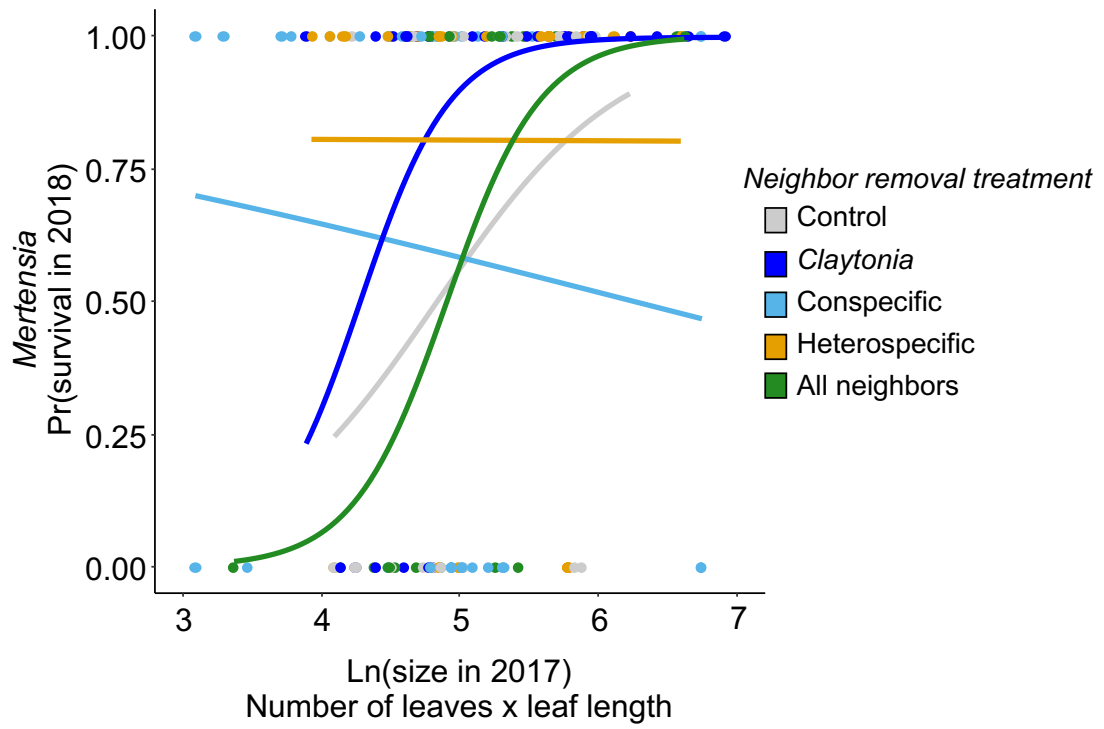


Figure 8. *Mertensia* probability of survival in 2018 in control and neighbor removal treatments.

**Table 5. Analysis of variance table for best fit models of vital rates in *Claytonia* and *Mertensia* in the neighbor removal and supplemental water experiment in 2017 and 2018. Significant p-values are bolded  $p \leq 0.05$ ).**

Spec.	Year	Fixed effects	Survival: Pr(survival)		Growth: Size in year $t+1$		Reproduction: Pr(flower)		Reproduction: Flower no.		Reproduction: Pr(fruit   flower)	
			$\chi^2$	p	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p
<i>Claytonia</i>	2017	Size in 2016	0.2	0.642	<b>4.1</b>	<b>0.040</b>					2.3	0.130
		Size in 2017					<b>9.1</b>	<b>0.003</b>	<b>616.8</b>	<b>&lt;0.001</b>		
		Neighbor removal							<b>122.5</b>	<b>&lt;0.001</b>	<b>90.8</b>	<b>&lt;0.001</b>
		Size x neighbor removal							<b>128.1</b>	<b>&lt;0.001</b>		
	2018	Size in 2017	7.4	0.007	<b>13.3</b>	<b>&lt;0.001</b>						
		Size in 2018					<b>6.0</b>	<b>0.014</b>	<b>254.1</b>	<b>&lt;0.001</b>	<b>5.9</b>	<b>0.015</b>
Neighbor removal				8.5	0.076			<b>14.0</b>	<b>0.006</b>	<b>17.5</b>	<b>0.002</b>	
Water				0.6	0.428			<b>4.0</b>	<b>0.046</b>	3.3	0.071	
Size x neighbor removal				<b>10.2</b>	<b>0.037</b>							
Neighbor removal x water								<b>20.4</b>	<b>&lt;0.001</b>	8.5	0.073	
Size x water									<b>15.0</b>	<b>&lt;0.001</b>		
<i>Mertensia</i>	2017	Size in 2016	0.3	0.614	<b>10.8</b>	<b>0.001</b>						
		Size in 2017					0.0	0.852	<b>1621.1</b>	<b>&lt;0.001</b>	<b>9.7</b>	<b>0.002</b>
		Neighbor removal	<b>14.8</b>	<b>0.005</b>					<b>20.8</b>	<b>&lt;0.001</b>	<b>34.9</b>	<b>&lt;0.001</b>
	2018	Size x neighbor removal	7.2	0.124					<b>26.0</b>	<b>&lt;0.001</b>	<b>31.0</b>	<b>&lt;0.001</b>
		Size in 2017			<b>6.2</b>	<b>0.013</b>						
		Size in 2018	1.1	0.304			<b>10.1</b>	<b>0.001</b>	<b>560.7</b>	<b>&lt;0.001</b>	<b>10.7</b>	<b>0.001</b>
		Neighbor removal	4.7	0.323					<b>20.1</b>	<b>0.002</b>	<b>12.7</b>	<b>0.013</b>
		Water	1.3	0.262							3.5	0.060
Size x neighbor removal	<b>11.9</b>	<b>0.018</b>					<b>9.5</b>	<b>0.049</b>	<b>34.2</b>	<b>&lt;0.001</b>		
Neighbor removal x water	7.9	0.097										
Size x water									<b>9.5</b>	<b>0.002</b>		

Neighbor removals and snowmelt date, but not supplemental water, significantly affected  $\lambda$ . In 2017, the difference in  $\lambda$  between the control and the all neighbor removal treatments was small but statistically significant in *Claytonia* (median  $\lambda$  (95% CI) in control: 1.00 (0.95 – 1.05), all neighbor removal: 1.02 (0.96 – 1.07)) (Table 6, Figure 9). Conversely, when only conspecific or *Mertensia* neighbors were removed,  $\lambda$  decreased (Table 6, Figure 9). Removing conspecifics and *Mertensia* plants were detrimental to  $\lambda$  in an average snowmelt year; however, when all neighbors (heterospecific and conspecific) were removed,  $\lambda$  increased. One potential reason for this result is that close neighbors may provide benefits (protection from frost damage), but the benefit provided from those few neighbors was overwhelmed by the effect of competitive interactions of the rest of the community.

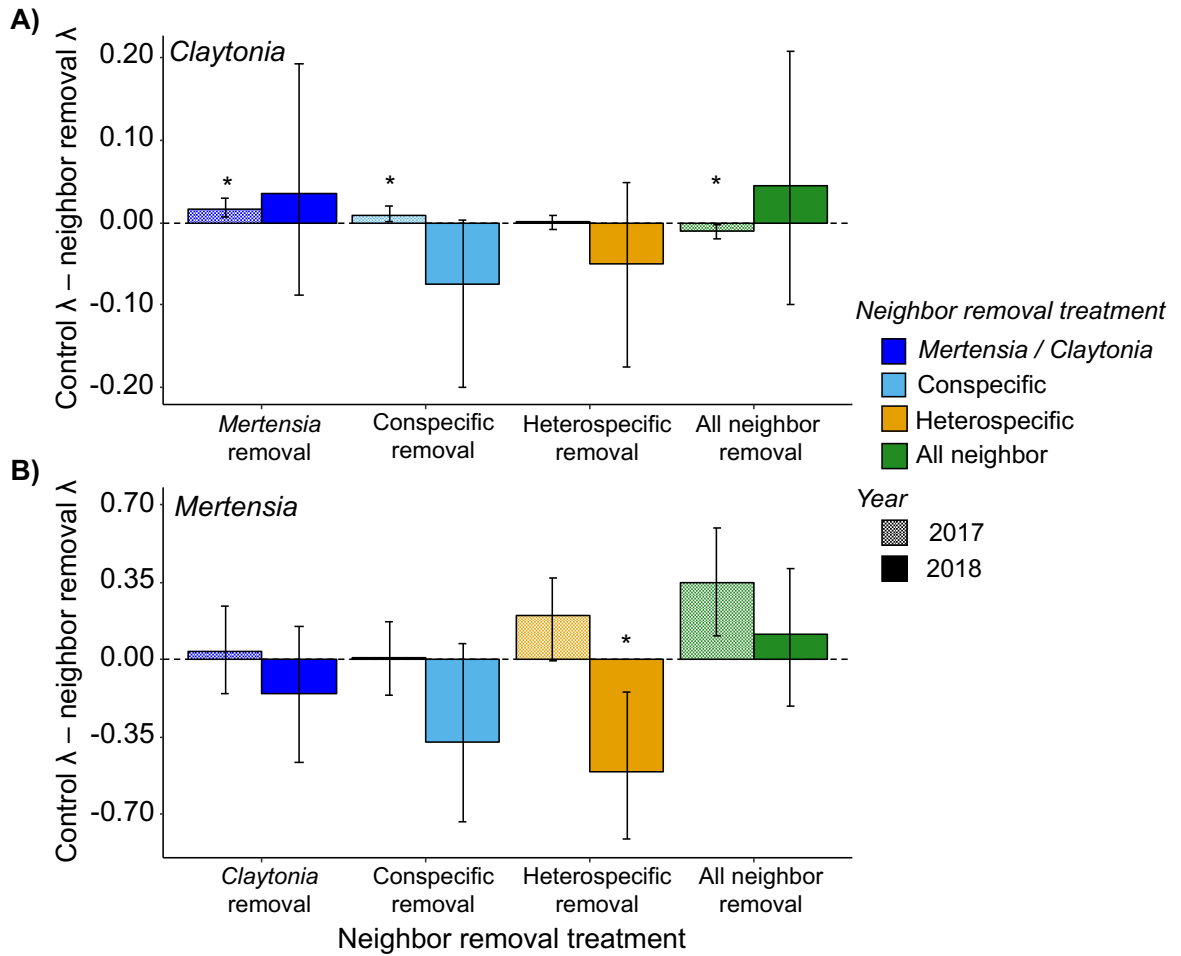
In 2018, *Claytonia*  $\lambda$  did not differ significantly between neighbor removal and water treatments (Table 6). However, median  $\lambda$  of the control treatment was lower in the early snowmelt year (median  $\lambda$  (95% CI): 1.00 (0.95 - 1.05) in 2017 vs. 0.69 (0.50 – 0.83) in 2018) (Table 6, Figure 9).

Unlike *Claytonia*, *Mertensia* plants benefited from the presence of all neighbors under average snowmelt conditions, as  $\lambda$  was higher for controls relative to all neighbor removals (median  $\lambda$  (95% CI) in control: 1.00 (0.81 - 1.14), all neighbor removal: 0.65 (0.46 – 0.86)) in 2017 (Table 6, Figure 9). In 2018 under early snowmelt conditions, removal of heterospecific neighbors resulted in an increase in  $\lambda$  (Table 6, Figure 9).

In summary, neighbors exerted both positive and negative effects on  $\lambda$  in *Claytonia* and *Mertensia* under average snowmelt conditions. However, when snowmelt was early and snowpack was low, neighbors did not have a significant impact on  $\lambda$  (except for heterospecific neighbors on *Mertensia*).

**Table 6. Median deterministic population growth rate ( $\lambda$ ) in *Claytonia* and *Mertensia* for water treatments (control or supplemental water) and neighbor removal treatments (control, *Mertensia* or *Claytonia*, conspecific, heterospecific, and all neighbor removals in 2017 and 2018.**

Species	Year	Water treatment	Neighbor removal treatment	Median $\lambda$ (95% Confidence Limits)
<i>Claytonia</i>	2017	NA	Control	1.00 (0.95 - 1.95)
			<i>Mertensia</i>	0.98 (0.93 - 1.03)
			Conspecific	1.00 (0.94 - 1.04)
			Heterospecific	1.00 (0.95 - 1.05)
			All neighbor	1.02 (0.96 - 1.07)
	2018	Control	Control	0.69 (0.50 - 0.83)
<i>Mertensia</i>			0.66 (0.43- 0.81)	
Conspecific			0.78 (0.64 - 0.87)	
Water		Heterospecific	0.75 (0.58 - 0.87)	
		All neighbor	0.65 (0.40 - 0.83)	
		All neighbor	0.65 (0.40 - 0.83)	
<i>Mertensia</i>	2017	NA	Control	1.00 (0.81 - 1.14)
			<i>Claytonia</i>	0.98 (0.80- 1.07)
			Conspecific	1.00 (0.85 - 1.09)
			Heterospecific	0.81 (0.67 - 0.93)
			All neighbor	0.65 (0.46 - 0.86)
	2018	Control	Control	0.47 (0.17 - 0.82)
<i>Claytonia</i>			0.65 (0.23 - 0.98)	
Conspecific			0.87 (0.55 - 1.00)	
Water		Heterospecific	1.00 (0.73 - 1.01)	
		All neighbor	0.34 (0.06 - 0.77)	
		All neighbor	0.34 (0.06 - 0.77)	
2018	Water	Control	0.46 (0.09 - 0.93)	
		<i>Claytonia</i>	0.57 (0.11 - 1.00)	
		Conspecific	0.99 (0.52 - 1.04)	
	Water	Heterospecific	1.01 (1.03- 1.11)	
		All neighbor	0.18 (0.01 - 0.80)	
		All neighbor	0.18 (0.01 - 0.80)	

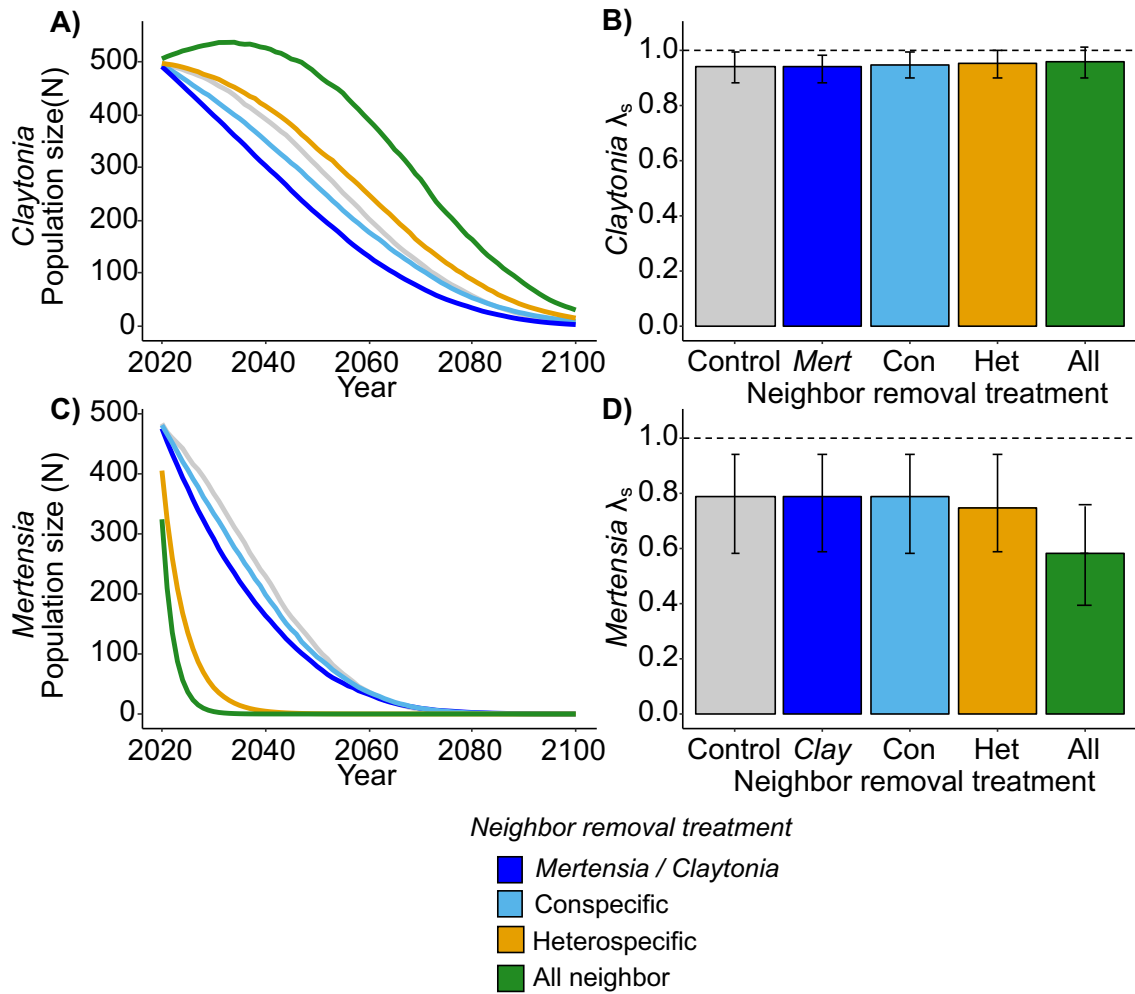


**Figure 9. Difference in deterministic population growth rate ( $\lambda$ , median  $\pm$  95% confidence intervals) between control and neighbor removal treatments in A) *Claytonia* and B) *Mertensia* in 2017 and 2018 estimated from 5000 bootstrap replicates. Asterisk indicate that control and the neighbor removals  $\lambda$  are significantly different. Positive values indicate that neighbors facilitate population growth rate, while negative values may indicate competition. Note the differences in the y-axis between species.**

When I simulated early snowmelt in the future, all populations, regardless of neighbor removal treatment, were negatively affected. However, the presence of heterospecific and all (heterospecific and conspecific) neighbors were detrimental to *Claytonia* and buffered *Mertensia* in the short term under early snowmelt predictions.

Under predictions of early snowmelt, median stochastic population growth rate ( $\lambda_s$ ) of *Claytonia* did not differ significantly among neighbor removal treatments (Figure 10A). Under simulated early snowmelt, population size declined in the control and all four neighbor removal treatments (Figure 10B). When all neighbors were removed,  $\lambda_s$  was higher than controls in the first 40 years of the simulation, but as the frequency of early snowmelt increased, populations nevertheless declined.

Simulated *Mertensia* populations all declined under early snowmelt predictions (Figure 10C), but when heterospecific and all neighbors were removed, populations crashed more quickly. Across the whole time series,  $\lambda_s$  was well below 1 for the control and all four neighbor removal treatments (Figure 10D).



**Figure 10. Simulated median population size (N) of A) *Claytonia* and B) *Mertensia* in neighbor removal treatments over time under early snowmelt predictions presented in Stewart, Cayan and Dettinger (2004). C) *Claytonia* and D) *Mertensia* median and 95% confidence intervals of mean stochastic population growth rate ( $\lambda_s$ ). There are four neighbor removal treatments in addition to the control: *Mertensia* or *Claytonia* (dark blue), conspecific (light blue), heterospecific (yellow) and all neighbors (green).**

### **3.4 Discussion:**

First, I found variation in how strongly neighbors affect vital rates under average and early snowmelt conditions. Second, neighbor removal resulted in stronger effects on population growth rate under average snowmelt conditions compared to early conditions, suggesting that the capacity for neighbors to facilitate or compete with one another may be overwhelmed by high abiotic stress. Third, under future projections of snowmelt date, median stochastic population growth rate was slightly lower in the control compared to some neighbor removals for *Claytonia* in the short term, but opposite for *Mertensia*. Fourth, neighbors neither mitigated or intensified detrimental effects of early snowmelt, as all simulated populations eventually declined.

*Neighbor effects on vital rates varied between years:* In an average snowmelt year, *Claytonia* plants set fewer fruits than plants in *Mertensia* neighbor removals. However, in an early snowmelt year, *Claytonia* reproductive success was higher in heterospecific and all neighbor removals. One potential reason for this trend is that under stressful environmental conditions, heterospecific neighbors with higher competitive ability outcompeted *Claytonia* for limited resources. However, under less abiotically stressful conditions, all plants received enough soil and light resources for high reproductive success. The probability of survival in *Mertensia* is a second example of varied effects of neighbors between year. In an average snowmelt year, the removal of all neighbors significantly reduced the probability of survival. In an early snowmelt year, the

probability of survival of small *Mertensia* plants in heterospecific and conspecific neighbor removal treatments were higher than in control plants, suggesting that neighbors were likely acting as competitors in a stressful year.

*High abiotic stress may overwhelm neighbor effects:* Deterministic population growth rate was significantly lower in *Claytonia* and *Mertensia* under early snowmelt conditions relative to average snowmelt conditions. In this study, I found that reproductive success and survival in the early snowmelt was lower than in the average year. Reproductive success may have suffered in an early snowmelt year due to frost exposure. In the early-flowering plant community at the RMBL, frost events have been documented to reduce reproductive success directly, through tissue damage of flowers and indirectly, through changes in floral traits and pollinator visitation rates (CaraDonna & Bain, 2016, Inouye, 2008, Pardee *et al.*, 2017). For example, when *Claytonia* plants were induced to flower earlier through snow removal, seed set was lower relative to control plants (Gezon *et al.*, 2016). In an observational study, seed set in *Mertensia fusiformis* was lower when frosts occurred more frequently (Forrest & Thomson, 2010).

Although average fruit set differed drastically between the two years of this study, population growth rate of most long-lived perennials is more sensitive to changes in survival and growth than changes in fecundity (Franco & Silvertown, 2004, Silvertown *et al.*, 1993). The probability of survival in both *Claytonia* and *Mertensia* was

significantly lower in the early snowmelt year relative to the average, which may have led declines in population growth rate.

Not only did the deterministic population growth rate differ between average and early snowmelt years, the effects of neighbors on population growth rate was also reduced under early snowmelt conditions. One potential hypothesis is that under benign environmental conditions, neighbors were more likely to affect fitness (indirect effects of climate), while under stressful abiotic conditions, the environment played a larger role (direct effects) (Chesson & Huntly, 1997, Hutchinson, 1961, Wiens, 1977). For *Claytonia*, the effect of all neighbors reduced population growth rate in average snowmelt years, but neighbor removal did not significantly affect growth rate under early snowmelt conditions. In more abiotically stressful years, the effect of the environment on population growth overwhelmed indirect effects.

There are caveats to this study. First, my sample size for constructing IPMs was low due to the number of neighbor removal treatments (n ~ 230 for each species across four neighbor removal treatments and a control). Therefore, the parameter estimates from the regressions used in the IPMs have high levels of uncertainty. Second, I only conducted this study over two demographic transitions and therefore may not have captured the entire range of temporal variation in vital rates. Therefore, future work should aim for a longer time series to adequately forecast population growth rate in the future. Third, I did not experimentally manipulate snowmelt date and instead relied on

natural variation in snowmelt date and annual snowpack between years. In addition to an early spring and low snowpack in 2018, the period before the monsoon season was extremely dry. This may have exacerbated the negative effects of early snowmelt, and therefore my estimates of population growth rate may be lower than what would be expected under most early snowmelt years. These estimates may therefore intensify the detrimental effects of early snowmelt date in my simulations beyond what is realistic.

Although there were limitations to this study, these results demonstrated that population growth rates of early flowering spring ephemerals were considerably negatively affected by early snowmelt and low snowpack. However, under future climate change, predicted early snowmelt and decreases in snowpack may be alleviated (for a short time) by the presence of neighbors for *Mertensia* and impeded by all vegetative neighbors for *Claytonia*. In conclusion, understanding both the direct and indirect effects of climate on species will be important for future predictions of population persistence under climate change.

## **4. Shifts in the phenology of the spring spawning of adult alewife (*Alosa pseudoharengus*): impacts of climate and population recovery**

### **4.1 Introduction**

The timing of many organism's recurring life cycle events, also known as their phenology, is highly sensitive to changes in the environment (Parmesan & Yohe, 2003, Poloczanska *et al.*, 2013, Reed *et al.*, 2013, Visser & Both, 2005). Organismal responses to climate change drivers via phenological responses have been well-studied in a diverse range of ecosystems, particularly in terrestrial and temperate regions (Parmesan & Yohe, 2003). Phenological shifts in marine and aquatic habitats have generally received less attention (Poloczanska *et al.*, 2013, Robinson *et al.*, 2009), leading to calls for additional studies and increased emphasis on understanding of directionality and magnitude.

Climate-induced shifts in phenological events that are linked to growth, reproduction, and survival can have ecological and evolutionary consequences (Miller-Rushing *et al.*, 2010, Rasmussen & Rudolf, 2015). One of these pivotal activities for many marine organisms, migration, is signaled by environmental cues (Ramenofsky & Wingfield, 2007). For example, phenological shifts in arrival dates by adults in birds to breeding grounds can affect mating/spawning timing, juvenile recruitment, and population dynamics (Cushing, 1990, Miller-Rushing *et al.*, 2010).

Anadromous fishes provide a unique case study for understanding phenological shifts in migration timing. This group of fishes have complex life cycles with strong seasonal movements, whereby they spend their early life in freshwater systems, mature in the open ocean, and return to freshwater to spawn as adults. Regional environmental drivers such as temperature, hydrology, and large-scale atmospheric processes (e.g., North Atlantic Oscillation index) have been useful in understanding migration in some anadromous species (Crozier & Hutchings, 2014, Juanes *et al.*, 2004, Otero *et al.*, 2014); however, drivers and responses vary across species and spatio-temporal scales throughout their geographical ranges (Jones *et al.*, 2003, Joyce *et al.*, 2000, Taylor *et al.*, 1998). Therefore, investigating regional and population-level shifts in phenology are needed to understand ongoing responses to climate change.

The Northwest Atlantic Ocean is an ideal system to study shifts in phenology due its strong seasonality and rapid warming (SST warmed by  $>0.4^{\circ}\text{C decade}^{-1}$  in Gulf of Maine and  $0.3^{\circ}\text{C decade}^{-1}$  in the Mid-Atlantic Bight between 1982 and 2014) during recent decades (Thomas *et al.*, 2017). The onset of spring has advanced by nearly two weeks since the 1980s. In addition, fall is occurring later, which has led to longer summers and shorter winters (Friedland *et al.*, 2015; Thomas *et al.*, 2017). While the timing of spring phytoplankton blooms has been shown to be positively related to changes in spring onset (Friedland *et al.*, 2015), effects on many components of the ecosystem and higher trophic levels remain largely unresolved.

In this study, we investigated the relationship between climate drivers and timing of adult migration of the anadromous fish species, alewife (*Alosa pseudoharengus*, Clupeidae), into coastal spawning ponds along the eastern United States. Alewife is well suited for this study because it has been identified as highly vulnerable to climate change, its passage points across the region are well-monitored, and it is a species of high conservation concern to state and federal agencies (Hare *et al.*, 2016). We examined long-term trends in the timing of spawning migration in alewife by asking the following questions: 1) Has migration timing shifted over recent decades? 2) How does the direction and magnitude of phenological shifts vary across the region?, and, 3) What regional-scale environmental factors best predict migration timing across spawning runs?

## **4.2 Materials and methods**

### **4.2.1 Study System**

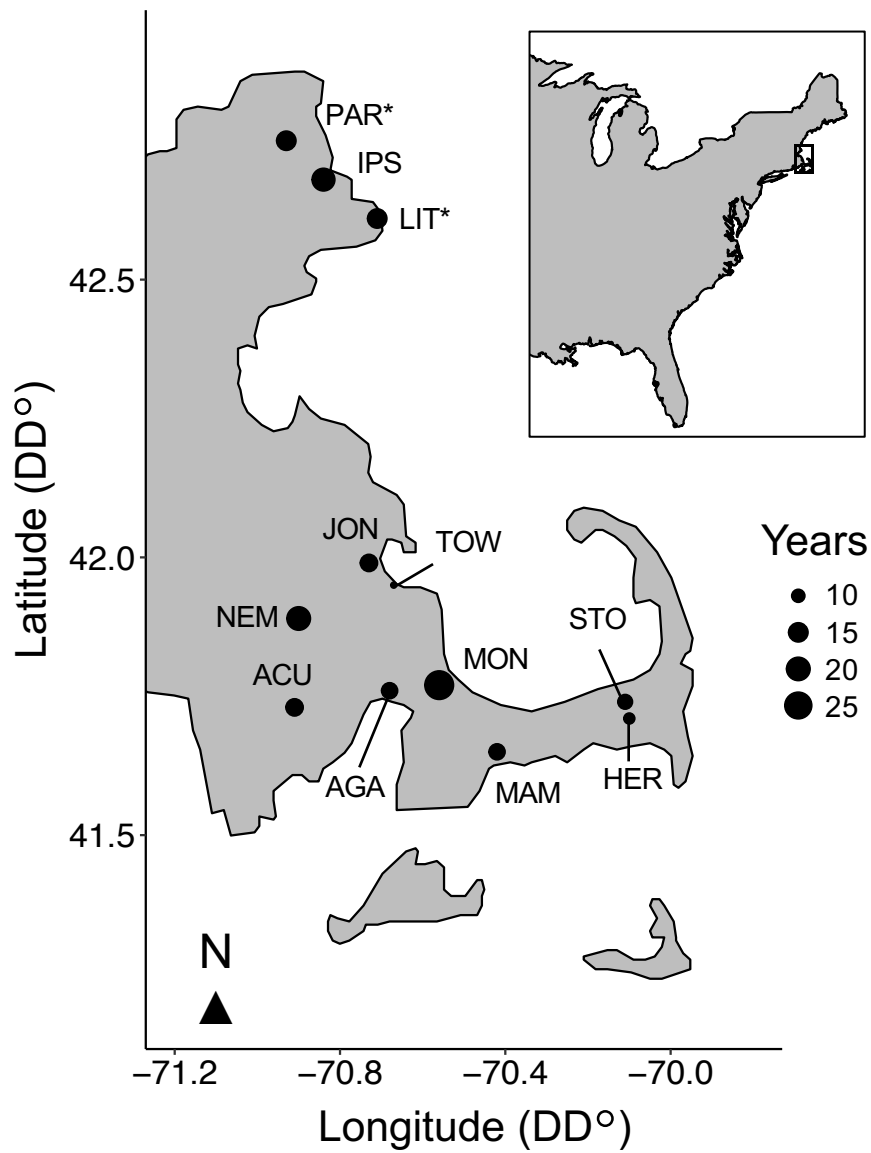
Alewife (*Alosa pseudoharengus*, Clupeidae) is an anadromous fish and one of the two species collectively known as river herring found in coastal habitats throughout eastern North America from Newfoundland, Canada to North Carolina, USA (Mullen *et al.*, 1986). Alewife has a long history of economic importance to regional commercial and recreational fisheries as well as to indigenous cultures as food and bait (Alexander *et al.*, 2017, Hall *et al.*, 2012, Mattocks *et al.*, 2017). Alewife serve as important links between lower and upper trophic levels as planktivores as well as key forage to higher-level

fishes, marine mammals, and seabirds (Moring & Mink, 2002, Mullen *et al.*, 1986). They provide other important ecosystem services as conduits of marine-derived nutrients between freshwater and ocean environments (Durbin *et al.*, 1979). Like other anadromous species, they rely on a variety of habitat types for completion of their life cycle; spending the adult portion of their lives in marine waters of the continental shelf, staging in estuaries until they move upstream to the spawning ponds, and completing their early life history in coastal freshwater ponds. Alewife initiate spawning migration when stream temperatures reach 5°C and 10°C (Loesch, 1987), migrations slow or delay between 8°C and 18°C (Ellis & Vokoun, 2009, Richkus, 1974), and cease when temperatures reach 20°C (Kissil, 1974). Alewife are iteroparous, and adults typically reach sexual maturity at four years old. Given the complexity of their reproductive cycle and early life history and the risks imposed by high exposure (e.g., increasing sea surface temperature) to regional climate change, alewife has been classified as a highly climate-vulnerable species (Hare *et al.*, 2016). Furthermore, alewife has experienced significant declines in abundance in the northeastern United States primarily as a result of habitat loss through damming of coastal rivers, overfishing, changing oceanic conditions, and increased abundance of native and non-native predator species (ASMFC, 2012, Hall *et al.*, 2012, Mattocks *et al.*, 2017).

#### 4.2.2 Study locations and fish counts

We synthesized fish count data from 12 coastal streams representing five major drainage areas across coastal Massachusetts (Table 7, Figure 11). Daily fish counts across the 12 sites go as far back as 1990 and span 8 - 28 years of data collection (Table 7, Figure 11). The Massachusetts Division of Marine Fisheries (MA DMF) worked collaboratively with municipalities, watershed associations and citizen science groups to record the daily number of river herring passing at eight coastal streams by visually counting of fish (Nelson, 2006, Rideout *et al.*, 1979). We estimated daily passage following the protocol detailed in Nelson (2006). We selected visual counting sites based on a minimum time series > 5 years, the use of a consistent sampling design provided by Nelson (2006), and a high probability to detect year-to-year changes in abundance and trends using the power analysis procedures of Gerrodette (1987). The MA DMF monitored four of the 12 streams using video monitoring systems or electronic resistivity counting systems (Smith-Root® 1101 and 1601). Raw daily passage counts derived from these systems were standardized and corrected based on associated error and correction methods by Sheppard and Bednarski (2015).

Another anadromous fish, blueback herring (*Alosa aestivalis*), may potentially inflate the daily fish counts at some of our sampling locations (Table 7). However, blueback herring typically move into systems later than alewife (Saunders *et al.*, 2006).



**Figure 11. Monitoring locations of alewife migration in Massachusetts, USA by the Massachusetts Division of Marine Fisheries and partnering organizations. Abbreviations of sampling locations are labeled next to monitoring location. Asterisks next to the sampling location abbreviations indicate non-continuous sampling since the first year. Total number of sampling years are indicated by size of the point (range: 8 – 28 years).**

**Table 7. Location (name of stream), abbreviation (three letter code), drainage, latitude (decimal degrees), longitude (decimal degrees), fish count method (E = electronic counter, V = visual counts, C = camera), years (number of sampling years) of data collection, and blueback presence (yes or no) of adult alewife migrating into coastal Massachusetts streams. Data was provided by the Massachusetts Division of Marine Fisheries and Rosset *et al.* (2017).**

Location	Abbreviation	Drainage Basin	Latitude (DD)	Longitude (DD)	Method	Years	Annual size (mean ± S.E.)	Blueback herring?
Parker River	PAR	Ipswich Bay	42.75	-70.93	EVC	16	11709 ± 16553	Yes
Ipswich River	IPS	Ipswich Bay	42.68	-70.84	V	19	873 ± 853	No
Little River	LIT	Ipswich Bay	42.61	-70.71	V	16	1890 ± 1446	No
Jones River	JON	Cape Cod Bay	41.99	-70.73	V	13	2784 ± 1650	No
Town Brook	TOW	Cape Cod Bay	41.95	-70.67	V	8	153907 ± 28868	No
Nemasket River	NEM	Mount Hope Bay	41.89	-70.9	V	20	571239 ± 280608	No
Monument River	MON	Cape Cod Bay	41.77	-70.56	E	28	174175 ± 108219	Yes
Agawam River	AGA	Buzzards Bay	41.76	-70.68	E	12	41203 ± 23591	No
Stony Brook	STO	Cape Cod Bay	41.74	-70.11	V	11	89657 ± 93985	Yes
Acushnet River	ACU	Buzzards Bay	41.73	-70.91	E	13	3555 ± 3117	No
Herring (Harwich) River	HER	Nantucket Sound	41.71	-70.1	EV	9	80572 ± 76496	No
Marstons Mills River	MAM	Nantucket Sound	41.65	-70.42	V	12	27338 ± 23309	No

### 4.2.3 Phenology metrics

We calculated annual run initiation date, median run date, and end of run date as indicators of spawning run timing for each site using daily fish count data (example of dataset for one site, Figure 12). Run initiation date was the Julian day when 5% of the population has passed the sampling location. Median run date (an indicator of peak run timing) was the day of the year when 50% of the population passed, and end of run date was the day of the year when 95% of the population passed. Run duration (number of days) was the difference (in days) between run initiation date and end of run date. We chose metrics that provided somewhat conservative estimates of population movements (e.g., rather than the absolute first and last observations) (Dufour *et al.*, 2010), to account for early-season sentinels that may begin to migrate upstream and return to the estuary if conditions are not adequate.

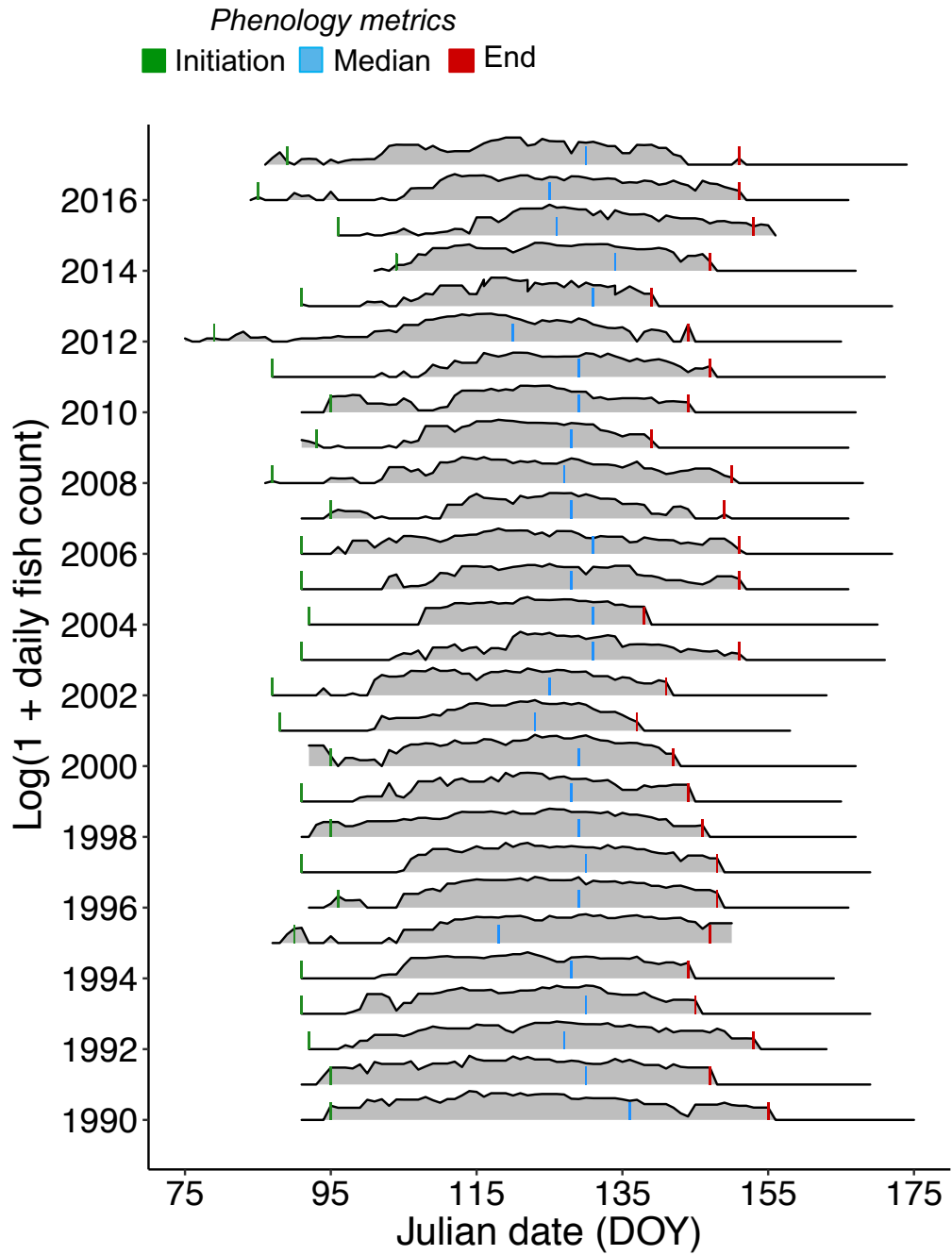


Figure 12. Daily counts of alewife in Monument River in Massachusetts, USA from 2005 to 2017. Run initiation (5% quantile, green lines), median run date (50% quantile, blue lines), and end of run date (95%, red lines) are marked for each year.

#### 4.2.4 Environmental variables

Seasonal sea surface temperature: Daily sea surface temperatures (SST) were downloaded from the National Oceanic and Atmospheric Administration's National Data Buoy Center (<http://www.ndbc.noaa.gov/>). We selected two buoys, one in the northern and one in the southern portion of our study region that aligned with distinct ecoregions separated by Cape Cod (Gulf of Maine 44005 and Nantucket 44008, respectively). We calculated seasonal mean, maximum, and minimum temperatures for fall (October - December), winter (January - March), and spring (April - June) to match other quarterly indices used in our models.

Seasonal transition dates and winter duration: We used fall and spring transition dates to assess how the annual timing of fall cooling and spring warming in the ocean affects fish migration. Spring transition date (STD) is the first day of the year when the SST exceeds the average annual temperature (10.3°C in the Gulf of Maine and 13.0°C in the Middle Atlantic Bight) for eight consecutive days (Friedland *et al.*, 2015). Similarly, fall transition date (FTD), is the day of the year that ocean temperatures drop below the average annual temperatures as noted above for a period of eight days (Friedland *et al.*, 2015). Seasonal transition dates of the closest 0.5° grid to our sampling sites were provided by K. Friedland (NOAA, NEFSC). We calculated winter duration as the difference between STD and the previous FTD for each year.

North Atlantic Oscillation index: Over the continental shelf of the northwest Atlantic, the North Atlantic Oscillation index (NAO) characterizes the difference in sea level atmospheric pressure between the low atmospheric pressure zone between Iceland and Southern Greenland and the high-pressure zone near the Azores (Hurrell, 1995, Hurrell & Deser, 2010). The NAO affects decadal, annual, and seasonal weather patterns over the eastern United States. Positive NAO phases result in warmer ocean surface waters and increased regional precipitation, while negative phases lead to colder ocean surface waters and drier conditions (Hurrell, 1995, Hurrell & Deser, 2010). Positive NAO phases typically encompass shorter summers and longer winters and are associated with more northerly positions of the Gulf Stream current (Thomas *et al.*, 2017). We obtained monthly North Atlantic Oscillation indices (NAO) from The National Weather Service's Climate Prediction Center (<http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml>). We averaged indices by season for use in modeling (fall, winter, spring).

Gulf Stream index: The Gulf Stream index (GSI) characterizes oceanographic conditions driven by the north-south position of the Gulf Stream Current and is a good indicator of bottom water temperatures at 200m (Chi *et al.*, 2018, Joyce *et al.*, 2000, Nye *et al.*, 2011). Although we used seasonal indices (fall, winter, and spring) for SST and NAO, annual values of the GSI were more appropriate since seasonal GSI values were all

highly correlated with one another ( $r$  values  $\geq 0.75$ ) during the time period evaluated in our models (1990 to 2015).

#### **4.2.5 Analyses**

Has adult alewife migration timing changed over recent decades? To determine if phenology metrics have shifted over time, we used the R package “lme4” to perform a series of linear mixed-effects regressions (LMMs) (Bates *et al.*, 2014). We used phenology metrics (run initiation, median, end dates, and run duration) as the response variable, year and annual run size as fixed effects, and site as a random effect. We z-score transformed annual run size for each sampling location by subtracting the variable mean from each value and then dividing by the standard deviation. All transformed variables then have a mean of zero and a standard deviation of one, preventing us from emphasizing a predictor a priori. Next, we confirmed these trends were robust by running all models without outliers. To determine whether a data point was an outlier, we calculated Cook’s distance (Cook’s SD) for each LMM. We removed points with a Cook’s SD above a threshold of  $4 * \text{mean}(\text{Cook’s SD})$  (Cook, 1977, Fox & Monette, 2002). In addition to running models with the complete dataset and a reduced one without outliers, we additionally ran the models without data from Acushnet, as this site has seen significant restoration events. Results from all of these analyses are presented in Appendix C (Table 12 Table 13). We conducted all statistical analyses in R version 3.5.1 (R Core Team, 2018).

How does the direction and magnitude of phenological shifts vary across the region? We estimated the magnitude and direction of shifts in phenology for each sampling location by running separate linear models (LMs). We used phenology metrics as the response variable and fixed effects of annual run size (z-score transformed) and year.

What are regional-scale environmental factors that best predict movements across spawning runs? First, we determined how seasonal environmental factors have changed over time of our study period. We used LMs to assess the relationship between each environmental variable (SST, transition dates, NAO indices, and annual GSI) and year. We also included buoy identification, which provided location information for the nearest corresponding seasonal temperature and ecological region (for transition dates) as fixed effects.

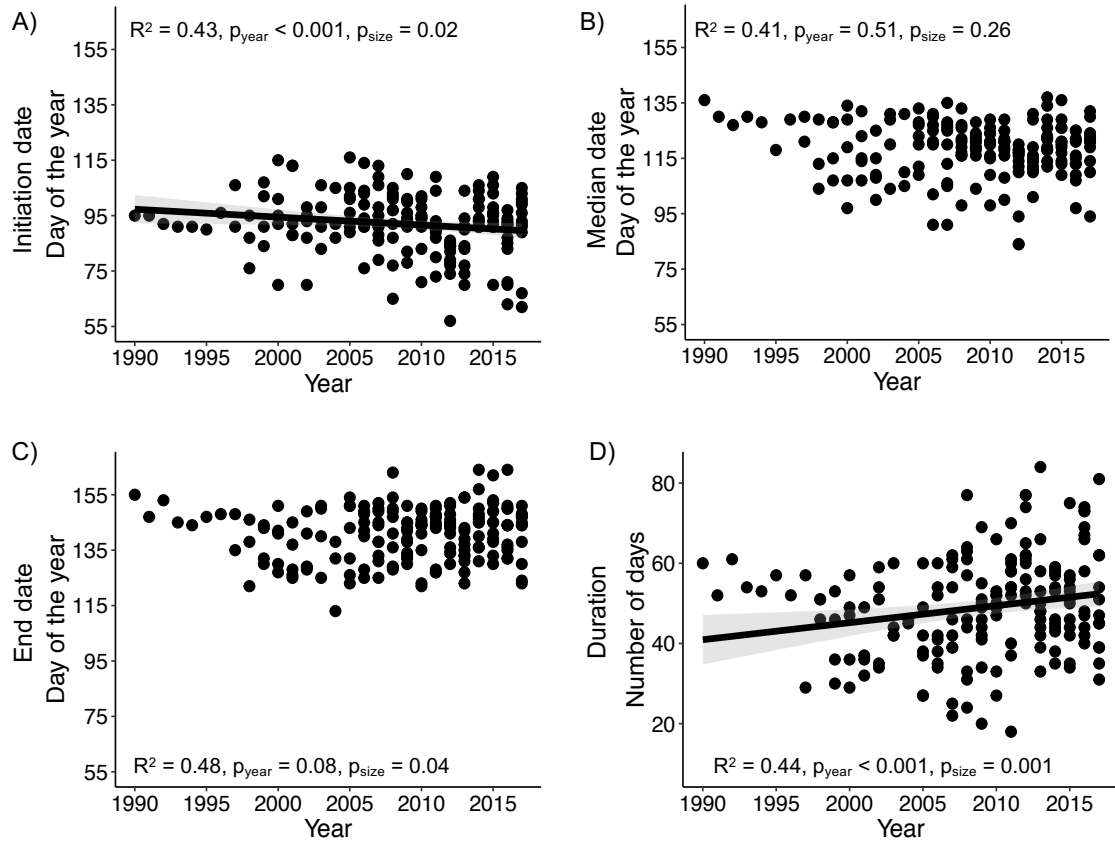
Next, we assessed multicollinearity between our predictor variables by calculating Pearson product-moment correlation coefficients. We reduced our list of variables to those with correlation coefficients less than the threshold of  $|r| < 0.7$  (Dormann et al., 2013). We ran four separate models with run initiation date, median run date, end of run date, and duration as the response variables. We first determined the structure of our random effects by building a series of global mixed effects models with ecoregion, and sampling location. We used a restricted maximum likelihood (REML) approach and Akaike's Information Criterion (AIC score) to select the best-fit

model (Zuur et al., 2009). Next, we selected between using seasonal minimum, mean, and maximum SST by running three competing global models for each phenology metric. We selected the best-fit model using AIC score for each metric, and found that minimum temperatures performed best in most cases (3 of 4 models). Next, we used the function *dredge()* in the R package “MuMIn” to generate a series of models with subsets of all of fixed effects (Barton & Barton, 2018). We then used a model averaging approach to create a top-model set of all models with  $\Delta AIC < 2$  (Burnham & Anderson, 2003). To estimate parameters and standard errors of the top-model set, we substituted a zero for a model in which the parameter was absent and then averaged the estimates of that parameter over all of the top models (Grueber et al., 2011).

### **4.3 Results**

*Run initiation date shows strongest shift over time.* We found a significant positive correlation between run initiation and median dates ( $r = 0.59$ ,  $p < 0.001$ ) and median and end dates ( $r = 0.69$ ,  $p < 0.001$ ). Initiation and end dates were not significantly correlated ( $r = 0.17$ ,  $p = 0.06$ ). When we ran the analysis with the full dataset, the average initiation date of adult alewife migration across all sites had advanced by  $10.7 \pm 3.9$  (mean  $\pm$  S.E) days ( $-0.42 \pm 0.15$  days/year) since 1990 (Figure 13A). Larger runs exhibited earlier migration initiation (LMM:  $\chi^2 = 16.5$ ,  $p < 0.001$ ). Median and end of run dates showed no relationship with year (Figure 13B and Figure 13C). As a consequence of earlier initiation date and constant end dates, run duration lengthened over time on

average by  $0.56 \pm 0.15$  days per year (LMM:  $\chi^2=15.2$ ,  $p < 0.001$ ) (Figure 13D). These trends held whether we ran these analyses with the full dataset or a reduced dataset without outliers. All results are reported in Appendix C (Table 12Table 13).



**Figure 13. Phenology metrics of adult alewife migration into coastal streams in Massachusetts, USA from 1990 to 2017. A) Run initiation date occurred earlier over time, while B) median and C) end of run dates showed no trend over time. D) Run duration (number of days) also increased over time.  $R^2$  values are conditional.**

The direction and magnitude of phenological shifts varies among sites. The occurrence, magnitude and direction of phenological shifts across 12 study streams were highly variable. Most streams showed earlier timing in phenology metrics but significant trends were only detected at a subset of sites (Table 8, Figure 14 and Figure 21). Run initiation (LM:  $t = -6.49$ ,  $p < 0.001$ ) and median (LM:  $t = -7.28$ ,  $p < 0.001$ ) run dates were significantly earlier in the Acushnet River (ACU). Over a 13-year period, run initiation at ACU advanced by  $5.2 \pm 0.81$  days per year and median date by  $3.3 \pm 0.45$  days per year (Table 8, Figure 14 and Figure 21). The total annual count of adult alewife migrating through the ACU increased since 2005, which was also significantly correlated to earlier run initiation (LM:  $t = 2.29$ ,  $p = 0.045$ ) and median run dates (LM:  $t = 3.48$ ;  $p = 0.005$ ). Run initiation in the Ipswich River (IPS) occurred significantly earlier over a 19-year period, shifting  $0.95 \pm 0.29$  days per year (LM:  $t = -3.27$ ,  $p = 0.005$ ) (Table 8, Figure 14 and Figure 21). In contrast, run end dates terminated later in the Parker River (PAR) over the 16-year sampling period ( $0.89 \pm 0.37$  days per year; LM:  $t = 2.40$ ,  $p = 0.029$ ).

**Table 8. Summary of linear regression analyses predicting phenology metrics of adult alewife spawning migration in 12 coastal streams in Massachusetts, USA. For each phenology metric (initiation date, median date, end of run date, and run duration), we ran models with fixed effects of year and annual run size. Regression coefficients  $\pm$  standard errors are on top, t-values are reported in parentheses. Adjusted R<sup>2</sup> for each model are reported. Significance is indicated by bold typeface and asterisks.**

Location	Fixed effects	Initiation (DOY)	Median (DOY)	End (DOY)	Duration (days)
Parker River (PAR)	Year	0.05 $\pm$ 0.33 (0.15)	0.50 $\pm$ 0.46 (1.10)	<b>0.89 <math>\pm</math> 0.37*</b> <b>(2.40)</b>	0.84 $\pm$ 0.41 (2.03)
	Annual Size	-2.54 $\pm$ 2.16 (-1.18)	0.91 $\pm$ 2.96 (0.31)	5.05 $\pm$ 2.41 (2.10)	<b>7.59 <math>\pm</math> 2.68*</b> <b>(2.83)</b>
	R <sup>2</sup>	-0.03	-0.02	0.42	0.47
Ipswich River (IPS)	Year	<b>-0.95 <math>\pm</math> 0.29**</b> <b>(-3.27)</b>	-0.06 $\pm$ 0.48 (-0.14)	0.12 $\pm$ 0.52 (0.23)	1.07 $\pm$ 0.52 (2.06)
	Annual Size	-1.64 $\pm$ 1.64 (-1.00)	-3.00 $\pm$ 2.71 (1.11)	2.38 $\pm$ 2.87 (0.83)	4.02 $\pm$ 2.92 (1.38)
	R <sup>2</sup>	0.33	-0.04	-0.08	0.14
Little River (LIT)	Year	-0.32 $\pm$ 0.21 (-1.50)	0.15 $\pm$ 0.53 (0.28)	-0.02 $\pm$ 0.34 (-0.06)	0.29 $\pm$ 0.40 (0.74)
	Annual Size	-0.81 $\pm$ 1.16 (-0.70)	3.90 $\pm$ 2.93 (1.33)	0.83 $\pm$ 1.88 (0.44)	1.64 $\pm$ 2.19 (0.75)
	R <sup>2</sup>	0.02	-0.01	-0.14	-0.09
Jones River (JON)	Year	-0.60 $\pm$ 0.58 (-1.03)	-0.62 $\pm$ 0.40 (-1.55)	-0.82 $\pm$ 0.54 (-1.52)	-0.22 $\pm$ 0.79 (-0.28)
	Annual Size	1.58 $\pm$ 2.28 (0.70)	0.96 $\pm$ 1.56 (0.62)	0.52 $\pm$ 2.10 (0.25)	-1.06 $\pm$ 3.04 (-0.35)
	R <sup>2</sup>	-0.08	0.09	0.16	-0.11
Town Brook (TOW)	Year	0.39 $\pm$ 1.58 (0.25)	-0.07 $\pm$ 0.76 (-0.09)	-0.03 $\pm$ 0.17 (-0.18)	0.84 $\pm$ 0.41 (2.21)
	Annual Size	-3.78 $\pm$ 3.86 (-0.98)	-1.33 $\pm$ 1.86 (-0.71)	0.70 $\pm$ 0.31 (1.69)	<b>7.60 <math>\pm</math> 2.68*</b> <b>(2.83)</b>
	R <sup>2</sup>	-0.17	-0.23	0.15	0.47
	Year	-0.49 $\pm$ 0.45 (-1.09)	-0.21 $\pm$ 0.24 (-0.90)	0.20 $\pm$ 0.14 (1.46)	0.69 $\pm$ 0.47 (1.48)

Nemasket River (NEM)	Annual Size	-1.41 ± 2.68 (-0.53)	-3.8 ± 1.41 (-0.27)	0.67 ± 0.82 (0.82)	2.08 ± 2.78 (0.75)
	R <sup>2</sup>	-0.04	-0.07	0.02	0.01
Monument River (MON)	Year	-0.03 ± 0.11 (-0.29)	-0.07 ± 0.10 (-0.76)	-0.07 ± 0.13 (0.59)	-0.04 ± 0.15 (-0.24)
	Annual Size	1.28 ± 0.94 (1.36)	-0.78 ± 0.79 (-0.99)	-1.04 ± 1.04 (-1.00)	-2.32 ± 1.27 (-1.83)
	R <sup>2</sup>	0.02	-0.03	-0.04	0.06
Agawam River (AGA)	Year	0.003 ± 1.23 (0.002)	-0.08 ± 0.50 (-0.17)	-0.57 ± 0.47 (-1.21)	-0.57 ± 1.41 (-0.40)
	Annual Size	-1.00 ± 4.45 (-0.23)	-2.85 ± 1.80 (-1.58)	-2.54 ± 1.69 (1.50)	-1.54 ± 5.08 (-0.30)
	R <sup>2</sup>	-0.21	0.08	0.05	-0.20
Stony Brook (STO)	Year	-0.08 ± 0.68 (-0.12)	-0.28 ± 0.46 (-0.62)	-0.33 ± 0.54 (-0.61)	-0.25 ± 0.81 (-0.31)
	Annual Size	3.03 ± 2.25 (1.34)	2.65 ± 1.51 (1.75)	2.68 ± 1.80 (1.49)	-0.35 ± 2.70 (-0.13)
	R <sup>2</sup>	0.02	0.10	0.02	-0.22
Acushnet River (ACU)	Year	<b>-5.21 ± 0.81***</b> <b>(-6.49)</b>	<b>-3.35 ± 0.46***</b> <b>(-7.28)</b>	-0.43 ± 0.61 (-0.70)	<b>4.79 ± 1.20**</b> <b>(4.00)</b>
	Annual Size	<b>7.17 ± 3.13*</b> <b>(2.29)</b>	<b>6.22 ± 1.79**</b> <b>(3.48)</b>	2.20 ± 2.36 (0.93)	<b>-4.97 ± 4.67**</b> <b>(-1.06)</b>
	R <sup>2</sup>	0.85	0.86	-0.1	0.71
Herring River (HER)	Year	0.23 ± 0.60 (0.38)	0.17 ± 0.58 (0.29)	0.59 ± 0.76 (0.78)	0.36 ± 0.96 (0.37)
	Annual Size	-2.86 ± 1.64 (-1.74)	-1.93 ± 1.60 (-1.21)	0.12 ± 2.07 (0.06)	2.97 ± 2.64 (1.13)
	R <sup>2</sup>	0.11	-0.07	-0.20	-0.04
Marston Mills River (MAM)	Year	-0.96 ± 0.57 (-1.67)	-0.74 ± 0.45 (-1.67)	-0.40 ± 0.51 (-0.79)	0.56 ± 0.65 (0.87)
	Annual Size	-4.30 ± 2.06 (-2.09)	-1.52 ± 1.60 (-0.95)	1.91 ± 1.83 (1.05)	<b>6.21 ± 2.32*</b> <b>(2.67)</b>
	R <sup>2</sup>	0.44	0.23	-0.07	0.44
*** p < 0.001, ** p < 0.01, * p ≤ 0.05					

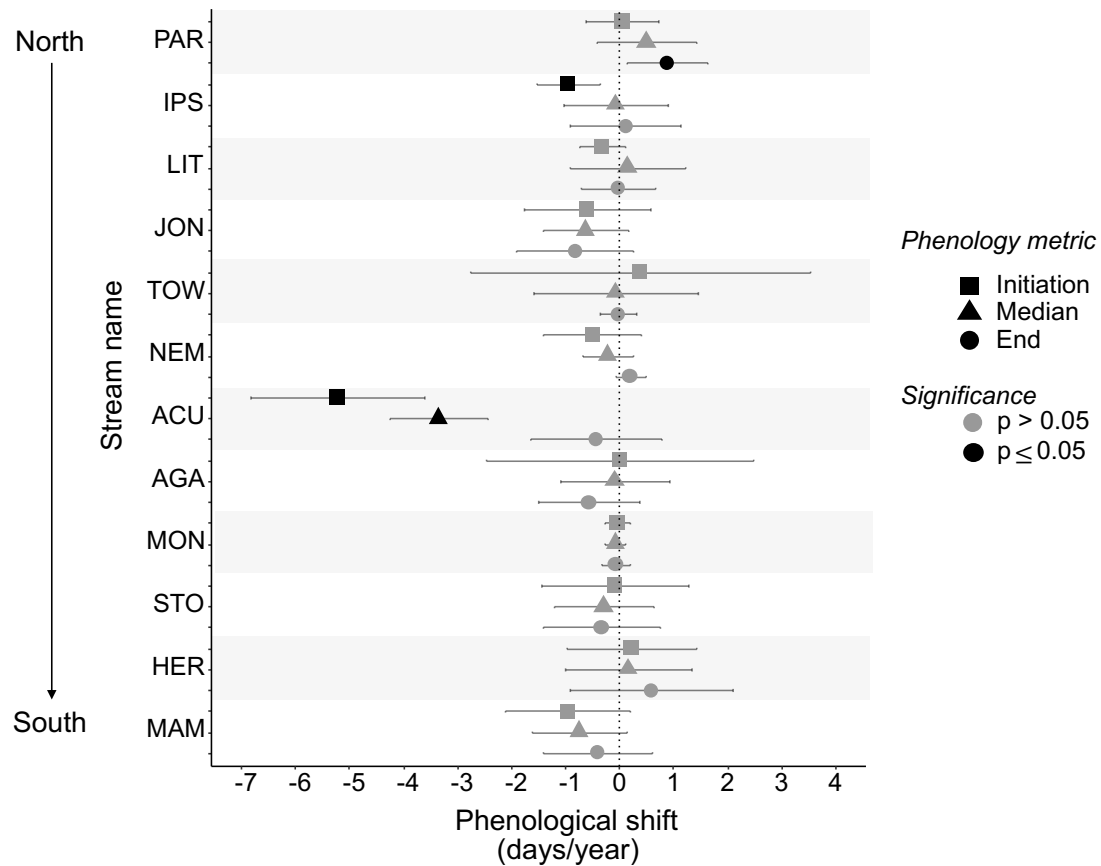
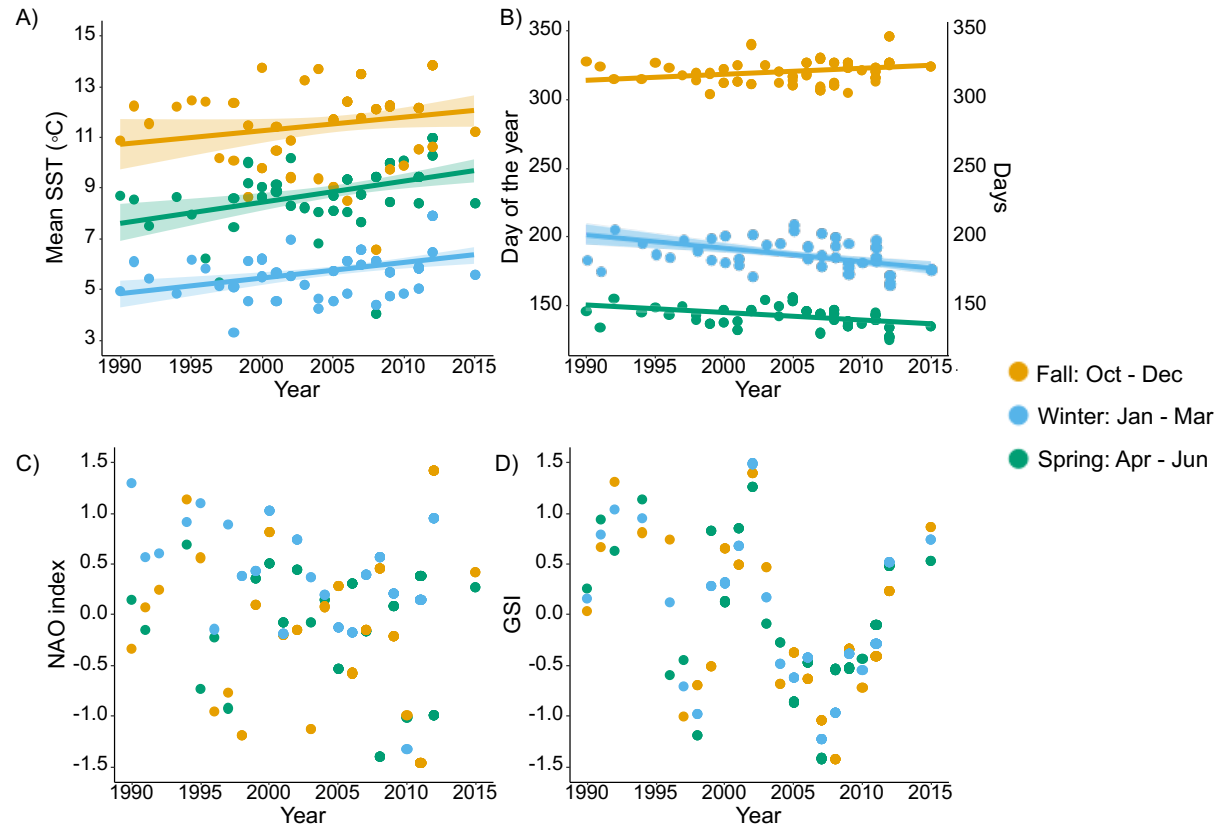


Figure 14. Phenological shift (days per year) in run initiation (square), median run (triangle) and end of run date (circle)  $\pm$  standard error per year for adult alewife migration in Massachusetts, USA between 1990 and 2017. Black symbols indicate a significant advancement or delay in phenology ( $p \leq 0.05$ ), while gray symbols indicate no significant shift in phenology ( $p > 0.05$ ). Sampling locations are ordered from north to south (see Table 7 for more information).

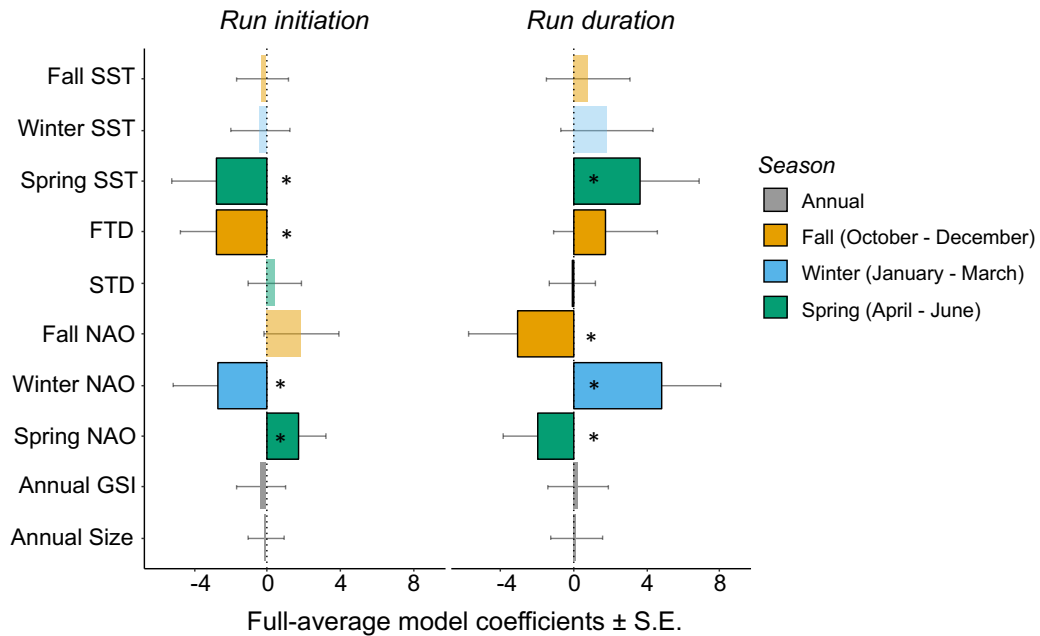
Spring minimum temperature and winter NAO predict run initiation date and duration. Seasonal SSTs have increased significantly from 1990 to 2015 (Figure 15A). From 1990 to 2015, the fall minimum and mean SSTs increased by  $1.85 \pm 0.54^{\circ}\text{C}$  (LM:  $t = 3.43$ ,  $p = 0.001$ ) and  $1.31 \pm 0.54^{\circ}\text{C}$  (LM:  $t = 2.4$ ,  $p = 0.02$ ), respectively; however, fall maximum SST showed no trend over time (LM:  $t = 0.09$ ,  $p = 0.93$ ). Winter mean SST increased by  $1.37 \pm 0.40^{\circ}\text{C}$  (LM:  $t = 3.45$ ,  $p = 0.001$ ), and winter maximum SST increased by  $2.49 \pm 0.61^{\circ}\text{C}$  (LM:  $t = 4.03$ ,  $p < 0.001$ ). Winter minimum SST did not show significant increases over time (LM:  $t = 1.15$ ,  $p = 0.26$ ). Spring mean SST increased by  $1.60 \pm 0.61^{\circ}\text{C}$  since 1990 (LM:  $t = 2.06$ ,  $p = 0.01$ ), while spring minimum (LM:  $t = 1.51$ ,  $p = 0.14$ ) and maximum (LM:  $t = 1.13$ ,  $p = 0.27$ ) SSTs did not significantly increase.

Spring transition dates became earlier ( $-0.43 \pm 0.02$  day per year,  $t = -23.64$ ,  $p < 0.001$ ) and fall transition dates became later ( $0.61 \pm 0.02$  day per year,  $t = 28.12$ ,  $p < 0.001$ ), resulting in a significant decrease in winter duration of  $26.81 \pm 0.76$  days over sampling period (LM:  $t = -35.2$ ,  $p < 0.001$ ) (Figure 15B). The NAO index and GSI varies intra- and interannually, both show no significant trend over time (Figure 15C and Figure 15D).

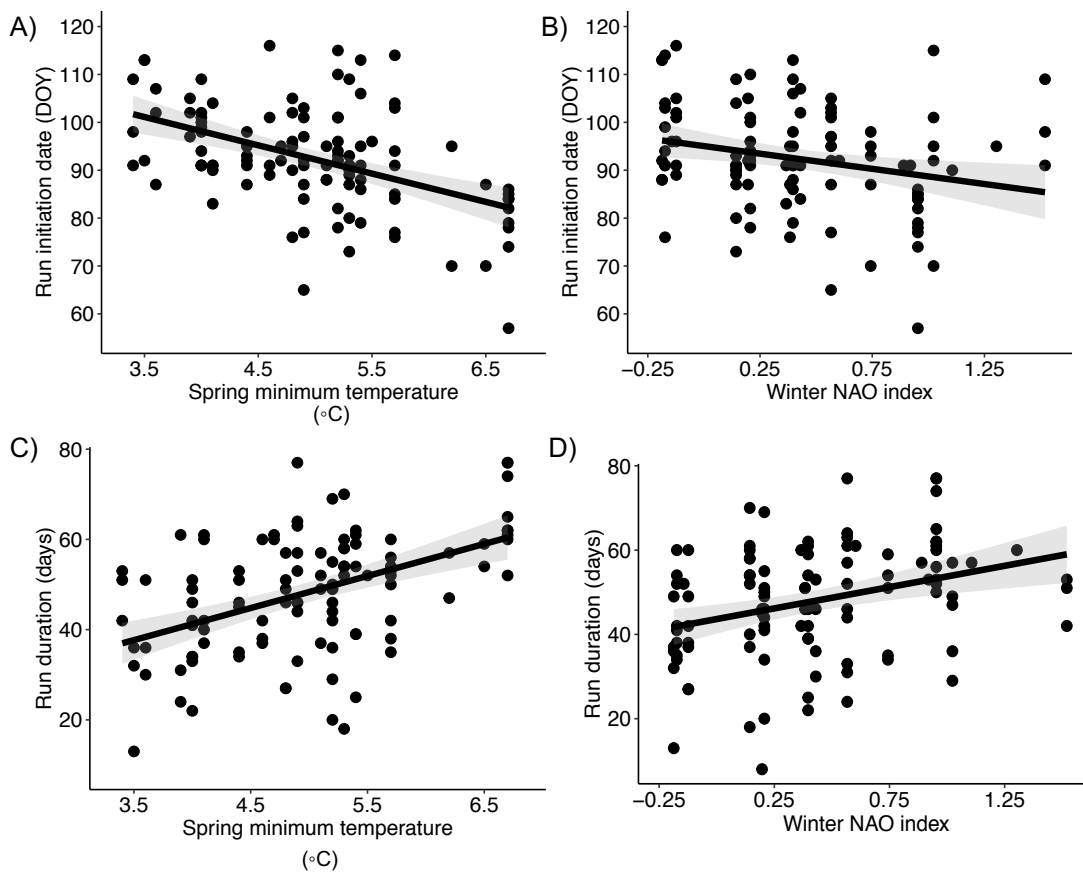


**Figure 15. Environmental variables from 1990 – 2015 in fall (orange: October – December), winter (blue: January - March), and spring (green: April – June). A) Mean temperature ( $^{\circ}\text{C}$ ) from Gulf of Maine and Nantucket ocean buoys, B) fall (orange), spring (green) transition dates (day of the year), and winter duration (blue, number of days), C) North Atlantic Oscillation index, and D) Gulf Stream index.**

Run initiation date was earlier during years when spring minimum temperature was warmer, the previous year's fall transition date was earlier, the winter NAO Index was negative, and the spring NAO was positive (Table 14). Warmer spring minimum temperatures, later fall transition dates, and more positive NAO phases were correlated with earlier run dates (Figure 16, Figure 17). Median and end of run dates were not significantly correlated to any environmental variables assessed in these models. Run duration was positively correlated to spring minimum temperature and winter NAO, but negatively correlated to fall and spring NAO indices (Table 14, Figure 16, Figure 17).



**Figure 16. Full-average model coefficients ± adjusted standard errors of all environmental variable effects on initiation date and duration of adult alewife spawning migration in Massachusetts, USA. Coefficient magnitude is represented by the size of each bar with negative relationships to the left and positive relationships to the right of each dotted line. Significant variables are indicated by asterisks ( $p \leq 0.05$ ).**



**Figure 17. Run initiation date (day of year) and duration (days) of adult alewife migration in Massachusetts, USA across from 1990 to 2015 in relation to minimum spring temperature ( $^{\circ}\text{C}$ ) and winter NAO. Run initiation was negatively correlated to A) spring minimum SST and B) winter NAO. Run duration was positively correlated to both C) spring minimum temperature and D) winter NAO.**

#### **4.4 Discussion**

A general trend towards earlier spring migration timing of adult alewife into coastal freshwater streams was found in Massachusetts between 1990-2017; however, shifts varied widely across individual systems. Many streams showed earlier timing in phenology metrics but significant trends overtime were only detected at a subset of sites. Run duration was found to increase, primarily due to earlier run initiation and constant

run end dates. A combination of several regional seasonal factors influenced run initiation, including warmer minimum spring SST, later fall transition dates from the previous year, as well as positive winter and negative spring NAO indices. Later fall transition dates were strongly correlated with shorter winter duration, and when considered in combination with the positive phase of the winter NAO index and warmer spring minimum SSTs, results suggest winter severity influences early migration behavior in alewife. We hypothesize that during warmer, shorter, and wetter winters alewife move inshore and test the system earlier in comparison to longer, colder winters with less precipitation, where they may remain offshore in search of (warmer) thermal refuge (Lynch *et al.*, 2014). Warmer minimum spring SST and a negative spring NAO index characterize the regional conditions effecting within-season movements by alewife. We hypothesize that these factors act to moderate hydrological conditions as has been shown previously (Huntington *et al.*, 2003). Additional insights into environmental influences on this system would benefit from the consideration of river flow, salinity and ice dynamics (ice thickness and ice-out) in future modeling efforts. Overall, multiple environmental and ecological factors, which were not captured by our models are likely working in concert to influence migration phenology including behavioral, demographic, food availability, and physiology.

The Northwest Atlantic has experienced strong ocean warming and earlier spring onset (Thomas *et al.*, 2017). However, alewife did not show concurrent shifts in

migration timing across comparable time periods despite observed changes in the environment and their hypothesized sensitivity to climate change (Hare et al., 2015). It is possible that thermal thresholds have not yet been crossed that would cause alewife behavior to change systematically across their range. Although stream, estuary, and shelf water temperatures were found to be correlated in our system, they may still differ significantly in magnitude with offshore waters of the outer continental shelf and slope offering (warmer) thermal refugia in comparison to inshore and inland waters (Sims *et al.*, 2004).

Furthermore, shifts in migration timing do not correlate with changes in timing of spawning. A recent study by Rosset *et al.* (2017) found that despite differences in migration timing of river herring among sites, spawning generally occurs at the same time across coast Massachusetts. Finally, alewife behavior may be plastic enough to take advantage of and move in response to optimal short-term (daily or even hourly) conditions within individual systems.

Other anthropogenic and ecological factors likely confounded and overwhelmed our results at certain locations. Three streams showed significant shifts in run timing, but changes manifested in different metrics, varying magnitudes, and opposite directions (run initiation and median run date in the Acushnet River, run initiation in the Ipswich River, and run end in the Parker River). First, in the Acushnet River, the number of adult alewife increased significantly over the sampling period as a result of

conservation and restoration efforts (range: 395 - 10,144 fish) (Sheppard & Block, 2013, Sheppard *et al.*, 2014). The second system that showed a significant advance in migration timing, Ipswich River, was stocked with over 13,000 fish in 2003, 2004, 2006, and 2007. These increases in population size likely increased the demography (size, age, sex ratios) and genetic diversity in the system, which can affect migration timing (Lambert, 1987, Marjadi *et al.*, 2018, Tillotson & Quinn, 2018) and may have influenced inter-annual trends observed over time. In contrast, migration timing in Parker River showed a delay in run termination date. The run size remained relatively stable from 1997 to 2013, and then increased substantially from 2014 to 2017 (mean  $\pm$  S.E.: 1997 – 2013: 6719  $\pm$  1238, 2014 – 2017: 38325  $\pm$  18439). Perhaps, more importantly, the data collection process changed during the sampling period. From 1997 – 2012, visual counts were used at this site (Nelson *et al.*, 2011), but then switched in 2013 to an electronic counter, and then switched again to video recordings from 2014 – 2017 (Sheppard, *personal communication*). Previous research has shown that visual counts can underestimate the number of fish passing and potentially truncate the end of season prematurely when numbers drop to just a few individuals per day (Sheppard & Bednarski, 2015). While our choice of phenology metric (95th percentile of run) should have buffered against such variation to some degree, it seems likely that later run end dates, were affected at least in part by changes in sampling method.

Understanding changes in the migratory behavior of alewife and other anadromous species in response to climate have important management implications (Peer & Miller, 2014). Specifically, many rivers along coastal Massachusetts are located in highly developed areas, and as a result, alewife spawning and nursery habitats in these rivers have been impacted by various development activities such as dams, water withdrawals and other forms of watershed development (Moring, 2005). For example, several coastal Massachusetts watersheds have impoundments that are utilized as water supplies for irrigation and municipal use (Acushnet, Herring (Harwich), Ipswich, Jones, Little, and Nemasket Rivers) (Reback *et al.*, 2004). Water withdrawals can hinder adult alewife spawning migrations in the spring as well as juvenile emigration in the summer and fall by lowering flows and making upstream and downstream passage problematic. Withdrawals often coincide with periods of low precipitation when the demand for water is high, which in turn further complicates fish passage and water quality parameters (Evans *et al.*, 2015).

Management actions are designed to protect these populations and habitats primarily through time-of-year restrictions on habitat alteration activities as well as best management practices on water withdrawals during critical migration periods (Evans *et al.*, 2015). These activities are based on known life history traits and migratory behavior from long-term monitoring programs. The results of this study emphasize the need to develop adaptive management strategies to account for temporal changes in adult

alewife spawning and juvenile emigration patterns from both climate and restoration activities. In addition, the results of this study indicate the need to explore models designed to forecast the timing of spawning migrations in response to predicted environmental change.

In conclusion, migration timing of adult alewife correlated with several broad-scale seasonal environmental drivers and population restoration actions. However, phenological shifts were inconsistent among spawning locations. A site-specific approach that considers local habitat characteristics such as stream flow, salinity, tidal cycles, and stream-pond habitat characteristics (e.g., distance from coast to pond, change in elevation, pond area, impediments to passage, restoration actions) considered in this study would improve understanding of the local thresholds and conditions causing the high variability in timing among sites. Although many of the metrics reported here did not show significant shifts in timing across all coastal streams, they are still noteworthy. Stable phenology could be indicative of local populations adapting in place or that populations are not keeping pace with the rapid environmental changes occurring around them (Beever *et al.*, 2016, Parmesan, 2007). If the latter is true of alewife in these systems, continued monitoring is important for detecting when the population is approaching a critical threshold or phenological mismatches are imminent.

## ***4.5 Funding***

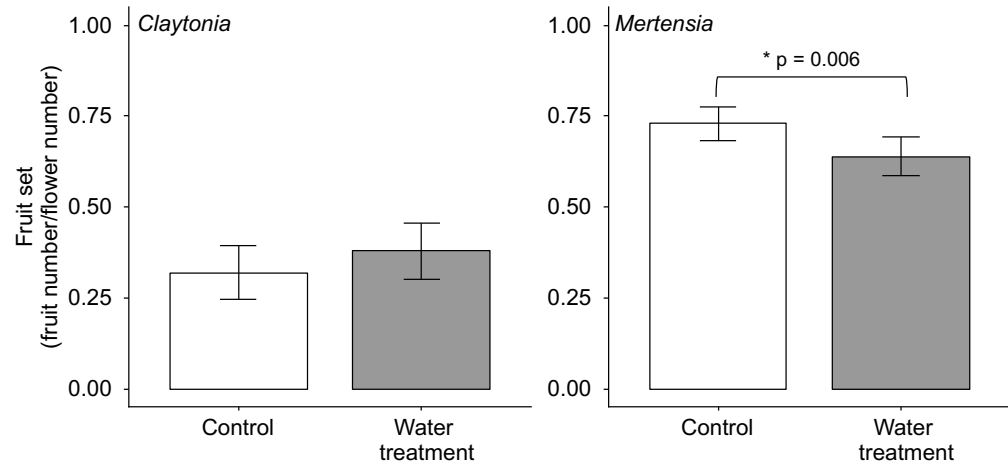
### **4.5.1 Funding Information**

This work was supported by the Department of the Interior Northeast Climate Adaptation Science Center (G14AC00441) for M.D.S. and A.J. R.M.D was funded by National Science Foundation Graduate Research Fellowship and Graduate Research Internship Program (Grant No. DGE-1644868).

## **5. Conclusions**

I combined observations, experiments, and demographic modeling to assess how climate affects species interactions in a terrestrial and an aquatic study system. In the future, I hope to combine the tools that I learned in this dissertation to study how phenological shifts affect species coexistence.

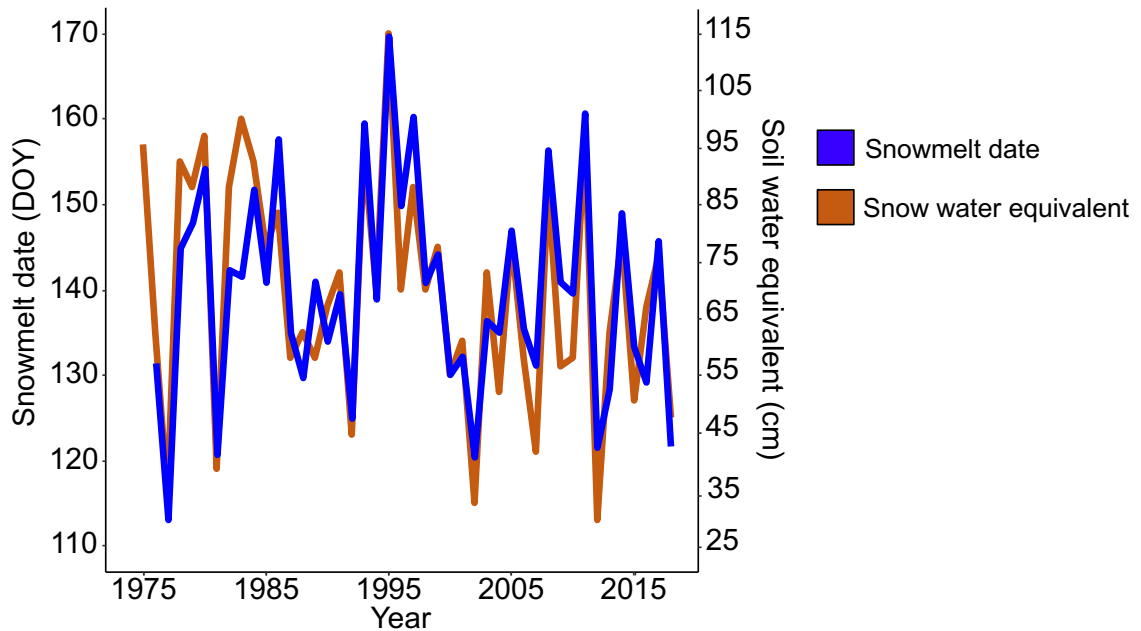
## Appendix A



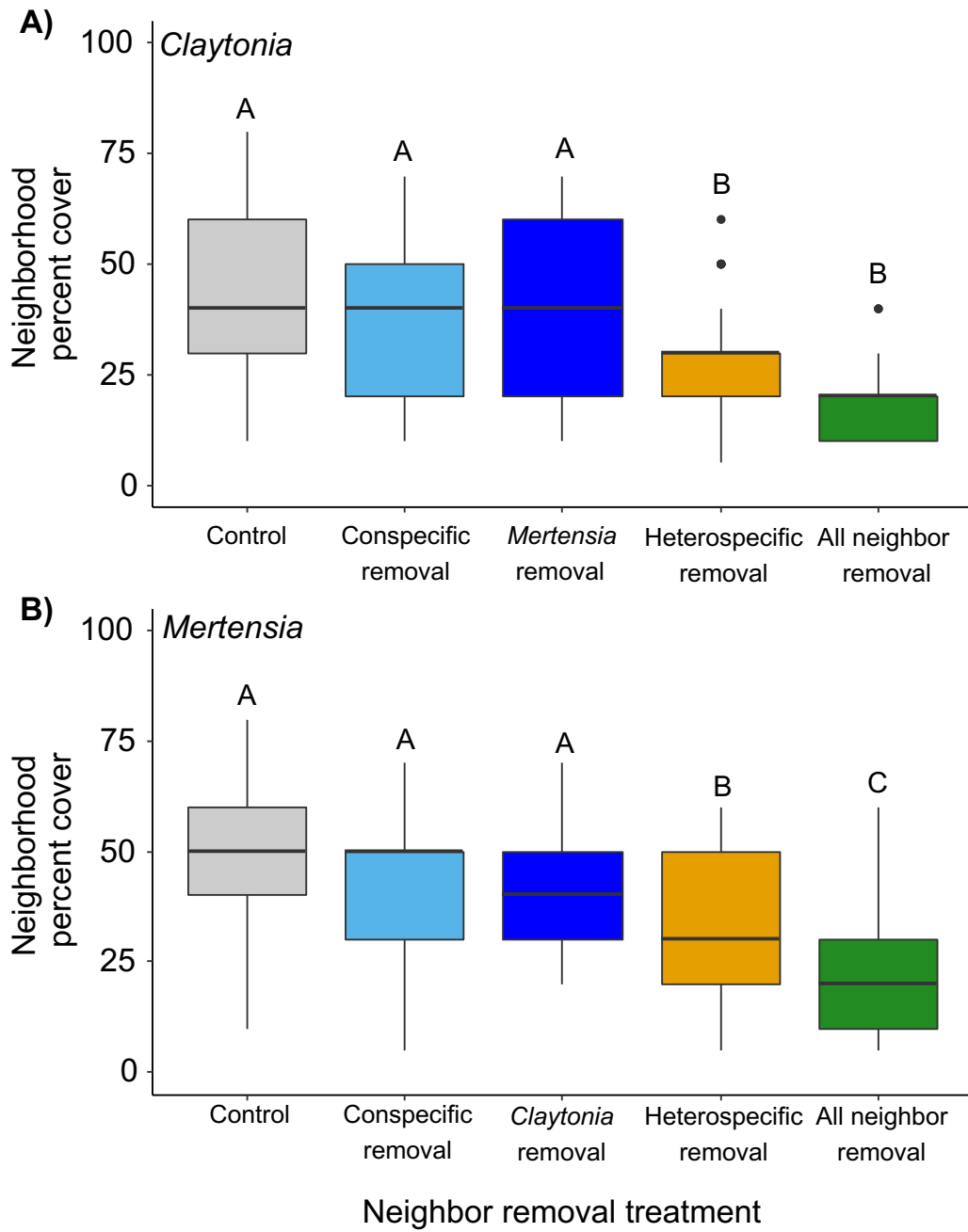
**Figure 18. Fruit set (fruit number/flower number, least squares means  $\pm$  S.E.) produced by A) *Claytonia* and B) *Mertensia* in control (white) and water treatment plots (gray) in 2018. Asterisk indicates significant differences ( $p \leq 0.05$ ).**

## Appendix B

Supplemental material for Chapter 3. Early snowmelt and neighbors interact to influence population growth of two subalpine spring ephemerals.



**Figure 19. Julian date of bare ground (day of the year, blue lines) and snow water equivalent (cm, orange lines) from 1975 to 2018 at the Rocky Mountain Biological Laboratory (barr 2019).**



**Figure 20. Percent cover of neighborhood in 2018 of A) *Claytonia* and B) *Mertensia* in neighbor removal treatments. Significant differences are indicated by letters (Tukey's HSD,  $p \leq 0.05$ ).**

**Table 9. Summary table for linear models of percent cover around *Claytonia* and *Mertensia* focal plants. Fixed effects include neighbor removal treatment (control, *Mertensia* or *Claytonia*, conspecific, heterospecific, and all neighbor removals), water treatment (control or supplemental water), and site (KP or RG). Supplemental water was only added in 2018, and therefore NAs indicate this factor is not included in analyses in 2017.**

Species	Year	Neighbor removal				Water treatment				Site				Residuals	
		df	SS	F	p	df	SS	F	p	df	SS	F	p	df	SS
<i>Claytonia</i>	2017	4	2.63	30.85	<0.001	NA	NA	NA	NA	1	1.19	55.81	<0.001	212	4.51
	2018	4	1.67	18.48	<0.001	1	0.0004	0.02	0.90	1	0.63	27.75	<0.001	211	4.77
<i>Mertensia</i>	2017	4	1.62	25.53	<0.001	NA	NA	NA	NA	1	1.62	61.02	<0.001	241	6.40
	2018	4	1.77	22.17	<0.001	1	0.01	0.72	0.40	1	0.51	25.41	<0.001	240	4.80

**Table 10. Summary of differences between vital rates in control and neighbor removal treatments in *Claytonia* in 2017 and 2018.**

<i>Claytonia</i> Vital rate	Year	Neighbor removal treatment	Summary of plants in neighbor removal treatment relative to the control
Growth	2018	All neighbor	Larger plants in the removal grew more from 2017 to 2018.
Flower number	2018	Heterospecific	Plants in removal with supplemental water produced more flowers than plants in removal without water.
Fruit set	2017	Conspecific	Plants in the removal set fewer fruits.
Fruit set	2017	<i>Mertensia</i>	Plants in the removal set fewer fruits.
Fruit set	2018	All neighbor	Plants in the removal set more fruits.
Fruit set	2018	Heterospecific	Plants in the removal set more fruits.
Fruit set	2018	<i>Mertensia</i>	Plants in the removal set more fruits.

**Table 11. Summary of differences between vital rates in control and neighbor removal treatments in *Mertensia* in 2017 and 2018.**

<i>Mertensia</i> Vital rate	Year	Neighbor removal treatment	Summary of plants in neighbor removal treatment relative to the control
Probability of survival	2017	All neighbor	Plants in the removal had lower probability of survival.
Probability of survival	2018	Heterospecific	Small plants in the removal were more likely to survive relative to small control Larger plants were less likely to survive.
Probability of survival	2018	Conspecific	Small plants in the removal were more likely to survive relative to small control plants. Larger plants were less likely to survive
Flower number	2018	Heterospecific	Larger plants in the removal produced more flowers.
Fruit set	2017	<i>Claytonia</i>	Small plants in the removal set more fruits, but larger plants set fewer fruits.
Fruit set	2017	Conspecific	Plants in the removal set more fruits.
Fruit set	2018	Conspecific	Small plants in the removal set more fruits, larger plants set fewer fruits.
Fruit set	2018	Heterospecific	Small plants in the removal set fewer fruits, larger plants set more fruits.

## Appendix C

Supplemental material for Chapter 4. Shifts in the phenology of the spring spawning of adult alewife (*Alosa pseudoharengus*): impacts of climate and population recovery.

**Table 12. Analysis of variance table for linear mixed effects models predicting phenology metrics of alewife spawning migration in Massachusetts, USA. For each phenology metric, we ran the model with the complete dataset (“full dataset”), a dataset without outliers (“remove outliers”), and a dataset without Acushnet River (“remove ACU”). Significant effects are in bolded typeface.**

Model	Data	Fixed effects	$\chi^2$	p	AIC
Initiation (DOY)	Full dataset	<b>Year</b>	<b>12.71</b>	<b>&lt; 0.001</b>	1295.58
		<b>Annual Size</b>	<b>4.48</b>	<b>0.030</b>	
	Remove outliers	<b>Year</b>	<b>10.82</b>	<b>0.001</b>	1135.74
		<b>Annual Size</b>	<b>9.83</b>	<b>0.002</b>	
	Remove ACU	<b>Year</b>	<b>7.13</b>	<b>0.008</b>	1174.43
		Annual Size	3.29	0.070	
Median (DOY)	Full dataset	Year	0.64	0.424	1259.37
		Annual Size	1.38	0.241	
	Remove outliers	Year	1.40	0.237	1089.57
		Annual Size	3.33	0.068	
	Remove ACU	Year	0.01	0.932	1163.16
		Annual Size	0.84	0.360	
End (DOY)	Full dataset	Year	2.58	0.108	1238.58
		Annual Size	0.01	0.939	
	Remove outliers	Year	0.08	0.773	1086.42
		Annual Size	0.01	0.930	
	Remove ACU	Year	2.49	0.115	1156.06
		Annual Size	0.02	0.898	
Duration (days)	Full dataset	<b>Year</b>	<b>16.07</b>	<b>&lt; 0.001</b>	1368.12
		<b>Annual Size</b>	<b>10.62</b>	<b>0.001</b>	
	Remove outliers	<b>Year</b>	<b>13.22</b>	<b>&lt; 0.001</b>	1281.18
		Annual Size	2.05	0.152	
	Remove ACU	<b>Year</b>	<b>10.05</b>	<b>0.002</b>	1260.60
		Annual Size	1.61	0.204	

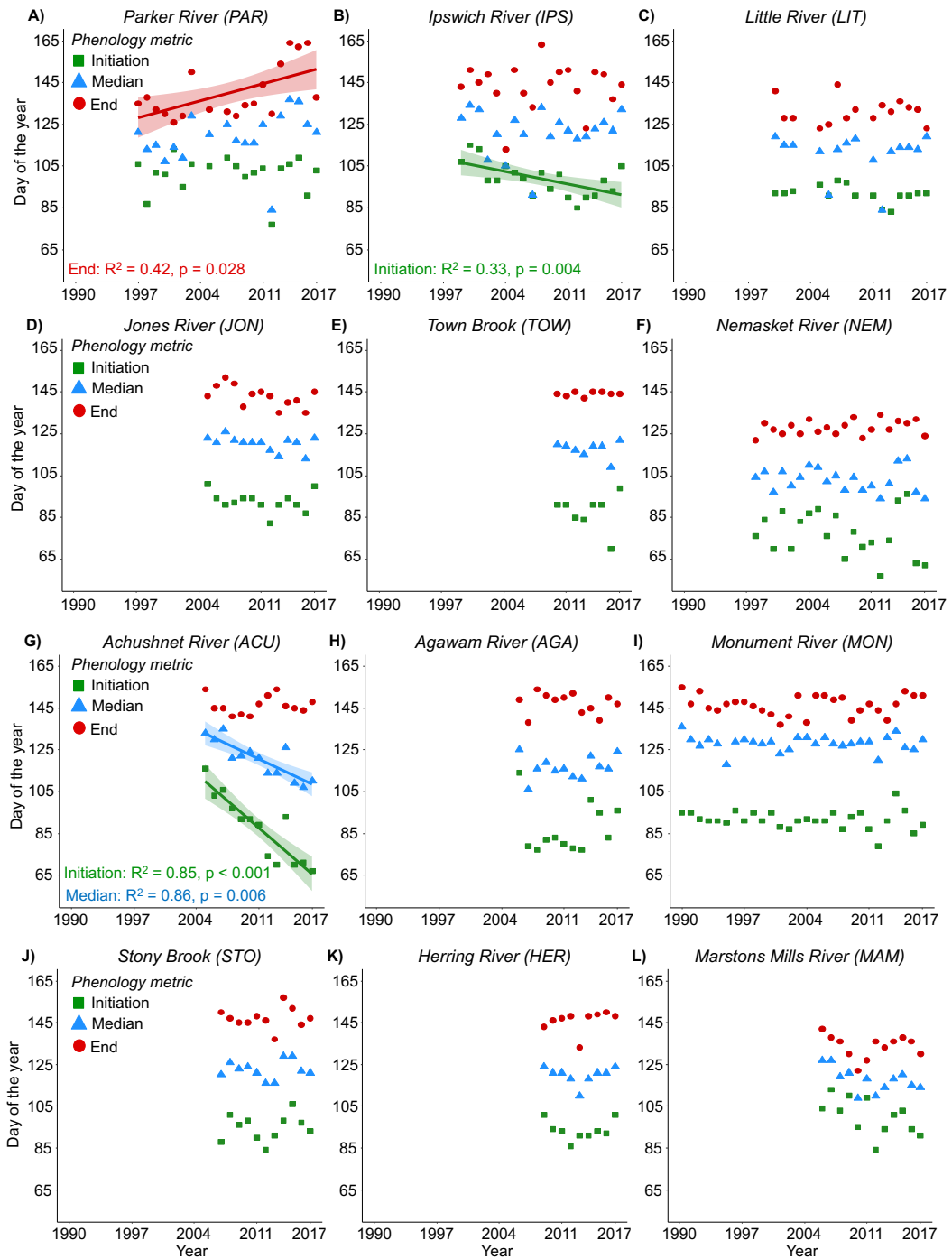
**Table 13. List of outliers in dataset of phenology metrics of adult alewife spawning migration in Massachusetts, USA. For each LMM presented in the results section, we calculated Cook's distance ("Cook's SD") and removed the ones above the threshold.**

Phenology Model	Location	Year	Response variable	Cook's SD	Cook's SD Threshold
Initiation (DOY)	ACU	2005	116	0.250	0.099
	ACU	2013	70	0.113	
	ACU	2015	70	0.107	
	ACU	2017	67	0.144	
	AGA	2006	114	0.240	
	NEM	2012	57	0.099	
	NEM	2015	96	0.231	
	NEM	2017	62	0.180	
	PAR	1998	87	0.106	
	PAR	2012	77	0.124	
	STO	2015	106	0.115	
TOW	2016	70	0.167		
Median (DOY)	ACU	2007	106	0.103	0.090
	IPS	2004	105	0.094	
	IPS	2007	91	0.295	
	LIT	2006	91	0.186	
	LIT	2012	84	0.316	
	NEM	2017	62	0.114	
	PAR	2012	77	0.417	
	PAR	2014	106	0.133	
	PAR	2015	109	0.128	
End (DOY)	HER	2013	133	0.129	0.090
	IPS	2004	113	0.352	
	IPS	2008	163	0.153	
	IPS	2013	123	0.180	
	MAM	2010	122	0.092	
	PAR	2014	164	0.241	
	PAR	2015	162	0.209	
PAR	2016	164	0.276		
Duration (days)	ACU	2013	84	0.150	0.103
	AGA	2006	35	0.153	
	AGA	2008	77	0.133	
	IPS	2004	8	0.214	
	NEM	2012	77	0.103	
	NEM	2015	34	0.110	
PAR	2016	73	0.255		

**Table 14. Summary of mixed-effects multiple regression analyses predicting phenology metrics of adult alewife spawning migration in Massachusetts, USA.**

Fixed effects	Initiation (DOY)	Median (DOY)	End (DOY)	Duration (days)
Intercept	<b>92.32 ± 1.96***</b> (47.18)	<b>117.71 ± 2.31***</b> (51.17)	<b>140.96 ± 2.12***</b> (66.41)	-250.99 ± 492.93 (0.05)
Year				0.15 ± 0.25 (0.61) 11
Fall minimum SST	-0.27 ± 0.71 (0.38) 15	-0.62 ± 0.96 (0.64) 273	0.24 ± 0.64 (0.37) 56	0.77 ± 1.15 (0.67) 15
Winter minimum SST	-0.40 ± 0.62 (0.49) 15	-0.17 ± 0.76 (0.23) 173	0.97 ± 0.93 (1.04) 106	1.81 ± 1.26 (1.43) 25
Spring minimum SST	<b>-2.82 ± 1.22*</b> (2.31) 31	-97 ± 1.31 (0.74) 273	0.59 ± 1.05 (0.56) 83	<b>3.68 ± 1.62*</b> (2.27) 25
Fall transition date	<b>-2.78 ± 1.00**</b> (2.77) 31	-1.43 ± 1.16 (1.24) 338	-0.15 ± 0.62 (0.25) 52	1.73 ± 1.43 (1.21) 23
Spring transition date	0.40 ± 1.22 (0.55) 15	0.01 ± 0.58 (0.01) 140	0.21 ± 0.56 (0.37) 52	-0.06 ± 0.64 (0.09) 8
Fall NAO	1.84 ± 1.02 (1.78) 31	-0.42 ± 0.86 (0.50) 197	-0.89 ± 0.95 (0.94) 99	<b>-3.11 ± 1.33*</b> (2.34) 25
Winter NAO	<b>-2.69 ± 1.23*</b> (2.19) 31	0.05 ± 0.98 (0.05) 191	2.06 ± 1.22 (1.69) 134	<b>4.85 ± 1.60**</b> (3.03) 25
Spring NAO	<b>1.73 ± 0.74*</b> (2.35) 31	0.28 ± 0.61 (0.47) 170	-0.07 ± 0.35 (0.21) 30	<b>-1.99 ± 0.95*</b> (2.1) 25
Annual GSI	-0.35 ± 0.61 (0.52) 15	-0.11 ± 0.56 (0.20) 144	-0.24 ± 0.55 (0.44) 50	0.26 ± 0.83 (0.31) 13
Annual Size	-0.10 ± 0.50 (0.20) 15	-0.40 ± 0.75 (0.54) 191	-0.03 ± 0.34 (0.09) 30	0.16 ± 0.72 (0.22) 11
Top model count	31	376	134	25
ΔAICc < 2				

\*\*\* p < 0.001, \*\* p < 0.01, \* p ≤ 0.05



**Figure 21. Phenology metrics of adult alewife migration in Massachusetts, USA across from 1990 to 2017 in 12 coastal streams. Run initiation (green square), median (blue triangle), and end of run (red circle) are presented for all 12 streams. Adjusted  $R^2$  and p-values are noted for significant relationships ( $p < 0.05$ ).**

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## Biography

Rebecca Dalton attended the University of Pittsburgh and graduated in 2014 with a B.A in Environmental Studies. During this time, she worked with Drs. Tia-Lynn Ashman and Matthew Koski studying sexual system evolution in wild strawberries. Since beginning her time at Duke University, she received an NSF Graduate Research Fellowship (GRFP) and a Graduate Research Internship Program (GRIP) fellowship. Her scientific publications include: (1) "Microenvironment and functional-trait context dependence predict alpine plant community dynamics", (2) "Multilocus sex determination revealed in two populations of gynodioecious wild strawberry, *Fragaria vesca* subsp. *bracteata*," and (3) "Maternal sex effects and inbreeding depression under varied environmental conditions in gynodioecious *Fragaria vesca* subsp. *bracteata*." After completing her degree, Rebecca will begin the Postdoctoral Synthesis Fellowship at the Rocky Mountain Biological Laboratory. She will work with Brian Inouye (Florida State University), Nora Underwood (Florida State University), Rebecca Irwin (North Carolina State University), Aimée Classen (University of Vermont), and David Inouye (University of Maryland).