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Effectiveness of Salmon Carcass Analogs as a Form of Nutrient Enhancement for Juvenile Coho Salmon (Oncorhynchus kisutch) in Three Lower Columbia Watersheds

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Effectiveness of Salmon Carcass Analogs as a Form of Nutrient Enhancement for Juvenile Coho Salmon (*Oncorhynchus kisutch*) In Three Lower Columbia Watersheds

By:

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A Thesis

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In Partial Fulfilment

Of the Requirements for the Degree

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Abstract

Adult Pacific salmon exhibit a form of parental care after spawning and perishing by depositing a subsidy of marine derived nutrients (MDN) that may be incorporated into the stream food web and feed juvenile salmon. Adult salmon populations have significantly declined since the late 19th century, thereby reducing the amount of MDN within Pacific Northwest Streams. This loss in nutrients within stream food webs may be limiting the growth and survival of juvenile salmon and therefore reducing the population sizes of adult salmon. One strategy to mitigate for nutrient deficiencies within a stream is the use of salmon carcass analogs (SCA), pellets composed of pulverized and pasteurized marine forage fish. We investigated the effectiveness of SCA in enhancing the size and abundance of juvenile coho salmon within a complex of three watersheds (Abernathy, Germany, and Mill Creek) that empty into the lower Columbia River near Cathlamet, WA. SCA applications occurred in the fall (2010-2013) on Germany Creek and in the spring (2013-2015) on Abernathy Creek, while Mill Creek served as a reference watershed and did not receive SCA applications. We periodically gathered samples of periphyton, macroinvertebrates, and juvenile coho (fin clips) before and after SCA application at approximately two month intervals. Juvenile coho were also sampled for fork length and weight. Samples were taken at three sites at the lower, middle, and upper extent of adult coho spawning within each watershed. During the final sampling event of each year, while juvenile coho were outmigrating, fin clips were taken at smolt traps located near each river's confluence with the Columbia River. Data from smolt traps were used to estimate the average fork length and abundance of juvenile coho during each year of this project. To evaluate the timing and extent of nutrients from SCA being incorporated into the stream food web, samples were processed and analyzed for $\delta^{15}N$, a measure of the abundance of the heavier isotope of nitrogen that occurs more abundantly in the marine environment. Seasonal trends of $\delta^{15}N$ in periphyton, macroinvertebrates, and juvenile coho, as well as seasonal trends of juvenile coho fork length and weight were compared between fertilized and unfertilized watersheds. We detected SCA effects on seasonal trends of macroinvertebrate and juvenile coho $\delta^{15}N$ for the fall and spring treatments, indicating SCA nutrients were incorporated by these communities. We detected SCA effects on the seasonal trends of juvenile coho fork length and weight for the spring treatment, but not for the fall treatment. We could not detect SCA effects on seasonal trends of periphyton $\delta^{15}N$ for either the fall or spring treatment, potentially due to smaller than needed sample sizes. Overall the effect of fall SCA application was to disrupt the seasonal trend of $\delta^{15}N$ values among trophic levels by causing an increase in $\delta^{15}N$ during the late fall/early winter when values are normally decreasing. The effect of spring SCA application was to enhance the seasonal trend, causing increases in $\delta^{15}N$ values greater than those seen in the absence of SCA applications. Comparing juvenile coho sizes and abundances between years with and without SCA application and between fertilized and unfertilized watersheds indicated that neither the fall or spring treatment had a significant effect on coho growth and

survival. Where SCA are to be used as a salmonid recovery tool, we recommend that careful watershed selection and subsequent monitoring be employed to ensure investments are worthwhile.

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Original project design was developed in part by Mara Zimmerman. I would like to highlight her constant guidance and mentorship throughout the course of this study. This project would not have been a success without her involvement.

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Table of Contents

List of Tables

List of Figures

Introduction

Adult Pacific salmon (*Oncorhynchus* spp*.)* migrate from the ocean back to their natal streams to spawn and perish, thereby depositing a subsidy of nutrients from the fertile North Pacific Ocean to the comparatively nutrient-poor freshwater and terrestrial ecosystems (Naiman et al. 2002, 2009). In Pacific Northwest streams, salmon-borne marine-derived nitrogen may account for as much as 20.7 percent of the total nitrogen in periphyton (mixture of autotrophic and heterotrophic organisms), as much as 24.8 percent in macroinvertebrates, and 30.6 percent within the body tissue of juvenile salmon (Bilby et al. 1996). From the late 19th century to the present, salmon biomass across their historical range has been reduced from approximately 160-226 million kilograms to 11.8-13.6 million kilograms, representing a net loss of 93-94 percent (Gresh et al. 2000). Without the historical magnitude of this annual influx of marine-derived nutrients (MDN), the productivity of salmon-bearing watersheds has potentially been reduced. Juvenile salmon rely on their stream's food-web to sustain them for as long as three years after they emerge from the gravel until they migrate downstream to saltwater (Sandercock 1991). Because of this reliance on lower trophic levels, reduced populations of primary producers and primary consumers in the freshwater environment can have a dramatic impact on growth and survival rates of salmon fry and parr.

MDN have been shown to contribute to the overall productivity of freshwater and terrestrial ecosystems (Helfield and Naiman 2001, Helfield and Naiman 2006). Contributions to stream productivity from MDN vary on a seasonal basis in Pacific Northwest aquatic systems depending on the run timing and numbers of returning adult

salmon and the feeding habits of aquatic organisms (Reichert et al. 2008). A bottom-up trophic cascade model offers an effective explanation of the pathways through which MDN reach juvenile salmon (Kiernan et al. 2010). Periphyton has been shown to respond to varying inputs of nutrients (Zhang and Mei 2013). Additional inputs of MDN would be expected to produce a corresponding increase in periphyton production. Higher trophic levels, such as macroinvertebrates and fish, may also experience corresponding increases in growth or abundance either due to direct consumption of the nutrient source or by indirect consumption of lower trophic levels that have directly consumed the nutrient source (Johnston et al. 1990). However, the addition of nutrients to the stream food web does not consistently result in increases in productivity of the stream food web. For example Davis et al. (2010) observed nutrient enrichment increasing production of primary consumers, but not macroinvertebrate predators within the stream. The benefit of the addition of nutrients was truncated at the primary consumer trophic level with no corresponding benefit to secondary consumers due to an increase in large, predator-resistant prey. The MDN may also bypass certain trophic levels, as macroinvertebrates and fish may feed directly on the source of MDN (e.g. decaying salmon carcasses), circumventing the trophic levels beneath them (Kiernan et al. 2010). For example, in a southwest Washington stream over 60 percent of stomach contents by mass in juvenile coho (*Oncorhynchus kisutch*) were of salmon egg and carcass material after salmon carcasses were placed within the stream during the fall and winter (Bilby et al. 1998).

Salmon are unlikely to rebound to historical run sizes in the near future, so strategies have been developed and implemented to mitigate for MDN deficiencies in streams. One technique uses treatments of inorganic fertilizer, but is typically used to enhance primary producers at the bottom of the food web (Perrin et al. 1987). Another technique involves the strategic placement of salmon carcasses in and along the stream (Bilby et al. 1998, Wipfli et al. 1998). Typically, carcasses are acquired from local salmon hatcheries and deployed at a density that attempts to mimic historical salmon escapements. There are at least three issues that complicate the effectiveness of carcass enhancement. First, the availability of carcasses at any given hatchery varies from year to year in response to variation in returning adult salmon. There may not be enough fish to satisfy carcass saturation goals. Secondly, watersheds lacking a hatchery program treated with out-of-basin carcasses become susceptible to diseases transmitted from out-of-basin populations. Lastly, there are logistical challenges to transporting and dispersing thousands of 2-9 kilogram salmon carcasses. An alternative strategy is to transport and disperse salmon carcass analogs (SCA), which consist of marine fish material that has been pasteurized and then ground and shaped into approximately 2 – 5 cm diameter pellets (Pearson et al. 2007). These analogs can act as a safe and effective substitute for actual carcasses because the analogs are consistent in availability, harbor no known diseases, and are easier to distribute. However studies have shown mixed results with respect to the benefits of SCA as a source of nutrient enhancement (Wipfli et al. 2004, Kohler et al. 2012).

Among the Pacific salmon, coho are a good subject for testing SCA effectiveness because of their relatively long residence times in freshwater and their wide spatial dispersals (Bilby et al. 1998, Pollock et al. 2004). After emergence, the vast majority of coho spend between one and two years in fresh water before outmigrating to the marine environment in the spring (Quinn 2005). Coho juveniles are also widely dispersed within their watersheds. Adult coho are able to access spawning grounds inaccessible to other salmonid species because stream flows are typically greater during the late fall months when coho return to spawn (Quinn 2005). As a result, juvenile coho have year-round access to nutrient sources from the headwaters to the mouth of each watershed.

Although declining salmon runs have certainly reduced the amount of MDN delivered to freshwater systems over the past century, caution may be warranted before concluding that nutrient deficiencies are the most significant current bottleneck to juvenile salmon production in Pacific Northwest streams (Collins et al. 2015). For example, Lessard et al. (2009) found that macroinvertebrate abundance did not increase in the presence of an MDN influx in several Alaskan watersheds. Within the Smith and Klamath River watersheds, Wilzbach et al. (2005) reported that the addition of salmon carcasses did not detectably increase the biomass or density of juvenile salmonids, while increasing the amount of available light by opening sections of the riparian canopy did increase juvenile salmonid biomass. If this is the case within our study site, juvenile salmonid food sources may not vary based on availability of MDN.

There are a number of factors other than the availability of nutrients that may affect growth and survival of juvenile coho, especially where land use practices have altered suitable habitat and flow regimes. Habitat alteration effects on juvenile salmonid populations may negate the benefits of an increased subsidy of MDN. For example, if availability of off-channel habitat, which acts as refuge for juvenile coho (Sandercock 2012), is limiting juvenile salmon survival, an increase in physical growth of fish in response to SCA placement in the watershed may not ultimately result in greater abundances of juvenile coho. Another freshwater factor that may currently influence juvenile coho growth and survival is summer temperature. Myrvold and Kennedy (2014) demonstrated that higher summer temperatures negated the competitive advantage of larger body size in a population of age-0 steelhead. That is, as stream temperatures increased, larger fish had a greater metabolic cost than smaller fish. Consequently, temperature can act as the main bottleneck limiting growth and survival. If stream nutrient and food resources do not currently limit salmon growth or survival, then investment in nutrient enhancement strategies may not be worthwhile as the maintenance of artificial levels of MDN in freshwater systems represents a long-term restoration strategy requiring continued annual treatments.

The goal of our research was to elucidate the extent to which nutrients from SCA applications are incorporated into the aquatic food web and the effectiveness of SCA applications in enhancing juvenile coho growth and production at the watershed scale. We evaluated the food web response to one set of SCA applications in the fall and a second set of SCA applications in the spring. We assessed the extent to which SCA

were incorporated into the stream food web by tracking the isotopic signatures of nitrogen in periphyton, macroinvertebrates, and juvenile coho. We determined the number and body size of coho smolts to evaluate if a population-level response occurred. By quantifying responses from the stream food web and juvenile coho population, we evaluated whether SCA represent a practical and effective habitat restoration tool to be applied in other, similar situations.

Methods

Study Location

The study location consisted of three adjacent Columbia River tributaries (Mill, Abernathy, and Germany Creeks) that enter the Columbia River 54-56 miles from the Pacific Ocean near the town of Cathlamet, Washington. The three watersheds have similar spatial areas and maximum elevations (Table 1, Figure 1). Land composition is classified as coastal temperate forests with predominantly Douglas fir (*Pseudotsuga menziesii*) in the uplands and red alder (*Alnus rubra*) in the riparian zones. The majority of land ownership within the Mill Creek and Abernathy Creek watersheds is public, while land ownership in the Germany Creek watershed is nearly all private. The upper portions of each watershed are managed for timber harvest, while the lower portions support a mixture of residential and agriculture uses. Hydrology is rain-dominated with seasonal precipitation characterized by wet winters and dry summers. The most substantial high flows occur in the fall and winter months and typically take place when a large rain event follows a snow event, resulting in the combined discharge from precipitation and melting snow. All three tributaries support populations of Chinook (*O. tshawytscha*), coho, and chum salmon (*O. keta*) as well as steelhead (*O. mykiss*) and cutthroat trout (*O. clarkii*; Washington Department of Fish and Wildlife 2012).

These watersheds form the Lower Columbia stream complex that is part of the statewide Intensively Monitored Watersheds (IMW) project (Bilby et al. 2004, Bennett et al. 2016). The IMW effort aims to evaluate the effectiveness of salmon habitat

restoration projects by measuring various fish metrics at a population scale, including juvenile salmonid growth, survival, and abundance (WDFW 2012). Each IMW complex has at least one treatment stream and one reference stream. Habitat restoration projects are conducted within treatment streams, but not within reference streams. Reference streams are similar in size and located near to the treatment streams. Within the Lower Columbia IMW, Germany and Abernathy Creeks are designated as treatment streams and Mill Creek is designated as the reference stream.

Analog Applications

Our project included seasonal applications of SCA: fall applications were applied in Germany Creek and spring applications were applied in Abernathy Creek. Fall applications were applied between September and November for four consecutive years (2010-2013). Spring applications were applied between May and June for three consecutive years (2013-2015). Analogs used in the fall application during 2010 were manufactured by Skretting USA (Tooele, UT; T. Meyers, *pers. comm*.). All other analogs used in the project were manufactured by NutraDine, Inc.(Healdsburg, CA). In addition to Mill Creek, two tributaries (Cameron and Wiest creeks) within the Abernathy Creek watershed were held as secondary reference tributaries (i.e., no SCA additions) to evaluate responses to spring applications. Watersheds (Abernathy and Germany) that received SCA applications will be referred to as fertilized watersheds. Mill Creek and the Abernathy tributaries that did not receive SCA will be referred to as the unfertilized watersheds and the unfertilized tributaries, respectively.

Analogs were distributed throughout the anadromous reaches of the mainstem of each fertilized watershed (Table 2). Application rates of the SCA were calculated based on the total mass of SCA applied to each watershed, the known lengths of the stream where SCA were applied and average bankfull widths of the mainstem within each watershed. SCA were applied at rates ranging from 0.065 to 0.134 kg/m^2. Since nutrients are approximately five times more concentrated in SCA than in salmon carcasses, SCA applications were equivalent to carcass densities ranging from 0.33 to 0.67 kg/m^2. Bilby et al. (1998) demonstrated that densities of carcasses greater than 0.15 kg/m^2 do not further enrich nitrogen content within the body tissues of juvenile salmon. Since our equivalent SCA densities were well above this saturation threshold, we expected to observe a response if MDN entered the stream food web.

The isotopic composition of N in SCA differed from that of actual salmon carcasses ($\delta^{15}N$ = 10.4‰ vs. 14.2‰), but nonetheless differed even more significantly from those of alternate sources of nitrogen, to the extent that SCA enrichment of freshwater biota should be readily detected (Bilby et al. 1996). For example, in the absence of MDN influence, leaf litter from terrestrial vegetation typically has $\delta^{15}N$ values ranging from approximately – 1 to – 4 (Helfield and Naiman 2001, 2002). See below for further explanation of $\delta^{15}N$ values.

Sampling Schedule

Sampling of the stream food web occurred at three sites (upper, middle, and lower) within each watershed plus one site in each of the two secondary unfertilized tributaries of Abernathy Creek. Each site consisted of a stream reach no longer than 50 m in length and contained at least one riffle-pool sequence. In Mill Creek, sampling sites were located 1800, 6500, and 18700 m, respectively, from the confluence with the Columbia River. The lengths of stream below these sites comprise 9%, 33%, and 94% of total coho distribution in the unfertilized mainstem, as determined from annual spawner surveys (data provided by T. Johnson, WDFW) Abernathy Creek sampling sites were located 200, 7600, and 14500 m from the confluence representing 2%, 48%, and 91% of total coho distribution. Germany Creek sampling sites were located 400, 9500, and 16500 m from the confluence representing 2%, 54%, and 93% of total coho distribution. The secondary unfertilized site within Wiest Creek was located 6700 m upstream from the confluence with the Columbia River. The site within Cameron Creek was 1900 m from the confluence with the Columbia River.

For fall SCA applications in Germany Creek, sampling commenced prior to analog placement and occurred every other month through the April-June sampling event the following spring, for a total of six sampling events per year (Table 3). There were only three sampling events associated with the 2010 SCA application (August/September, November, and April-June). From the 2011 SCA application onward, the full sampling schedule was employed. For spring SCA applications in Abernathy Creek, pre-application periphyton and macroinvertebrate samples were collected prior to SCA

application and sampling continued every other month through the following April-June sampling event. Juvenile coho sampling associated with spring SCA applications commenced six weeks after analog placement and then followed the same schedule as the other food web sampling. Juvenile coho sampling prior to SCA application in Abernathy was not feasible due to a lack of parr-sized coho juveniles large enough to survive fin tissue clips in February/March. The April/May periphyton/macroinvertebrate sampling event acts as a pre-application sample for the subsequent year and the last sampling event for the previous year. Since Mill Creek acts as the unfertilized watershed for both fall and spring treatments, it was sampled during every sampling event.

During each sampling event we collected periphyton, macroinvertebrates, and juvenile coho from all sites within each watershed. One exception is the final sampling event of each schedule (April-June) during which coho emigrating from all areas of the watershed were captured and sampled at a rotary screw smolt trap located near the confluence of each watershed with the Columbia River. Periphyton and macroinvertebrates were still collected at all sites during the April-June sampling event. Sampling typically occurred in the same location within each site during each event, but the sampling locations within each site were adjusted to obtain the necessary samples if changes in habitat characteristics occurred.

Sampling Protocol

Periphyton

Periphyton is made up of complex assemblages of autotrophic and heterotrophic organisms attached to the stream substrate, including algae, cyanobacteria, microbes, and detritus (Allan and Castillo 2007). We collectively refer to this mixture as periphyton. During each sampling event periphyton was removed from several rocks in the same location at each site. A stiff nylon brush was used to scrub periphyton and organic matter off each rock from the upper surface exposed to daylight. The rock and scrub brush were rinsed in a plastic container filled with approximately 100 ml of water from the stream. This process was repeated until the water in the container was a tea-colored brown, indicating enough matter had been collected to analyze the isotopic composition of nitrogen in the sample. Typically, 3-7 approximately fist-sized rocks were required. Water was poured from the container into a smaller plastic container with some head space for freezing. The small plastic container was capped, labeled with site number and date, stored on ice, and processed within one week.

Macroinvertebrates

Macroinvertebrates were collected with a D-frame net. The goal was to acquire a mass of aquatic macroinvertebrate material representing diverse taxonomic groups. During each sampling event, the net was placed with its bottom flush against the stream bed downstream of a riffle. Substrate in the riffle was overturned by foot so as to wash

benthic macroinvertebrates into the net. For reaches with smaller substrate (small cobble, gravel, sand), one or two D-frame net samples from the same riffle were collected from each site. For reaches with larger substrate (larger cobble), three or four D-frame net samples from the same riffle were collected from each site in order to obtain enough macroinvertebrate material. During each sampling event, all of the D-frame net samples were amalgamated into one sample per site and emptied into a container filled with stream water. Large stoneflies were placed into separate, individual vials so that they did not consume other macroinvertebrates in the sampling container. The macroinvertebrate containers were capped, labeled with site number and date, and stored on ice. Samples were processed within one week and sorted into functional feeding groups (e.g. filter-feeders, collector-gatherers, predators, scrapers, and shredders), as defined by Vannote et al. (1980), prior to stable isotope analysis.

Fish

Fish were collected using electrofishing, stick seines, minnow traps, and screw traps. During the late summer sampling events, fish were collected with a backpack electrofisher. During the fall and winter sampling events, fish were collected with stick seines or minnow traps. In the spring sampling events, fish were collected from screw traps located at the mouth of each watershed.

At each site, fish were collected from habitat with a depth of at least 0.3 m and sufficient structure or cover. This was generally limited to pools or off-channel zones with woody

debris, leaves, or overhanging structure. Electrofishing occurred across the entire site. Fish were captured after being stunned by the electrofisher or were herded into a block net located at the downstream end of the site. Seining was typically effective in pools without structure. Minnow traps were a more effective option in current speeds greater than a casual walking pace and in habitat with too much structure to seine effectively. Locations selected for using traps were similar to those where seining was used, but sampling in areas with greater amounts and sizes of wood or boulders was possible. Other desirable features included undercut banks and debris jams. Traps were baited with approximately one-ounce portions of sharp cheddar cheese and deployed for up to 24 hours.

Fish were sampled using a nonlethal method previously shown to be effective for stable isotope analysis (Sanderson et al. 2009). A small (~2 mm length) upper caudal clip was taken as a tissue sample from each fish. During each stream sampling (i.e., non-smolt trap) event, tissue was collected from a minimum of 15 and a maximum of 30 coho parr at each site. During each smolt trap sampling event, up to 10 coho samples per week were collected over an 8 to 10 week period. Additional information taken from each coho included fork length and weight. Tissue samples were placed in vials filled with stream water and frozen within six hours. They were processed for stable isotope analysis at a later date.

Stable Isotope Analysis

Naturally-occurring stable isotopes provide an effective tracker for the movement of MDN through the food web (Naiman et al. 2002, 2009). Since ratios of ^{15}N to ^{14}N are greater in nitrogen from the marine environment than from freshwater and terrestrial sources, the ^{15}N stable isotope works well as an indicator of MDN enrichment within freshwater food webs (Schoeninger et al. 1983, Owens 1987). Ratios of ^{13}C to ^{12}C are similarly greater within marine sources versus freshwater and terrestrial sources (Kline et al. 1993). Nitrogen stable isotope ratios are expressed as $\delta^{15}N$ values, indicating the per-mil deviation in ^{15}N:^{14}N ratio relative to a recognized isotopic standard, atmospheric N^2, whereas carbon stable isotope ratios are expressed as $\delta^{13}C$ values, indicating the per-mil deviation in ^{13}C:^{12}C relative to the Pee Dee Belamnite standard (Nadelhoffer and Fry 1994). The practicality of using stable isotopes to track diet changes in salmonids was verified by Williamson (2005), who found ^{15}N:^{14}N ratios in juvenile salmonid tissue increased with corresponding increases in ^{15}N enriched food. Additionally, $\delta^{15}N$ values can be investigated in macroinvertebrates and periphyton to determine whether MDN are used by multiple trophic levels within the stream food web (Bilby et al. 1996). $\delta^{13}C$ values can be used to delineate the relative contributions of marine food sources to an organism.

All samples were dried and ground into a fine (i.e., $\leq$212 µm) powder for analysis. $\delta^{15}N$ and $\delta^{13}C$ values were analysed using an isotope ratio mass spectrometer at Cornell University.

Chinook Carcass Density

A potential confounding variable when evaluating the effects of SCAs is the uptake of nutrients from natural salmon carcasses in the stream environment. In all three watersheds that encompass our project, Chinook salmon spawn in the highest densities compared to other salmonid species, and they are limited to the lower reaches of these watersheds due to lower discharges during early fall when they are spawning. In contrast, coho and steelhead spawn in much lower densities and spawning is spread out over a greater area of each watershed. Chum salmon are also known to generally spawn in high densities, but spawner survey observations and smolt trap collections indicated that the presence of chum salmon in these watersheds was negligible for the duration of our study (data provided by T. Johnson, WDFW).

The influx of nutrients provided by coho, chum, or steelhead is unlikely to explain $\delta^{15}N$ variation or influence differences in fertilized watershed and unfertilized watershed response variables because it is relatively small. On average, the amount of nitrogen available via SCA was 5-10 times the amount of nitrogen available from salmonid carcasses (Table 4). However, Chinook carcass densities may occur at high enough densities to influence the flow of nitrogen into the stream food web and therefore affect our interpretation of response variables measured in our study. Because MDN from Chinook carcasses were available at the lower and middle sampling sites within both the fertilized and unfertilized watersheds, carcass density for Chinook was incorporated into the analyses. To test whether carcass densities differed at sampling sites in the

fertilized versus unfertilized watersheds, we calculated Chinook carcass densities within 100 m upstream and downstream of each sampling site. We assumed size of the Chinook did not significantly differ among watersheds and expressed densities in terms of carcasses per m. Calculations were an index of relative Chinook densities as they were based on carcasses observed during spawning grounds surveys and were not extrapolated to an estimate of total Chinook escapement. In the secondary unfertilized tributaries of the spring treatment, Chinook carcass densities were zero, since low flows made these streams inaccessible to Chinook in each year of the project.

To evaluate whether differences existed among sampling sites and between watersheds, we fitted an ANOVA model with carcasses per m as the response variable and site and watershed as predictor variables. All upper sites were excluded from carcass density analysis since Chinook spawners were never in these upper sites. The density of Chinook carcasses did not significantly vary between watersheds or sampling sites (Tables 5 and 6). The density of Chinook carcasses was added to the analysis in order to understand the importance of natural spawning carcasses as a source of MDN in our study streams and to disentangle the food web response to natural carcasses versus SCA. Because densities did not significantly vary between the fertilized and unfertilized watersheds, the presence of Chinook carcasses did not confound our evaluation of SCA by introducing a greater source of MDN into any of the watersheds. Therefore, if $\delta^{15}N$ values within the food web are elevated in one watershed relative to another watershed, Chinook carcass densities cannot explain the difference.

Data Analysis

If SCA additions to the watershed are to have an effect on juvenile coho salmon we would expect to see changes on an individual fish level and at the population level. Individual fish from fertilized watersheds should show greater growth rates (length and weight) with tissue more enriched with ^{15}N than individual fish from the unfertilized watershed. These individual responses should translate into a population level increase in abundance at the smolt stage because larger fish typically have greater survival rates (Holtby et al. 1990, Sandercock 1991).

Response variables analyzed included periphyton, macroinvertebrate, and juvenile coho $\delta^{15}N$ as well as juvenile coho fork length (mm) and weight (g). For each response variable, results were plotted as the mean plus or minus one standard error of values observed during each sampling period. Values from fertilized and unfertilized watersheds were plotted separately.

We used linear mixed effects models in order to identify factors that help explain variations in periphyton, macroinvertebrate, and juvenile coho $\delta^{15}N$ values and juvenile coho size metrics. The fixed factors were watershed (e.g. fertilized vs. unfertilized), sample period, watershed-sample period interaction, and Chinook density. Watershed represents levels from each separate watershed in the project (Abernathy, Germany, and Mill Creeks). The two secondary unfertilized tributaries were also combined into a single level. Each level of sample period represents all values taken across all sites and

years during that sample period. Chinook densities were added in the sample period immediately following SCA application assuming that carcasses were not available before or following that time period. For the model evaluating macroinvertebrate $\delta^{15}N$, macroinvertebrate functional feeding group was added as a fixed factor. The random factor in the periphyton and macroinvertebrate models was site, with year acting as replication. For models evaluating coho response variables, year was a random factor with individual fish acting as replicates.

Modeling was done using R statistical software and the packages lme4 and MuMIn (Bates et al. 2015, Barton 2016). All models were tested for heteroscedasticity by observing residuals versus fitted values plots. Departure from normality was evaluated by generating and observing normal quantile plots. Both equal variance and normality assumptions were met by the data. To evaluate the predictive capacity of each model, the goodness of fit of fixed factors versus all factors (fixed and random) was calculated using the method developed by Nakagawa and Schielzeth (2013). The total R-squared for each model was produced to determine the relative importance of fixed and random factors. The marginal R-squared values represent evaluation of the model with only fixed factors while conditional R-squared values represent evaluation of the model with both fixed and random factors. If conditional R-squared values were greater than the marginal R-squared values, then including random factors improved the model's fit.

We evaluated the statistical significance of each fixed factor in the model using a likelihood ratio test where the full model was iteratively compared with reduced nested

models by removing the factor being evaluated. If the likelihood ratio test was statistically significant (alpha = 0.05), then the factor was retained. Final models retained only factors that were significant predictors of the response variable ($\delta^{15}N$, coho length, or coho weight).

To evaluate pairwise comparisons between sample periods, we calculated and plotted standard error for each mean. If two standard errors did not overlap, we concluded the differences in means were not likely due to random variation. Post-hoc power analysis evaluated the statistical power associated with sample size for each analysis and was performed using the software package G*Power (Faul et al. 2007).

Population Level Analysis

Population level analysis was set up as a before-after-control-impact (BACI) design (Roni et al. 2005). This design compares response variables between years before and after treatment as well as between control and experimental study sites. For the purposes of our study, ‘after’ years represent years when SCA application occurred, and ‘before’ years represent years when SCA application did not occur. Working under the assumption that SCA applications in a given year did not affect size and abundance of coho broods from future years (e.g., SCA application in the fall of 2013 did not affect juvenile coho outmigrating in the spring of 2015), we included years after SCA applications had ceased as ‘before’ years. For fall treatment analyses, ‘before’ years include 2001-2010 and 2015-2016, and ‘after’ years include 2011-2014. For spring

treatment analyses, 2001-2013 represent ‘before’ years and 2014-2016 represent ‘after’ years.

Population level responses by juvenile coho were evaluated by comparing smolt lengths and abundances in fertilized versus unfertilized watersheds and between years with and without SCA applications. Coho smolt lengths (data provided by T. Johnson, WDFW) were measured on a weekly basis at each screw trap throughout the spring outmigration period. Coho smolt abundances (data provided by T. Johnson, WDFW) were estimated using a mark-recapture abundance methodology (Volkhardt et al. 2007). Coho smolt weights were not available in the pre-application years and were therefore not included in these analyses. If a population level response occurred, we would expect that differences in smolt lengths or abundances between the fertilized and unfertilized watershed would be greater in magnitude during years with SCA application than during years without SCA application.

Results

Overall Food Web

The three trophic levels (primary producers, macroinvertebrates, and fish) that make up the food web within our study watersheds show clear separation when comparing $\delta^{15}N$ and $\delta^{13}C$ values (Figure 2). Larger $\delta^{15}N$ values represent a combination of higher trophic levels (due to fractionation) and diets more rich in MDN. Larger (less negative) $\delta^{13}C$ values indicate diets more rich in marine food sources versus freshwater or terrestrial sources. Alder leaves represent a nearly entirely terrestrial input (low $\delta^{13}C$) and as primary producers they are at the lowest trophic level (low $\delta^{15}N$) and have minimal incorporation of MDN because alder trees fix their own atmospheric nitrogen although alder trees can use nitrogen from soil containing MDN. Periphyton has similar $\delta^{15}N$ values to alder leaves, but higher $\delta^{13}C$ values. This indicates minimal incorporation of MDN, but potentially the presence of heterotrophic organisms in the periphyton community. Macroinvertebrates (primary consumers) have higher $\delta^{15}N$ values than primary producers indicating nitrogen fractionation and potential incorporation of MDN. Fish (secondary consumers) have even higher $\delta^{15}N$ and $\delta^{13}C$ values representing food sources potentially influenced by the presence of MDN and of higher trophic levels. In some cases, higher $\delta^{15}N$ or $\delta^{13}C$ values may be partially explained by fractionation due to biogeochemical processes in soils or rivers such as denitrification (Nadelhoffer and Fry 1994).

Fall Treatment

1. Periphyton $\delta^{15}N$

The final periphyton model for the fall SCA application includes only watershed as a statistically significant predictor of periphyton $\delta^{15}N$ (Tables 7 and 8). The $\delta^{15}N$ of periphyton in the unfertilized watershed (mean = 0.150, SD = 2.163) was higher than in the fertilized watershed (mean = -1.170, SD = 2.163. Sampling period, Chinook density, and the watershed-sampling period interaction term were not significant factors. This was the only model where a sample period main effect, reflecting a change in periphyton $\delta^{15}N$ over time, was not detected. The periphyton model had the lowest goodness of fit R-squared value compared to other fall treatment models (Table 9). There was no difference between the marginal and conditional R-squared values, indicating fixed factors alone explained variation in periphyton $\delta^{15}N$.

For periphyton, the $\delta^{15}N$ values in fertilized and unfertilized watersheds were most similar in the four months following SCA application, but $\delta^{15}N$ values in the fertilized watershed were lower than in the unfertilized watershed at other times (Figure 3). This observed difference in seasonal patterns between watersheds suggests a watershed-sample period interaction effect, but neither sample period nor the interaction term were statistically significant using likelihood ratio tests. The non-significant result was potentially due to low statistical power. Periphyton samples from multiple rocks were amalgamated to produce one sample per site or three samples per sampling period, which is many fewer total samples available for analysis compared to the macroinvertebrates or juvenile coho. The result is greater variability in periphtyon $\delta^{15}N$

values, as reflected by the large standard errors. Post-hoc power analysis indicates relatively low statistical power at 0.11, indicating we had only an 11 percent chance of detecting a statistically significant difference between treatments given our sample size. Therefore, the periphyton $\delta^{15}N$ in the fertilized watershed may have increased following the SCA application, but we could not detect it statistically.

2. Macroinvertebrate $\delta^{15}N$

The final macroinvertebrate model for the fall SCA application included watershed, sample period, watershed-sample period interaction, and functional feeding group as fixed factors (Tables 7 and 12). Including functional feeding group as a factor significantly improved the goodness of fit, increasing the marginal R^2 value from 0.280 to 0.462 (Table 9). The macroinvertebrate $\delta^{15}N$ model for the fall SCA treatment more accurately predicted $\delta^{15}N$ values when compared to the periphyton model. Random effects did not improve model fit.

Macroinvertebrate $\delta^{15}N$ values changed among sampling periods, and the pattern of change differed between the two watersheds (Figure 4). The difference in seasonal trends (i.e., changes in $\delta^{15}N$ values among sampling periods) is reflected in the significant interaction effect between sampling period and watershed, which suggests the SCA affected the seasonal uptake of $\delta^{15}N$ among the macroinvertebrate feeding groups. Prior to SCA application, macroinvertebrate $\delta^{15}N$ values were lower in the fertilized watershed than in the unfertilized watershed. For the two sampling periods

following SCA application (November, December), macroinvertebrate $\delta^{15}N$ values were similar between the two watersheds reflecting an increase in $\delta^{15}N$ values in the fertilized watershed relative to the unfertilized watershed. In the final two sampling periods (February, April-June), macroinvertebrate $\delta^{15}N$ values diverged again with the $\delta^{15}N$ values in the unfertilized watershed remaining constant and the $\delta^{15}N$ values in the fertilized watershed decreasing over this time period.

Similar to the periphtyon, the overall macroinvertebrate $\delta^{15}N$ values were greater within the unfertilized watershed (mean = 2.865, SD = 1.841) than in the fertilized watershed (mean = 1.030, SD = 2.177 SD, Tables 13 and 14). Seasonal patterns in the macroinvertebrate $\delta^{15}N$ values were highest during the month of November (mean = 2.716, SD = 2.209) and lowest during the April-June sample period (mean = 1.425, SD = 2.343). During July, August/September, and April-June values were similar.

Differences among functional feeding groups were important in describing macroinvertebrate $\delta^{15}N$ values. We identified five feeding groups within our samples: filter-feeders, collector-gatherers, predators, scrapers, and shredders. Predators had the highest $\delta^{15}N$ values (mean = 3.615, SD = 2.284) while collector-gatherers had the lowest (mean = 1.515, SD = 2.043, Table 15). The relative abundance of each functional feeding group in our collection varied among sampling periods. In some cases, no representatives of a functional feeding group were observed in any year during a particular sampling period. For example, no filter feeders were observed at Germany Creek in July. In other cases, only one year had a particular functional feeding

group present. Because of these smaller sample sizes, some values do not have a standard error displayed or are missing values entirely from a specific sample period.

With the exception of predators, each functional feeding group displayed a seasonal pattern of $\delta^{15}N$ values similar to that of the combined macroinvertebrate community (Figures 5-9). Predator samples were only collected once in the first post-application sampling period (Nov) and never in the second post-application sampling period (Dec). Predator samples collected during the third post-application sampling period (Feb) had $\delta^{15}N$ values that appeared to be higher than the pre-application values, so it is possible that there was an increase in predator $\delta^{15}N$, but we were unable to detect it due to low sample size. Filter feeders experienced a significant increase in $\delta^{15}N$ following SCA application, but the magnitude of this increase was less than was observed for other functional feeding groups. Fertilized watershed filter feeder $\delta^{15}N$ values did not appear to change after SCA application, but because only one sample was collected in both February and the April-June sampling period we cannot determine the trend after December.

The largest post-application increases in $\delta^{15}N$ values within the fertilized watershed occurred with gatherers, scrapers, and shredders ($\geq$2‰). The post-application fertilized watershed samples (except shredders) all show a similar pattern: an increase in $\delta^{15}N$ values is followed by decreases through the spring. Unfertilized watershed values did not display the same magnitude of seasonal change. The exception was with fertilized watershed shredders, but that could be because we only collected one sample for the

third and fourth post-application fertilized watershed sampling periods and did not have enough observations to detect a decrease during this time period. With gatherers and scrapers, the $\delta^{15}N$ values in the spring are not significantly different than the values immediately preceding SCA application.

In all cases, macroinvertebrate $\delta^{15}N$ values in the unfertilized watershed were greater than fertilized watershed $\delta^{15}N$ values before SCA application. With the exception of scrapers, macroinvertebrate $\delta^{15}N$ values in the unfertilized watershed did not appear to differ between sampling periods before and after SCA application. Among the sample periods following SCA application, there was either no detected difference or a general decrease in unfertilized watershed $\delta^{15}N$ values. Unfertilized watershed shredders were an exception as there appeared to be an increase in $\delta^{15}N$ values between February and the spring. Overall, fertilized watershed combined macroinvertebrate $\delta^{15}N$ values and individual feeding group $\delta^{15}N$ values increased following SCA application to a level comparable to unfertilized watershed values, but decreased during the post-application period so that by the spring they had returned to pre-application levels.

3. Juvenile Coho $\delta^{15}N$

The juvenile coho $\delta^{15}N$ model for the fall SCA treatment included sample period, watershed-sample period interaction, and Chinook density as fixed factors. Fixed factors explained most of the variance relative to the random effects (Tables 7, 9, and 16). The model predicting $\delta^{15}N$ for the fall SCA treatment had the lowest goodness of fit

R-squared value among the juvenile coho models (Table 6). There was no difference between the marginal and conditional R-squared values indicating fixed factors alone explained variation in juvenile coho $\delta^{15}N$.

Seasonality (sample period) was an important factor in juvenile coho $\delta^{15}N$ for both the fertilized and unfertilized watersheds, but the seasonal patterns differed between watersheds. In both the fertilized and unfertilized watersheds, juvenile coho $\delta^{15}N$ generally increased over time both before and following SCA application (Figure 10). For the first three sampling periods (two pre-application, one post-application), juvenile coho $\delta^{15}N$ values were greater in the unfertilized watershed than in the fertilized watershed. By December (two months after the fall SCA application), juvenile coho $\delta^{15}N$ values in the fertilized watershed were greater than those in the unfertilized watershed due to a relatively large decrease of coho $\delta^{15}N$ from the previous sampling period in the unfertilized watershed. In comparison, juvenile coho $\delta^{15}N$ values in the fertilized watershed were nearly identical between November and December (i.e., significant watershed-sample period interaction effect). Juvenile coho $\delta^{15}N$ values in the February and April-June sample periods did not differ between the fertilized and unfertilized watersheds.

Overall, juvenile coho $\delta^{15}N$ values were largest in February (mean = 7.843, SD = 2.159) and were lowest during the previous July (mean = 3.924, SD = 1.394, Table 17). Values were similar between November and April-June. The presence of Chinook carcasses in both the fertilized and unfertilized watersheds was positively correlated with the $\delta^{15}N$

values of juvenile coho (Table 18). At sites and sample periods where Chinook carcasses were present, juvenile coho $\delta^{15}N$ values were greater (mean = 7.655, SD = 2.575) than juvenile coho $\delta^{15}N$ values at sites and sample periods when Chinook carcasses were not present (mean = 6.736, SD = 1.682, Figure 11)

4. Juvenile Coho Size

The final models predicting juvenile coho size (fork length and weight) in response to the fall SCA application include watershed, sample period and watershed-sample period interaction as fixed factors (Tables 7, 9, 19, and 20). The length and weight models had similar goodness of fits (Table 6). These fixed factors explained most of the variance relative to the random effects. Juvenile coho size (length and weight) increased over time after SCA application in both the unfertilized and fertilized watersheds (Figure 12 and 13). Coho sizes were greater in the fertilized watershed than in the unfertilized watershed for all sample periods. Minimal difference was observed between watersheds in the month of July, whereas the largest magnitude of difference between the two watersheds was observed during outmigration, as indicated by the sample period - watershed interaction effect. The magnitudes of the post-application increases are similar in size in both watersheds except between December and February. During that time period coho size in the unfertilized watershed slightly increased, while fertilized watershed values did not.

Juvenile coho length was greater overall in the fertilized watershed (mean = 89.8 mm, SD = 17.86) versus the unfertilized watershed (mean = 85.2 mm, SD = 16.4, Tables 21 and 22). Coho weight was also greater in the fertilized watershed (mean = 8.7 g, SD = 4.8) versus the unfertilized watershed (mean = 7.4 g, SD = 3.9, Tables 23 and 24). Coho length (mean = 108.4 mm, SD = 11.85) and weight (mean = 13.92 g, SD = 4.22) were highest during April-June. Over time, the largest increase in coho sizes occurred between the February and April-June sample periods and the smallest increase in size occurred between the December and February sample periods.

Spring Treatment

5. Periphyton $\delta^{15}N$

The final periphyton model for the spring SCA treatment included watershed and sample period as statistically significant fixed factors (Tables 25 and 26). Chinook density and the watershed-sampling period interaction term were not significant predictors of periphyton $\delta^{15}N$. The spring treatment periphyton model performed better when compared to the fall treatment periphyton model, as it had a greater goodness of fit (Table 27). There was little difference between the marginal and conditional R-squared values indicating fixed factors explained the majority of variation in periphyton $\delta^{15}N$.

The $\delta^{15}N$ of periphyton in the fertilized watershed, unfertilized watershed, and secondary unfertilized tributaries had a seasonal pattern wherein $\delta^{15}N$ values were

consistently greater after SCA application (Figure 14). The largest increase in periphyton $\delta^{15}N$ after the time of SCA application was observed at the fertilized watershed, which had higher periphyton $\delta^{15}N$ values than did the unfertilized watershed in the month of July. By the February sampling period, periphyton $\delta^{15}N$ values in the fertilized watershed were less than those of either the unfertilized watershed or the unfertilized secondary tributaries. Based on visual observation, the fertilized watershed experienced greater seasonal variation (i.e., increases and decreases) in $\delta^{15}N$, compared to samples from the two unfertilized areas, but this observation was not reflected in a significant watershed by sample period interaction. Post-hoc power analysis indicated that smaller sample sizes contributing to our periphyton model resulted in a 16 % probability of detecting an interaction between watershed and sample period.

Periphyton $\delta^{15}N$ values were greatest overall in the unfertilized watershed (mean = 0.951, SD = 1.572) and lowest in the fertilized watershed (mean = -0.261, SD = 2.174, Tables 28 and 29). They were greatest during July (mean = 2.012, SD = 1.159) and lowest during April-June (mean = -0.363, SD = 1.514). Values were similar between February and April-June. The greatest overall change occurred between April-June and July (i.e., before and after SCA application).

6. Macroinvertebrate $\delta^{15}N$

The final macroinvertebrate model for the spring SCA treatments included all terms as significant fixed factors (Tables 25 and 30). This model had the second best goodness of fit among spring treatment models (Table 27). There was little difference between the marginal and conditional R-squared values indicating fixed factors explained the majority of variation in macroinvertebrate $\delta^{15}N$.

Model analysis indicates a significant watershed effect. The seasonal pattern was similar between the fertilized and unfertilized areas, but the magnitude of change was enhanced within the fertilized watersheds (Figure 15). Fertilized watershed $\delta^{15}N$ values increased by a greater magnitude between April-June and July and decreased by a greater magnitude between July and November. The $\delta^{15}N$ values in the fertilized watershed were higher than either the unfertilized watershed or the unfertilized secondary tributaries for the two sample periods after the SCA application but were lower than the unfertilized watershed and unfertilized secondary tributaries for the remainder of the sample periods.

On average macroinvertebrate $\delta^{15}N$ values were greatest in the unfertilized watershed (mean = 2.969, SD = 1.665) and lowest in the fertilized watershed (mean = 2.357, SD = 2.823, Tables 31 and 32). The macroinvertebrate $\delta^{15}N$ values in the secondary unfertilized tributaries (mean = 2.650, SD = 1.891) were intermediate in value between the unfertilized and fertilized watersheds. Sample period was also an important predictor of macroinvertebrate $\delta^{15}N$ values, with the highest values occurring in July

(mean = 4.388, SD = 2.826) and the lowest values occurring during April-June (mean = 1.619, SD = 2.079). Between November and February, macroinvertebrate $\delta^{15}N$ values were similar.

The density of Chinook carcasses was also a significant factor in predicting macroinvertebrate $\delta^{15}N$ values (Table 32). Macroinvertebrate $\delta^{15}N$ values were higher at sites (lower, middle) with Chinook carcasses and during the sample period (November) when Chinook carcasses were present. Values were widely dispersed around the mean, but overall were greater at sites with Chinook carcasses (mean = 2.932, SD = 1.871) than at sites without Chinook carcasses (mean = 1.807, SD = 1.545, Figure 16).

Functional feeding group was also an important predictor of macroinvertebrate $\delta^{15}N$ values. We identified five different feeding groups within our samples: filter-feeders, collector-gatherers, predators, scrapers, shredders. Predators had the highest $\delta^{15}N$ values (mean = 5.438, SD = 2.42), while collector-gatherers had the lowest (mean = 1.429, SD = 1.761, Table 33). The abundance of each functional feeding group in our collection varied among sampling periods. In some cases, no representatives of a functional feeding group were observed in any year during a particular sampling period. Because of these relatively low sample sizes, some values do not have a standard error displayed or are missing values entirely from a specific sample period.

For each functional feeding group, $\delta^{15}N$ values in the fertilized watershed appeared to increase after SCA application (Figures 17-21). Filter-feeder, scraper and shredder $\delta^{15}N$ values increased at a greater magnitude in the fertilized watershed than in the unfertilized watershed or the unfertilized secondary tributaries, but a similar pattern was not evident for collector-gatherers or predators. Values taken from gatherers in the fertilized watershed appeared to increase after SCA application, but not enough samples were collected to determine if the same occurred in both unfertilized watershed and tributaries.

For all functional feeding groups, $\delta^{15}N$ values in the fertilized watershed appeared to decrease between the first (July) and fourth (December) sampling periods following SCA application. With the exception of predators, $\delta^{15}N$ in fertilized watersheds for each feeding group decreased by November. Scrapers were the only functional feeding group to have $\delta^{15}N$ values decrease by August/September in the fertilized watershed. These decreases among all groups except shredders in the fertilized watershed $\delta^{15}N$ were similar in size to the previous increases, so that values had returned to their original level. By the final sampling event in February, $\delta^{15}N$ values were not greater in the fertilized watershed than in the unfertilized watershed and tributaries for any of the functional feeding groups.

7. Juvenile Coho $\delta^{15}N$

The final juvenile coho $\delta^{15}N$ model for the spring SCA treatment includes all terms as significant fixed factors (Table 25 and 34). Similar to the model predicting juvenile coho $\delta^{15}N$ following the fall SCA application, fixed factors did a relatively poor job of explaining juvenile coho $\delta^{15}N$, as evidenced by the low marginal R-squared value (Table 27). The conditional R-squared value was considerably larger indicating the random factors explain the majority of the spring treatment juvenile coho $\delta^{15}N$ variation.

Juvenile coho $\delta^{15}N$ values in the fertilized watershed were greater than those in the unfertilized watershed and unfertilized tributaries, with the greatest magnitude of difference occurring in the five months (three sample periods) after the spring SCA application (Figure 22). Between July and December, juvenile coho $\delta^{15}N$ values in the fertilized watershed were similar, whereas juvenile coho $\delta^{15}N$ values in the unfertilized watershed progressively increased over time towards levels observed in the fertilized watershed, suggesting a sample period by watershed interaction. In the December sampling event, the juvenile coho $\delta^{15}N$ values were not different between the unfertilized and the fertilized watershed. In the April-June sampling event (i.e., outmigration), juvenile coho $\delta^{15}N$ values in the unfertilized watershed and tributaries were greater than those in the fertilized watershed.

Overall juvenile coho $\delta^{15}N$ values differed between fertilized and unfertilized watersheds. Average juvenile coho $\delta^{15}N$ values were greatest in the fertilized watershed (mean = 7.666, SD = 2.137 SD) and lowest in the secondary unfertilized tributaries

(mean = 6.927, SD = 1.920 SD) over the course of the study (Table 35). Juvenile coho $\delta^{15}N$ values also differed seasonally (Table 36), with the highest values seen during the spring outmigration in April-June (8.159, 1.476 SD) and lowest in February (6.794, 1.484 SD).

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Juvenile coho $\delta^{15}N$ was positively correlated with the presence of Chinook carcasses (Table 33). Juvenile coho mean $\delta^{15}N$ values were higher at sites with Chinook carcasses (lower, middle) and during sample periods (November) when Chinook carcasses were present (mean = 7.578, SD = 2.593 SD), relative to sites and sample periods without Chinook carcasses (mean = 7.091, SD = 2.525, Figure 23).

8. Juvenile Coho Size

The final juvenile coho size models for the spring SCA treatment included watershed, sample period, and the watershed-sample period interaction effect (Table 25, 37 and 38). Upon initial analysis of fixed effects for the coho weight model, the interaction term was not significant. This non-significant result was not intuitive, given the observed seasonal trend wherein seasonal patterns appear to differ between fertilized and unfertilized watersheds (Figure 24). We redid the analysis omitting values from the final sample period (coho outmigration), as the large number of samples during the April-June sampling period appeared to be overriding the obvious interaction effect occurring around SCA application. Omitting these values resulted in a significant interaction effect, but did not change our conclusions regarding the significance of other fixed

factors. The marginal R-squared values were considerably larger indicating that fixed factors explain the majority of the spring treatment juvenile coho size variation (Table 27). Goodness of fit was higher for the length model than for the weight model, even after omitting weight samples from the final sample period.

The difference in juvenile coho length and weight between the fertilized and unfertilized areas was greatest immediately following SCA application and decreased over time (Figure 24 and 25). In July, coho size (length, weight) in the fertilized watershed was greater than the unfertilized watersheds/tributaries. The difference in coho size between the unfertilized watershed and tributaries and the fertilized watershed progressively decreased between July and December, similar to the pattern observed for coho $\delta^{15}N$ values. The different seasonal trends among watersheds is supported by the significant interaction effect between watershed and sampling period. During December and February, coho sizes in the fertilized watershed remained slightly higher than in the unfertilized watershed, but coho size in the fertilized watershed was not different from the unfertilized secondary tributaries. By the spring, when coho were outmigrating, we could not detect a difference in body size between fertilized and unfertilized watersheds.

Juvenile coho length was greater overall in the fertilized watershed (94.1 mm, 24.0 SD versus the unfertilized watershed (mean = 91.1 mm, SD = 26.5, Tables 39 and 40). Coho weight was also greater in the fertilized watershed (mean = 10.9 g, SD = 10.7) versus the unfertilized watershed (mean = 10.2 g, SD = 10.9, Tables 41 and 42). Coho length (mean = 124.3 mm, SD = 27.8) and weight (mean = 22.2 g, SD = 16.5) was

highest during the April-June sample period. Coho sizes increased by the greatest margin between February and April-June and by the least margin between December and February.

9. Population Level Analysis

For the fall-fertilized watershed, mean smolt abundance was 4011 (SD = 1829) during years before and after SCA application and 5594 (SD = 2675, Table 43) during SCA application years. Abundance was higher in the unfertilized watershed than in the fertilized watershed both outside of (mean = 9831, SD = 2977 SD) and during (mean = 10410, SD = 1689) SCA application years. Differences in the abundance of coho smolts in years with and without SCA application did not differ for either the fertilized or unfertilized watersheds (Figure 27). Smolt length in the fall-fertilized watershed was 114.4 mm (SD = 4.2) before and after SCA application and 113.4 mm (SD = 1.4) during SCA application years (Table 44). Smolt lengths were shorter in the unfertilized watershed than the fertilized watershed both during (mean = 103.8 mm, SD = 1.4) and outside of SCA application years (mean = 104.5 mm, SD = 4.2). In both the fertilized and unfertilized watersheds, there was no detectable difference in fork length during years with and without SCA application (Figure 26).

For the spring-fertilized watershed, mean smolt abundance was 6554 (SD = 2901) during years before and after SCA application and 5968 (SD = 1473) during application years (Table 45). Abundance was greater in the unfertilized watershed both during

(mean = 10447, SD = 1508) and outside of (mean = 9867, SD = 2911) application years. Smolt length in the spring-fertilized watershed was 109.5 mm (SD = 5.2) before and after SCA application years and 112.5 (SD = 2.7) during application years (Table 46). Smolt lengths were smaller in the unfertilized watershed both during (mean = 106.3 mm, SD = 0.6) and outside of (mean = 103.9 mm, SD = 3.9) SCA application years. No differences in length or abundance could be detected between years with and without SCA application in the fertilized watershed (Figures 28 and 29).

Discussion

Seasonal Trends

Our results demonstrate seasonal changes in $\delta^{15}N$ values at each trophic level in each watershed (although not statistically supported for the periphyton). Our interpretation of the results assumes that patterns observed in the unfertilized watershed represents natural patterns of $\delta^{15}N$ in the food web that would be observed in all watersheds within our study without the added input of SCA. In the absence of SCA applications, the seasonal $\delta^{15}N$ patterns of primary producers (periphyton) and primary consumers (macroinvertebrates) differed from those of secondary consumers (juvenile coho). The $\delta^{15}N$ values in periphyton and macroinvertebrate tissue were highest during the summer (July) sampling period while $\delta^{15}N$ values in juvenile coho tissue were highest during late fall and winter sample periods (Figures 30 and 31). Past work within the Skagit River basin has demonstrated that sub-yearling coho diets during the spring and summer are not strongly influenced by MDN but that the MDN in juvenile coho tissue during the winter months are affected by the presence of adult coho carcasses (Reichert et al. 2008). The seasonal pattern in juvenile coho $\delta^{15}N$ values observed by Reichert et al. (2008) is similar to the pattern seen in our study, although $\delta^{15}N$ values increased and peaked earlier in our lower Columbia River tributaries relative to what was seen within the Skagit River. The difference in the seasonal peak of juvenile coho $\delta^{15}N$ values in our study versus juvenile coho $\delta^{15}N$ values on the Skagit River may be because the principal source of carcasses overlapping with the juvenile coho in the lower Columbia River tributaries were Chinook salmon, which return and spawn in September and

October, as compared to coho salmon in the Skagit River tributaries, which primarily spawn between November and January.

Juvenile coho $\delta^{15}N$ values increased in Abernathy Creek (spring fertilized) and Mill Creek (unfertilized, not in secondary unfertilized tributaries, no April-June samples) between February and April-June, but the timing of this increase suggests that this pattern was unlikely to result from uptake of MDN. Curiously, spring increases in $\delta^{15}N$ values were observed only in coho and only during spring treatment years. While there are steelhead spawners present during the late winter and spring, most steelhead exit the streams as kelts and do not leave carcasses in concentrations high enough to explain this seasonal increase in juvenile coho $\delta^{15}N$ values. The springtime uptick in juvenile coho $\delta^{15}N$ values was not likely due to a shift in the stable isotope composition of lower trophic levels (periphyton and macroinvertebrates) because $\delta^{15}N$ values of these lower trophic levels did not follow a similar seasonal pattern. Juvenile coho are growing rapidly in the spring and as they become larger they may be changing their prey selection to macroinvertebrate feeding groups that contain higher $\delta^{15}N$ values, such as predator macroinvertebrates. If coho prey selection did not change, we would not expect coho $\delta^{15}N$ values to follow a seasonal pattern different from those of periphyton and macroinvertebrates. Because coho $\delta^{15}N$ values increased between the late winter and spring while lower trophic level $\delta^{15}N$ values remained constant, we can infer that juvenile coho switched to food sources containing $\delta^{15}N$ values higher than those of the prey items on which coho were feeding during the winter. A change in prey selection by juvenile coho influencing $\delta^{15}N$ values in the spring is also supported by the

fact that coho smolts were larger in both watersheds during the outmigrations corresponding to the spring treatment years (ocean entry year 2014-2016) relative to the fall treatment years (ocean entry year 2011-2014). Alternatively, it is possible that growing conditions were generally more favorable during the years of the spring treatment analyses versus the years of the fall treatment analyses. Larger coho are potentially more likely to switch to larger prey, which may be more likely to containing higher $\delta^{15}N$ values.

As stream temperatures and the intensity and availability of light decrease in the fall and winter, periphyton and macroinvertebrates become less productive. This time period also coincides with the presence of Chinook carcasses. Since periphyton and macroinvertebrates are less productive at in the late fall/early winter they may be less likely to incorporate MDN from Chinook carcasses (Hawkins and Sedell 1981). This is a potential explanation as to why periphyton and macroinvertebrate $\delta^{15}N$ values do not appear to increase when carcasses are present.

Throughout most of the year, periphyton and macroinvertebrate $\delta^{15}N$ values were consistently higher in the unfertilized watershed versus the fertilized watershed (Figures 30-33). This result is independent of SCA applications or the presence of salmon carcasses. Since salmon carcasses do not provide any substantial sources of ^{15}N-enriched nitrogen during the summer, the difference between the watersheds must be due to characteristics inherent to the watershed. We expect that background levels of $\delta^{15}N$ may be higher in the unfertilized watershed than in the two fertilized watersheds due to differences in the denitrification processes occurring in headwater reaches of

each watershed. Denitrification is the process by which nitrate (NO_3) is ultimately converted into nitrogen gas (N_2), and it can be more prevalent under anaerobic conditions within the stream environment (Naiman et al. 1988). Greater rates of denitrification can also lead to higher ambient levels of $\delta^{15}N$ within the food web because the lighter isotope of nitrogen (^{14}N) is preferentially lost as N_2 during the denitrification process, leaving behind the heavier nitrogen isotope (^{15}N; Nadelhoffer and Fry 1994).

The fertilized (Abernathy and Germany Creeks) and unfertilized (Mill Creek) watersheds are similar in size, but have different physical attributes. The upper extent of coho habitat in Mill Creek has a lower gradient, while the upper extent of Germany Creek and Abernathy Creek has a higher gradient. During the summer when stream discharges are at their lowest, the upper reaches of Mill Creek appear stagnant and swamp-like. This is contrasted with the upper reaches of Germany Creek where the stream appears less stagnant. While we have not measured water quality metrics that would confirm these conditions, it is possible that parts of upper Mill Creek may become anaerobic during the summer, thereby increasing denitrification. Greater rates of denitrification could increase the ambient $\delta^{15}N$ values within Mill Creek, leading to higher $\delta^{15}N$ values across the food web. Once discharges increased in the fall, these conditions would dissipate and $\delta^{15}N$ values would decrease.

Another possibility explaining the higher food web $\delta^{15}N$ values in Mill Creek (unfertilized) relative to Abernathy or Germany creek watersheds (fertilized) could be a difference in the densities of red alder, which represent a terrestrial source of nitrogen relatively low

in ^{15}N:^{14}N. Since alder fix atmospheric N_2, alder leaves and leaf litter produced in fall tends to have $\delta^{15}N$ values close to 0 (Helfield and Naiman 2002). Precipitation events beginning in the late fall could lead to increased leaching of soil nitrogen. If greater densities of alders are present, nitrogen leached from nearby soils will have lower $\delta^{15}N$ values when compared to areas with lower densities of alders. The combination of these processes could lead to overall lower $\delta^{15}N$ values within a watershed's food web, especially during the fall.

Response to Fall Treatment

If SCA nutrients were being incorporated into the periphyton community, we would expect $\delta^{15}N$ values in the sampled periphyton to respond relatively quickly following the SCA applications. Bilby et al. (1996) demonstrated that periphyton sequesters dissolved nitrogen relatively quickly from the water column. Nonetheless, we saw no detectable difference in periphyton $\delta^{15}N$ in the fertilized watershed before versus after the fall SCA application (Table 7). This may be due to the fact that our periphyton samples included autotrophic as well as heterotrophic organisms. The autotrophic components of the periphyton community (e.g., diatoms, cyanobacteria) would incorporate inorganic forms of nitrogen, while heterotrophic components (e.g., bacteria, fungi) would incorporate organic forms of nitrogen, which may have inherently different $\delta^{15}N$ values that cannot be accounted for in this study. The lack of a periphyton effect may also be due to low statistical power. These uncertainties limit our confidence in drawing a conclusion about the response of periphyton to the fall SCA treatment.

Overall, $\delta^{15}N$ values in the macroinvertebrates in the fertilized watershed were elevated after SCA application (November and December sample periods) relative to before the SCA application (July and August/September sample periods), and in comparison with $\delta^{15}N$ values of macroinvertebrates in the unfertilized watershed, which decreased between the July and December sample periods (Figure 4). A difference in the seasonal trend of macroinvertebrate $\delta^{15}N$ values between watersheds is likely due to SCA nutrient incorporation in the fertilized watershed, as suggested by the timing of the response following SCA application and the difference in observed response between the fertilized and unfertilized watersheds. The incorporation of nutrients from the SCA application was apparently short-lived because $\delta^{15}N$ values in macroinvertebrates begin decreasing within three months after SCA application in the fertilized watershed. Unfertilized values also decreased between December and the spring (April-June), but at a lesser rate. If we assume that, in the absence of SCA application, the $\delta^{15}N$ values of macroinvertebrates would follow the seasonal patterns observed in the unfertilized watershed, the analogs appear to have had the effect of reversing this seasonal trend.

Each functional feeding group we observed exhibited seasonal trends in $\delta^{15}N$ values similar to those of the other feeding groups within the watershed (Figures 5-9), suggesting they share a common source of nutrients that changes seasonally. Based on the feeding strategies associated with each feeding group (Vannote et al. 1980), we can make inferences as to how they acquired ^{15}N from the SCA. Collector-gatherers and shredders had $\delta^{15}N$ values that increased after SCA application in the fertilized watershed. Because these particular feeding groups do not feed on periphyton, they are

likely feeding directly on SCA material instead of incorporating SCA nutrients from primary producers. Shredders, which feed on course particulate organic matter (CPOM) on the stream bottom, have been observed feeding directly on salmon carcasses (Kline et al. 1997, Minikawa et al. 2002, Honea and Gara 2009) and may also target SCA in our study. We observed shredder caddisflies (Order Trichoptera, Family Limnephilidae) located directly on SCA material, presumably to feed. Collector-gatherers feed on finer particles and may have consumed SCA material that we observed to break down into finer particles and settle in depositional areas such as pools and eddies. While filter feeder $\delta^{15}N$ values did not respond as strongly to SCA application as other macroinvertebrate functional groups, there did appear to be an increase in $\delta^{15}N$ values in July, suggesting incorporation of nutrients from SCA. An increase in filter-feeder $\delta^{15}N$ values after SCA application could be an indication they were incorporating fine SCA particles that did not settle to the bottom. The increase in $\delta^{15}N$ values from scrapers after the SCA application is puzzling since we did not observe a $\delta^{15}N$ response from periphyton. Presumably, scrapers would acquire SCA nutrients by feeding on periphyton that had already been enriched in $\delta^{15}N$. Because scrapers appear to respond relatively strongly to the SCA treatment it is possible that autotrophic members of the periphyton in the fertilized watershed did incorporate SCA nutrients and we did not detect them (e.g., due to the presence of heterotrophs in the samples or low statistical power).

Unfertilized watershed shredders differed from other feeding groups as there appeared to be an increase in $\delta^{15}N$ values between February and April-June (Figure 9). Since

there is no meaningful influx of MDN between February and April-June, an increase in shredder $\delta^{15}N$ values cannot be attributed to the presence of SCA or salmonid carcasses. Interestingly, periphyton $\delta^{15}N$ values also appear to increase between February and July. While other feeding groups did not show an increase between February and April-June, collectively there is an increase in unfertilized watershed values between April-June and July (Figure 4). An increase in macroinvertebrate $\delta^{15}N$ values during the summer suggests a change in the nitrogen isotopic signature in these watersheds is occurring from the bottom up and not due to an influx of MDN. For the isotope composition of the food web to shift there needs to be a change in the composition of organic matter and primary producers (periphyton) which have different $\delta^{15}N$ values, leading to shifts in nitrogen isotopic signatures across all stream macroinvertebrates.

In the month of December, juvenile coho $\delta^{15}N$ values in the fall-fertilized watershed were greater than juvenile coho $\delta^{15}N$ values in the unfertilized watershed (Figure 10). After the SCA application, juvenile coho $\delta^{15}N$ values in the fertilized watershed increased by a greater margin relative to juvenile coho $\delta^{15}N$ values in the unfertilized watershed. This suggests that MDN from SCA were likely incorporated into the juvenile coho biomass. Conversely, juvenile coho growth does not appear to have responded to the fall application of SCA. While we determined there was a significant watershed-sample period interaction effect, changes in coho length and weight do not vary between the fertilized and unfertilized watersheds between August/September and December (Figures 12 and 13), which is the time frame we would expect to see the

analog application affect coho growth. The significant interaction of sample period and watershed on juvenile coho length is due to relative differences between the unfertilized and fertilized watersheds in July and August/September versus February and April-June the following spring and reflect juvenile coho growth in the winter months. The observation that the size of overwintering juvenile coho increased by a greater magnitude within the fertilized watershed relative to within the unfertilized watershed is not likely to be an indication of effects from SCA applications, since the analogs were not present during these time periods and juvenile coho $\delta^{15}N$ values actually decreased between the February and April-June sampling periods. If SCA were affecting coho size during the late winter and spring, we would expect to see coho $\delta^{15}N$ values also increasing within the fertilized watershed.

Response to Spring Treatment

$\delta^{15}N$ values of periphyton following the spring SCA application appeared to increase by a greater margin in the fertilized watershed than in the unfertilized areas (Figure 14), but the interaction term that would have statistically supported this observation was not significant. Periphyton $\delta^{15}N$ values in the fertilized watershed also appear to decrease by a greater margin than in the unfertilized watershed between July and February. Although these results hint at a response of periphyton to the spring SCA application, our confidence in interpretations about interactions of the sample period and watershed is low because results from our analysis may have been influenced by the low statistical power.

The spring treatment of SCA did increase macroinvertebrate $\delta^{15}N$ values within the fertilized watershed beyond the typical seasonal increase seen in the unfertilized areas, but the effect was relatively short-lived. In the sample period following spring SCA application, macroinvertebrate $\delta^{15}N$ values increased by a greater magnitude in the fertilized watershed versus the unfertilized areas (Figure 15). The difference in seasonal trend of macroinvertebrate $\delta^{15}N$ values in the fertilized and unfertilized watershed suggests SCA nutrients were incorporated by the macroinvertebrate community following the spring SCA applications. The elevated levels of $\delta^{15}N$ values in macroinvertebrates in the fertilized watershed persisted through the August/September sample period, but by the November sample period, macroinvertebrate $\delta^{15}N$ in the fertilized watershed had decreased to values less than those found in macroinvertebrates in the unfertilized areas. $\delta^{15}N$ values did not change between November and February in the fertilized watershed or unfertilized areas.

The seasonal $\delta^{15}N$ pattern shown by each functional feeding groups following the spring SCA application in the fertilized watershed is similar to those seen in periphyton and overall macroinvertebrates (Figures 17-21). In all macroinvertebrate feeding groups other than predators, there was an initial post-application increase in $\delta^{15}N$ values, followed by a noticeable decrease in $\delta^{15}N$ values after the July sampling period. The same pattern appears to occur within the unfertilized areas, but the increase in $\delta^{15}N$ values between the May and July sample period as well as the decrease after July in unfertilized areas were smaller in magnitude. As with the overall macroinvertebrate

results, a difference in seasonal trends suggests an interaction between watershed and sampling period occurring within each feeding group (Table 32). A difference in seasonal patterns of macroinvertebrate $\delta^{15}N$ values between the fertilized and unfertilized areas during the spring and winter is likely due to SCA application because there were not any other meaningful influxes of MDN during this time. Because each feeding group appeared to respond to SCA application and because feeding groups have differing feeding strategies, macroinvertebrates are likely accessing MDN from SCA both via primary producers (e.g., scrapers feeding on periphyton, even with no detected periphyton response) and directly feeding on the analogs (e.g., shredders).

While we do not have $\delta^{15}N$ values for juvenile coho prior to the spring SCA applications, we can make inferences based on post-application values and patterns. After the spring SCA application, $\delta^{15}N$ values of juvenile coho in the fertilized watershed were highly elevated (1.5-2.5 ‰) relative to the values in the unfertilized areas (Figure 22), suggesting that the juvenile coho were directly feeding on the analogs. Values remained elevated in the fertilized watershed relative to the unfertilized watershed through the November sampling period, five months after SCA application, likely due to SCA incorporation. The $\delta^{15}N$ values of juvenile coho did not remain elevated through the outmigration period, however. Between the December and February sampling periods, $\delta^{15}N$ values of juvenile coho in the fertilized watershed decreased to levels less than those in the unfertilized watershed which, likely indicated that the MDN were no longer available for uptake in the stream food web.

The pattern of an initial increase followed by a decrease in juvenile coho $\delta^{15}N$ values following spring SCA application in the fertilized watershed is similar to that observed for periphyton and macroinvertebrate $\delta^{15}N$ values during this same time frame (Figures 14, 15, and 22). The pattern observed for juvenile coho differs in that the decrease following the post-SCA application increase lags in time. The decrease does not occur until the fourth post-SCA sampling period, well after periphyton and macroinvertebrate $\delta^{15}N$ values have already decreased to pre-SCA values. A delay in a decrease of $\delta^{15}N$ values in fish relative to lower trophic levels is likely due to the slower nitrogen turnover rate in larger organisms (Sakano et al. 2005, McIntyre and Flecker 2006).

Interestingly, juvenile coho $\delta^{15}N$ values in the secondary unfertilized tributaries become more similar to $\delta^{15}N$ values in the fertilized watershed between July and August/September, and then decrease to values similar to the unfertilized watershed between August/September and November. Juvenile coho have been documented making downstream migrations in the late summer and early fall as sub-yearlings (Crone and Bond 1976, Hartman et al. 1982, Harke and Lucey 1999). It is possible an increase in juvenile coho $\delta^{15}N$ values in the secondary unfertilized tributaries during August/September is due to juvenile coho migrating from the mainstem of the fertilized watershed into the secondary unfertilized tributaries in early fall months. The sampling site within one of our secondary unfertilized tributaries (Wiest Creek) is <2,000 m from fertilized areas within Abernathy Creek and could be accessible by juvenile coho originally exposed to the SCA applications in the fertilized watershed.

The influence of spring SCA applications was also observed in the growth of juvenile coho. Immediately after the SCA applications, juvenile coho lengths and weights are greater in the fertilized watershed relative to the unfertilized areas (Figures 24 and 25). Coho size remains higher in the fertilized versus the unfertilized areas through November but these differences were not sustained to outmigration. By December there was little difference in coho size among fertilized watershed and unfertilized areas. Since juvenile coho $\delta^{15}N$ values in the fertilized watershed were also not different from the unfertilized areas by the winter, we can infer that responses due to SCA applications were no longer present by December.

Synthesis of SCA Effects

SCA applications appear to have differing effects on the seasonal pattern of food web $\delta^{15}N$ values, depending on whether the application occurred in the fall or spring (Figures 32 and 33). To illustrate these differences, we have created two conceptual diagrams, one for each treatment (Figures 34 and 35). Fall application of SCA occurred at a time when $\delta^{15}N$ values of periphyton and macroinvertebrates are generally decreasing and near their seasonal low. These bottom trophic levels are potentially less productive when fall treatment SCA application occurred because of decreasing water temperature and ambient light levels (Morin et al. 1999). In the fall-fertilized watershed we observed a fall-time increase in macroinvertebrate $\delta^{15}N$ values, opposite the pattern observed in the absence of SCA application. The seasonal trend within the fall treatment fertilized watershed appears to be a disruption of the seasonal pattern. Without SCA applications

we would expect fertilized watershed values to be decreasing during the late fall/early winter, following a pattern similar to that observed in the unfertilized watershed. The effect on the seasonal trend of $\delta^{15}N$ values from fall applications of SCA contrasts with the response of periphyton and macroinvertebrates following the spring SCA applications. The spring application of SCA occurred during a time when $\delta^{15}N$ values of periphyton and macroinvertebrates were naturally increasing in the unfertilized watershed as well. The MDN from the SCA enhanced the fertilized watershed's seasonal change in $\delta^{15}N$, increasing $\delta^{15}N$ values by a magnitude greater than that seen in the unfertilized watershed during this time frame.

A question arises as to whether the different seasonal trends between the fertilized and unfertilized watersheds were entirely due to the presence of SCA. We discussed earlier the possible difference in physical characteristics influencing stable isotope compositions of Mill Creek versus Germany and Abernathy Creeks. There may be other differing characteristics we have not considered influencing seasonal $\delta^{15}N$ patterns of these watersheds. To confirm whether SCA additions are impacting these seasonal patterns, future monitoring to compare $\delta^{15}N$ values in the fertilized watersheds without SCA application versus those of unfertilized watershed would be useful. This would help elucidate the extent to which seasonal patterns in the fertilized watersheds are influenced by SCA, as opposed to being inherently different from those of the unfertilized watershed.

Chinook Carcass Contributions

The contribution of Chinook carcasses to the $\delta^{15}N$ values of macroinvertebrates varied among the three watersheds. Macroinvertebrate uptake of MDN form Chinook carcasses was detected in the unfertilized watershed and the fertilized watershed that received the spring SCA application but not in the watershed that received the fall SCA application. This suggests that, to some extent, the macroinvertebrate community incorporated nutrients from Chinook carcasses. It also suggests that some macroinvertebrates were feeding directly on the carcasses rather than getting the nutrients from primary producers, because periphyton $\delta^{15}N$ values were not associated with Chinook carcass densities.

We would expect the density of Chinook carcasses to influence the $\delta^{15}N$ values of macroinvertebrates to a similar extent in both the fall and spring treatments. While parameter estimates for the fall treatment Chinook density effects indicated a positive correlation, the factor was not statistically significant ($p = 0.129$). The spring treatment parameter was significant, but not by a large margin ($p = 0.044$). Our density metric is somewhat rudimentary and may not be calculated at a precise enough detail to capture the effect of Chinook carcasses in the fall-fertilized watershed. Secondly, while our density metric encompasses only carcasses within 100 m of sampling sites, Chinook escapement is consistently smaller in Germany Creek (fall treatment fertilized watershed) versus Abernathy Creek (spring treatment fertilized watershed). Since there are on average more Chinook carcasses present in the spring treatment watersheds versus the fall treatment watersheds, our density metric may not be capturing the full

effect of carcasses on macroinvertebrate $\delta^{15}N$ values. It is possible that Chinook carcasses may influence $\delta^{15}N$ values of macroinvertebrates at distances significantly greater than 100 m. Therefore the amount of carcasses present at the watershed level may be of more importance in predicting macroinvertebrate $\delta^{15}N$ values.

Chinook carcass densities influenced the $\delta^{15}N$ values of juvenile coho salmon in all three watersheds, but were not observed to be associated with the length or weight of juvenile coho (Tables 16 and 34). Original parameter estimates prior to omitting the term for the final model indicate that Chinook density was negatively correlated with both size metrics (length and weight) in both fall and spring treatments, which is counter-intuitive. This suggest that while nutrients from Chinook carcasses did increase the $\delta^{15}N$ values of juvenile coho, the uptake of nutrients provided by the carcasses did not result in increased juvenile growth. These mixed results associated with the uptake of $\delta^{15}N$ by macroinvertebrates suggest that the influence of Chinook salmon carcasses on the $\delta^{15}N$ values of juvenile coho were either due to coho feeding directly on Chinook carcasses or incorporating the nutrients by feeding on macroinvertebrates. In either case, our results demonstrate a flow of nutrients from the Chinook salmon spawners to the juvenile coho during fall months in these watersheds.

Juvenile Coho Abundance and Size

Mean lengths and abundances of smolts were greater in the fall treatment fertilized watershed than in the unfertilized watershed, but the difference is not likely due to

enhancement from SCA applications (Figures 26 and 27). Prior to years with SCA application, coho smolt lengths were also greater in the fertilized watershed relative to the unfertilized watershed. Therefore, a before-after comparison of smolt lengths is a more appropriate way to evaluate the effects of the SCA application on juvenile coho growth. We could not detect a before-after difference between years with and without SCA applications in either watershed, indicating SCA applications did not significantly increase coho smolt sizes. Similarly, while mean abundance was higher in the fertilized watershed during SCA application years relative to years prior to SCA application, a similar difference was observed in the unfertilized watershed, suggesting that the temporal difference cannot be attributed to the SCA application itself.

Coho smolt size in the spring fertilized watershed was also greater than in the unfertilized watershed during SCA application years, but we cannot attribute the difference to SCA application (Figures 28) because, prior to SCA treatment years, coho smolts were of greater size in the fertilized watershed than in the unfertilized watershed. If SCA application had an effect on coho size at outmigration, we would expect the difference between the watersheds to be enhanced during the SCA application years. Instead there is no detectable difference in smolt size between SCA and non-SCA years in the fertilized watershed, while coho lengths were actually greater in the unfertilized watershed during SCA years versus non-SCA years. This indicates that the observed difference in juvenile coho lengths between watersheds was due to more favorable conditions in the spring-fertilized watershed unrelated to the presence of SCA. No differences could be detected in smolt abundance between SCA and non-SCA years for

either the fertilized or unfertilized watershed, indicating SCA applications did not significantly increase coho smolt abundances (Figure 29).

In summary, neither fall or spring applications of SCA increased the size or abundance of juvenile coho. While we did detect nutrients from the SCA entering the food web and being incorporated by juvenile coho, this did not translate into any apparent beneficial effects. Past projects, including work done in the Columbia basin, have indicated the potential for SCA to increase juvenile salmon growth (Wipfli et al. 2003, Kohler et al. 2012). We did observe temporarily increased sizes of juvenile coho immediately following spring SCA application, but larger body sizes relative to the unfertilized watershed did not persist to smolt outmigration. Because coho were not larger or more numerous at outmigration, we cannot claim SCA application had sustained effects that would will be translated into increased future adult coho escapements within our study watersheds.

Several potential explanations exist as to why SCA were ultimately ineffective at increasing juvenile coho size and survival. The watersheds where our project took place have relatively high gradients, little off channel habitat, and lack retentive structure such as large woody debris that can aid in reducing stream velocities and moderating rises in discharge during rain events. As a result, stream discharges can increase rapidly during large precipitation events. Fall treatment SCA applications took place in October, just before the commencement of high discharge events. These high flows potentially washed SCA downstream, especially smaller pieces that had broken up, before they

could be fully incorporated by the watershed's food web. In Germany Creek we observed an increase in discharge of approximately 500 CFS during a single rain event over 24 hours, after which most of the fully intact analogs were no longer present. Spring treatment $\delta^{15}N$ metrics showed a more dramatic response relative to fall treatment metrics. This may be because discharges are relatively lower during May, when the spring treatment SCA were distributed, than they are during October, when the fall treatment SCA were distributed. Discharges typically decrease between May through the month of September, allowing the SCA to be retained in the watershed, and making them available to the watershed's food web for a longer period of time. In addition, overall productivity of the food web is likely decreasing when fall treatment SCA were applied, while productivity is increasing or at the annual peak when spring treatment SCA application occurs. As stream temperatures and available light decrease during the fall, primary producers and primary consumers are less productive and therefore less likely to incorporate nutrients from SCA applications. If MDN are being incorporated by the lower trophic levels at a diminished rate in the fall, the effects of fall SCA applications would be more reliant on direct consumption by juvenile coho, suggesting that nutrients from fall treatment SCA applications may be less available overall when compared to nutrients from spring treatments.

SCA applications resulted in nitrogen inputs to the food web and, in the case of spring applications, increased the sizes of juvenile coho. However, these effects were not sustained through smolt outmigration. A lack of sustained effects on the food web and juvenile coho populations suggests that, despite the recognized decline in MDN

delivered to these watersheds over the past century, there are additional factors that currently limit juvenile coho production. For example, even if SCA application resulted in larger juvenile coho, density-dependent factors might constrain the number of fish that survive until outmigration. Benefits from an initial increase in size may not translate into an increase in population sizes if survival from SCA application to smolt outmigration is not influenced by fish size or condition. Past work within these watersheds has indicated that survival during the over-winter rearing period determines smolt abundance (Zimmerman et al. 2015). Survival during the over-winter period may be influenced by the lack of off-channel and low-flow rearing environments, especially during high winter flow events (Bechie et al. 1994). In effect, current stream conditions during the winter months may be having a bottleneck effect on juvenile coho size and abundance. Because applications of SCA did not result in increased size or survival of juvenile coho, it is likely nutrient deficiencies are not limiting coho production within the watersheds of our study.

Conclusions

The uptake of ^{15}N isotope into the stream food web exhibited a seasonal trend in all watersheds, and the fall and spring applications of SCA affected the seasonal trends for both macroinvertebrates and juvenile coho. Our interpretation of these results assumes similar seasonal patterns would exist among the three watersheds in the absence of SCA applications. Data to validate this assumption are currently being collected. Incorporation of MDN from spring applications of SCA temporarily increased the sizes of juvenile coho, but neither the spring nor fall applications of SCA translated into larger or more abundant smolts. SCA applications are most likely to be effective within streams that have a combination of gentle gradients, greater amounts of off-channel habitat, and retentive structures (i.e., log jams). These may be streams that are relatively productive for salmonids when compared to streams where habitat characteristics are limiting salmonid production. Nonetheless, SCA applications may have the greatest positive effect in already productive watersheds. Future nutrient enhancement projects intended to benefit juvenile salmonids should incorporate regular monitoring of responses by each trophic level and overall juvenile salmonid abundance. SCA applications require long-term effort and investment as this type of restoration technique necessitates annual application for a continued benefit to salmonid populations. To ensure these efforts are worthwhile, careful monitoring should be employed.

Tables

Table 1. Watershed size, land cover percentage, and max elevation of each watershed (WDFW 2012).

Watershed	Watershed Area (km^2)	Forested %	Max Elevation (m)	Annual Mean Discharge (m^3/s)
Mill	75.5	94	273	2.69
Germany	58.6	82	362	2.94
Abernathy	74.1	92	285	2.89

Table 2. Total amount and spatial coverage of analog deposits and corresponding analog densities for each treatment. Analog density calculations are based on an assumed average bankfull width of 6 m (based on habitat surveys).

Watershed	Year	Treatment	Analog (kg)	Distance (km)	Density (kg/m^2)
Germany	2010	Fall	9,630	12.1	0.133
	2011	Fall	11,567	18.7	0.103
	2012	Fall	10,206	18.7	0.091
	2013	Fall	7,257	18.7	0.065
Abernathy	2013	Spring	5,126	9.3	0.092
	2014	Spring	6,532	11.5	0.095
	2015	Spring	18,144	22.5	0.134

Table 3. Sampling event schedule for each watershed. April-June periphyton and macroinvertebrates were collected at the sampling sites during April while fish were sampled at the rotary screw trap between April and June. Germany Creek sampling occurred between sampling periods Aug/Sept of 2010 and Apr-June of 2014. Abernathy Creek sampling occurred between sampling periods Apr-June of 2013 (only periphyton and macroinvertebrates) and Apr-June of 2016. Mill Creek sampling occurred during all indicated sampling periods.

	July	Aug/Sept	Nov	Dec	Feb	Apr-June
2010-2011		X	X			
2011-2012		X	X	X	X	X
2012-2013		X	X	X	X	X
2013-2014	X	X	X	X	X	X
2014-2015	X	X	X	X	X	X
2015-2016	X	X	X	X	X	X

Table 4. Estimates of average influxes of nitrogen delivered by anadromous salmonid species, the total flux from all carcasses (combined), and the flux from SCA applications. Estimates from carcasses represent ranges of carcass weights larger and smaller than average carcass weights of salmon in Washington (Gresh et al. 2000). Nitrogen content is based on an assumed value of 3.03 percent by wet weight. Average nitrogen content for analogs used in the 2010 application was 8.6 percent and 10.4 percent for all other applications.

Year	Chinook (kg)	Coho (kg)	Steelhead (kg)	Combined (kg)	SCA (kg)
Fall	35.5-80.6	20.9-35.1	2.3-6.0	58.7-121.7	754.8-1202.9
Spring	22.4-50.7	41.1-69.0	2.2-5.6	65.7-125.3	533.1-1886.9

Table 5. Results of an ANOVA evaluating differences in Chinook carcass density between fall treatment watersheds (Germany and Mill Creeks) and sites (lower and middle). P values less than 0.05 indicate a significant result.

	Df	Sum of Squares	Mean Squares	F Value	Pr
watershed	1	2.57E-04	2.57E-04	0.778	0.397
site	1	6.29E-04	6.29E-04	1.902	0.195
residuals	11	3.64E-03	3.31E-04		

Table 6. Results of an ANOVA evaluating differences in Chinook carcass density between spring treatment watersheds (Abernathy and Mill Creeks) and sites (lower and middle). P values less than 0.05 indicate a significant result.

	Df	Sum of Squares	Mean Squares	F Value	Pr
watershed	1	2.10E-06	2.08E-06	0.010	0.924
site	1	1.02E-04	1.02E-04	0.471	0.510
residuals	9	1.95E-03	2.17E-04		

Table 7. Response variables and the fixed factors included in the final model predicting response to fall SCA treatment. FFG represents macroinvertebrate functional feeding group and was only evaluated for the macroinvertebrate model. An X signifies that the factor was statistically significant.

Response Variable	Watershed	Sample Period	W/S Interaction	Chinook Density	FFG
Periphyton δ15N	X				
Invertebrate δ15N	X	X	X		X
Coho δ15N		X	X	X	
Coho Length	X	X	X		
Coho Weight	X	X	X		

Table 8. Results of a likelihood ratio test evaluating the fixed factors included in the final fall treatment periphyton model. P-values less than 0.5 indicate a significant result.

Model	Df	Chisq	Chi Df	Pr
Watershed	8			
Partial	9	6.585	1	**0.01**

Table 9. Pseudo R-squared values for each fall treatment model. Marginal R-squared values represent the goodness of fit of just fixed factors. Conditional R-squared values represent the goodness of fit of the model as a whole.

Model	Marginal R-Squared	Conditional R-Squared
Periphyton δ15N	0.050	0.050
Invertebrate δ15N	0.462	0.462
Juvenile Coho δ15N	0.097	0.328
Juvenile Coho Length	0.620	0.634
Juvenile Coho Weight	0.620	0.636

Table 10. Means and standard deviations of each level of main effect from the fall treatment model evaluating periphyton δ15N.

Factor [Level]	Mean	SD
Watershed [Fertilized]	-1.170	2.922
Watershed [Unfertilized]	0.150	2.163

Table 11. Main effect coefficients and their standard errors for the model evaluating fall treatment periphyton δ15N.

Factor [Level]	Parameter Estimate	Standa	t-value
(Intercept)	-1.094	0.328	-3.333
Watershed-Unfertilized	1.177	0.462	2.545

Table 12. Results of a likelihood ratio test evaluating the fixed factors included in the final fall treatment macroinvertebrate δ15N mode. P-values less than 0.05 indicate a significant result.

Model	Df	Chisq	Chi Df	Pr
Watershed	13			
Partial	14	97.387	1	**<2.2E-16**
Sampling Period	10			
Partial	14	59.648	4	**3.44E-12**
Interaction	14			
Full	18	28.787	4	**8.64E-06**
Feeding Group	13			
Full	18	91.617	5	**<2.2E-16**

Table 13. Means and standard deviations of each level of main effect from the model evaluating fall treatment macroinvertebrate δ15N.

Factor [Level]	Mean	SD
Watershed [Fertilized]	1.030	2.177
Watershed [Unfertilized]	2.865	1.841
Sample Period [July]	1.556	3.503
Sample Period [Aug/Sept]	1.428	2.2
Sample Period [Nov]	2.716	2.209
Sample Period [Dec]	2.507	1.276
Sample Period [Feb]	1.852	1.95
Sample Period [Apr-June]	1.425	2.343

Table 14. Main effect coefficients and their standard errors for the model evaluating fall treatment macroinvertebrate δ15N.

Factor [Level]	Parameter Estimate	Standard Error	t-value
(Intercept)	1.411	0.440	3.207
Watershed [Unfertilized]	1.793	0.532	3.37
Sample Period [Aug/Sept]	-0.780	0.434	-1.798
Sample Period [Nov]	2.238	0.452	4.956
Sample Period [Dec]	2.441	0.493	4.957
Sample Period [Feb]	0.883	0.494	1.787

Table 15. δ15N Means and standard deviations of each functional feeding group for the fall treatment.

Factor [Level]	Mean	SD
FFG [Filter-Feeders]	2.642	1.954
FFG [Collector-Gatherers]	1.515	2.043
FFG [Predators]	3.615	2.284
FFG [Scrapers]	1.773	2.363
FFG [Shredders]	1.526	1.683

Table 16. Results of a likelihood ratio test evaluating the fixed factors included in the final fall treatment juvenile coho δ15N model. P-values less than 0.05 indicate a significant result.

Model	Df	Chisq	Chi Df	Pr
Sampling Period	6			
Partial	10	190.64	4	**<2.2E-16**
Chinook Density	13			
Full	14	4.75	1	**0.029**
Interaction	10			
Full	14	27.027	4	**1.96E-05**

Table 17. Means and standard deviations of each level of main effects from the model evaluating fall treatment juvenile coho δ15N.

Factor [Level]	Mean	SD
Sample Period [July]	3.924	1.394
Sample Period [Aug/Sept]	5.600	1.619
Sample Period [Nov]	7.298	2.312
Sample Period [Dec]	6.597	2.122
Sample Period [Feb]	7.843	2.159
Sample Period [Apr-June]	7.580	1.805

Table 18. Main effect coefficients and their standard errors for the model evaluating fall treatment juvenile coho δ15N.

Factor [Level]	Parameter Estimate	Standard Error	t-value
(Intercept)	7.137	0.529	13.500
Chinook Density	8.850	4.019	2.201
Sample Period [Aug/Sept]	-1.891	0.204	-9.293
Sample Period [Nov]	-0.329	0.189	-1.747
Sample Period [Dec]	-0.081	0.185	-0.439
Sample Period [Feb]	0.773	0.179	4.321

Table 19. Results of a likelihood ratio test evaluating the fixed factors included in the final fall treatment juvenile coho length model. P-values less than 0.05 indicate a significant result.

Model	Df	Chisq	Chi Df	Pr
Watershed	9			
Partial	10	122.43	1	**<2.2E-16**
Sampling Period	6			
Partial	10	308.48	4	**<2.2E-16**
Interaction	10			
Full	14	26.967	4	**2.02E-05**

Table 20. Results of a likelihood ratio test evaluating the fixed factors included in the final fall treatment juvenile coho weight model. P-values less than 0.05 indicate a significant result.

Model	Df	Chisq	Chi Df	Pr
Watershed	9			
Partial	10	135.2	1	**<2.2E-16**
Sampling Period	6			
Partial	10	158.13	4	**<2.2E-16**
Interaction	10			
Full	14	83.606	4	**<2.2E-16**

Table 21. Means and standard deviations of each level of main effects from the model evaluating fall treatment juvenile coho length (mm).

Factor [Level]	Mean	SD
Watershed [Fertilized]	89.800	17.860
Watershed [Unfertilized]	85.170	16.420
Sample Period [July]	61.340	10.320
Sample Period [Aug/Sept]	73.050	9.520
Sample Period [Nov]	79.340	9.620
Sample Period [Dec]	85.390	11.490
Sample Period [Feb]	86.68	9.08
Sample Period [Apr-June]	108.38	11.85

Table 22. Main effect coefficients and their standard errors for the model evaluating fall treatment juvenile coho length (mm).

Factor [Level]	Parameter Estimate	Standard Error	t-value
(Intercept)	112.715	1.667	67.610
Watershed [Unfertilized]	-8.098	0.820	-9.880
Sample Period [Aug/Sept]	-37.350	1.971	-18.980
Sample Period [Nov]	-31.607	1.836	-17.220
Sample Period [Dec]	-25.456	1.869	-13.620
Sample Period [Feb]	-25.771	1.873	-13.760

Table 23. Means and standard deviations of each level of main effects from the model evaluating fall treatment juvenile coho weight (g).

Factor [Level]	Mean	SD
Watershed [Fertilized]	8.700	4.800
Watershed [Unfertilized]	7.400	3.890
Sample Period [July]	2.930	1.530
Sample Period [Aug/Sept]	4.920	1.950
Sample Period [Nov]	6.030	2.060
Sample Period [Dec]	7.250	2.630
Sample Period [Feb]	7.55	2.24
Sample Period [Apr-June]	13.92	4.22

Table 24. Main effect coefficients and their standard errors for the model evaluating fall treatment juvenile coho weight (g).

Factor [Level]	Parameter Estimate	Standard Error	t-value
(Intercept)	15.657	0.394	39.710
Watershed [Unfertilized]	-3.270	0.237	-13.820
Sample Period [Aug/Sept]	-10.214	0.430	-23.750
Sample Period [Nov]	-9.300	0.384	-24.200
Sample Period [Dec]	-8.079	0.397	-20.350
Sample Period [Feb]	-8.165	0.398	-20.530

Table 25. Response variables and the fixed factors included in the final model to predict responses to the spring SCA treatment. FFG represents macroinvertebrate functional feeding group and was only evaluated for the macroinvertebrate model. An X signifies that the factor was statistically significant.

Response Variable	Watershed	Sample Period	W/S Interaction	Chinook Density	FFG
Periphyton δ15N	X	X			
Invertebrate δ15N	X	X	X	X	X
Coho δ15N		X	X	X	
Coho Length	X	X	X		
Coho Weight	X	X	X*		

Table 26. Results of a likelihood ratio test evaluating the fixed factors included in the final spring treatment periphyton model. P-values less than 0.05 indicate a significant result.

Model	Df	AIC	Chisq	Chi Df	Pr
Watershed	9	644.27			
Partial	11	633.98	14.283	2	**7.92E-04**
Sampling Period	6	657.8			
Partial	11	633.98	33.813	5	**2.59E-06**

Table 27. Pseudo R-squared values for each spring treatment model. Marginal R-squared values represent the goodness of fit of fixed factors. Conditional R-squared values represent the goodness of fit of all factors.

Model	Marginal R-Squared	Conditional R-Squared
Periphyton δ15N	0.327	0.348
Macroinvertebrate δ15N	0.305	0.305
W/ Feeding Group	0.545	0.577
Juvenile Coho δ15N	0.105	0.304
Juvenile Coho Length	0.565	0.595
Juvenile Coho Weight	0.359	0.394

Table 28. Means and standard deviations of each level of main effects from the model evaluating spring treatment periphyton δ15N.

Factor [Level]	Mean	SD
Watershed [Fertilized]	-0.261	2.174
Watershed [Unfertilized]	0.951	1.572
Watershed [Secondary]	0.474	1.983
Sampling Period [Apr-June]	-0.363	1.514
Sampling Period [July]	2.012	1.159
Sampling Period [Aug/Sept]	0.796	1.704
Sampling Period [Nov]	-0.253	2.177
Sampling Period [Dec]	0.646	2.438
Sampling Period [Feb]	-0.366	1.72

Table 29. Main effect coefficients and their standard errors for the model evaluating spring treatment periphyton δ15N.

Factor [Level]	Parameter Estimate	Standard Error	t-value
(Intercept)	0.749	0.450	1.665
Watershed [Fertilized]	-0.737	0.414	-0.59
Watershed [Unfertilized]	0.461	0.412	1.754
Sample Period [Apr-June]	-1.009	0.455	-0.468
Sample Period [July]	1.366	0.487	1.747
Sample Period [Aug/Sept]	0.119	0.465	0.925
Sample Period [Nov]	-0.899	0.487	-0.91
Sample Period [Feb]	-1.012	0.487	0.262

Table 30. Results of a likelihood ratio test evaluating the fixed factors included in the final spring treatment macroinvertebrate model. P-values less than 0.05 indicate a significant result.

Model	Df	AIC	Chisq	Chi Df	Pr
Watershed	14	1820.3			
Partial	16	1805.5	18.838	2	**8.12E-05**
Sampling Period	11	1889.3			
Partial	16	1805.5	93.846	5	**<2.2E-16**
Chinook Density	25	1755			
Full	26	1752.9	4.0579	1	**0.044**
Interaction	16	1870.5			
Full	26	1860.5	71.389	10	**2.39E-11**
Feeding Group	21	1936			
Full	26	1752.9	193.12	5	**<2.2E-16**

Table 31. Means and standard deviations of each level of main effects from the model evaluating spring treatment macroinvertebrate δ15N.

Factor [Level]	Mean	SD
Watershed [Fertilized]	2.357	2.823
Watershed [Unfertilized]	2.969	1.665
Watershed [Secondary]	2.650	1.891
Sample Period [Apr-June]	1.619	2.079
Sample Period [July]	4.388	2.826
Sample Period [Aug/Sept]	3.540	2.193
Sample Period [Nov]	2.084	1.689
Sample Period [Dec]	2.069	1.484
Sample Period [Feb]	2.319	1.476

Table 32. Main effect coefficients and their standard errors for the model evaluating spring treatment macroinvertebrate δ15N.

Factor [Level]	Parameter Estimate	Standard Error	t-value
(Intercept)	3.537	0.485	7.29
Chinook Density	36.784	18.188	2.022
Watershed [Fertilized]	-0.879	0.547	-1.609
Watershed [Unfertilized]	0.846	0.549	1.543
Sample Period [Apr-June]	-1.067	0.504	-2.118
Sample Period [July]	0.009	0.503	0.018
Sample Period [Aug/Sept]	0.078	0.504	0.154
Sample Period [Nov]	-0.701	0.503	-1.394
Sample Period [Feb]	-0.188	0.562	-0.334

Table 33. δ15N Means and standard deviations of each functional feeding group for the spring treatment.

Factor [Level]	Mean	SD
FFG [Filter-Feeders]	3.858	2.151
FFG [Collector-Gatherers]	1.429	1.761
FFG [Predators]	5.438	2.42
FFG [Scrapers]	2.366	1.777
FFG [Shredders]	1.812	1.53

Table 34. Results of a likelihood ratio test evaluating the fixed factors included in the final spring treatment juvenile coho δ15N model. P-values less than 0.05 indicate a significant result.

Model	Df	AIC	Chisq	Chi Df	Pr
Watershed	10	9027.8			
Partial	12	9011.4	20.427	2	**3.67E-05**
Sampling Period	7	9060.7			
Partial	12	9011.4	59.296	5	**1.70E-11**
Chinook Density	20	8874.5			
Full	21	8856.5	19.996	1	**7.76E-06**
Interaction	12	9011.4			
Full	21	8856.5	172.83	9	**<2.2E-16**

Table 35. Means and standard deviations of each level of main effects from the model evaluating spring treatment juvenile coho δ15N.

Factor [Level]	Mean	SD
Watershed [Fertilized]	7.666	2.137
Watershed [Unfertilized]	7.356	2.202
Watershed [Secondary]	6.927	1.920
Sample Period [July]	6.901	2.079
Sample Period [Aug/Sept]	7.259	2.826
Sample Period [Nov]	7.235	2.193
Sample Period [Dec]	8.022	1.689
Sample Period [Feb]	6.794	1.484
Sample Period [April-June]	8.159	1.476

Table 36. Main effect coefficients and their standard errors for the model evaluating spring treatment juvenile coho δ15N.

Factor [Level]	Parameter Estimate	Standard Error	t-value
(Intercept)	9.165	0.720	12.736
Chinook Density	41.300	8.382	4.927
Watershed [Fertilized]	-1.649	0.412	-4.005
Watershed [Unfertilized]	-0.864	0.382	-2.264
Sample Period [July]	-2.387	0.398	-6.001
Sample Period [Aug/Sept]	-1.438	0.555	-2.59
Sample Period [Nov]	-2.142	0.491	-4.36
Sample Period [Dec]	-18.000	0.496	-2.456
Sample Period [Feb]	-2.649	0.48	-5.517

Table 37. Results of a likelihood ratio test evaluating the fixed factors included in the final spring treatment juvenile coho length model. P-values less than 0.05 indicate a significant result.

Model	Df	AIC	Chisq	Chi Df	Pr
Watershed	10	22349			
Partial	12	22313	39.731	2	**2.36E-09**
Sampling Period	7	22899			
Partial	12	22313	595.34	5	**<2.2E-16**
Interaction	12	22313			
Full	21	22293	37.965	9	**1.77E-05**

Table 38. Results of a likelihood ratio test evaluating the fixed factors included in the final spring treatment juvenile coho weight model. P-values less than 0.05 indicate a significant result. The model evaluating interaction was fitted omitting samples taken in the final sample period.

Model	Df	AIC	Chisq	Chi Df	Pr
Watershed	10	18451			
Partial	12	18445	9.832	2	**7.33E-03**
Sampling Period	7	18578			
Partial	12	18445	143.4	5	**<2.2E-16**
Interaction	12	18445			
Full	21	18454	8.428	9	**1.52E-05**

Table 39. Means and standard deviations of each level of main effects from the model evaluating spring treatment juvenile coho length (mm).

Factor [Level]	Mean	SD
Watershed [Fertilized]	94.119	24.000
Watershed [Unfertilized]	91.107	26.529
Watershed [Secondary]	81.517	16.487
Sample Period [July]	70.682	10.783
Sample Period [Aug/Sept]	75.425	9.471
Sample Period [Nov]	82.393	9.889
Sample Period [Dec]	86.435	8.537
Sample Period [Feb]	93.178	13.273
Sample Period [April-June]	124.293	27.807

Table 40. Main effect coefficients and their standard errors for the model evaluating spring treatment juvenile coho length (mm).

Factor [Level]	Parameter Estimate	Standard Error	t-value
(Intercept)	119.191	3.359	35.49
Watershed-Fertilized	4.543	2.414	1.88
Watershed-Unfertilized	1.172	2.047	0.57
Sample Period [July]	-53.706	1.828	-29.39
Sample Period [Aug/Sept]	-44.821	3.283	-13.65
Sample Period [Nov]	-35.096	2.773	-12.65
Sample Period [Dec]	-31.173	2.780	-11.22
Sample Period [Feb]	-25.146	2.727	-9.22

Table 41. Means and standard deviations of each level of main effects from the model evaluating spring treatment juvenile coho weight (g).

Factor [Level]	Mean	SD
Watershed [Fertilized]	10.865	10.683
Watershed [Unfertilized]	10.176	10.907
Watershed [Secondary]	6.939	4.474
Sample Period [July]	4.500	2.090
Sample Period [Aug/Sept]	5.382	2.077
Sample Period [Nov]	6.871	2.155
Sample Period [Dec]	7.644	1.805
Sample Period [Feb]	9.315	5.147
Sample Period [April-June]	22.17	16.466

Table 42. Main effect coefficients and their standard errors for the model evaluating spring treatment juvenile coho weight (g). The final sample period (April-June) was omitted from this model.

Factor [Level]	Parameter Estimate	Standard Error	t-value
(Intercept)	10.196	0.452	22.537
Watershed-Fertilized	-0.880	0.427	-2.064
Watershed-Unfertilized	-1.544	0.434	-3.555
Sample Period [July]	-6.752	0.391	-17.278
Sample Period [Aug/Sept]	-5.141	0.517	-9.95
Sample Period [Nov]	-3.208	0.392	-8.175
Sample Period [Dec]	-2.180	0.395	-5.523

Table 43. Means and standard deviations of fall treatment coho smolt outmigration estimates (abundance) in the fertilized and unfertilized watersheds during years with and without SCA application.

Treatment	Watershed	Mean	SD
Non-SCA	Fertilized	4011	1829
SCA	Fertilized	5594	2675
Non-SCA	Unfertilized	9831	2977
SCA	Unfertilized	10410	1689

Table 44. Means and standard deviations of fall treatment coho smolt length (g) in the fertilized and unfertilized watersheds during years with and without SCA application.

Treatment	Watershed	Mean	SD
Non-SCA	Fertilized	114.4	4.2
SCA	Fertilized	113.4	1.4
Non-SCA	Unfertilized	104.5	4.2
SCA	Unfertilized	103.8	1.4

Table 45. Means and standard deviations of spring treatment coho outmigration estimates (abundance) in the fertilized and unfertilized watersheds during years with and without SCA application.

Treatment	Watershed	Mean	SD
Non-SCA	Fertilized	6554	2901
SCA	Fertilized	5968	1473
Non-SCA	Unfertilized	9867	2911
SCA	Unfertilized	10447	1508

Table 46. Means and standard deviations of spring treatment coho length (mm) in the fertilized and unfertilized watersheds during years with and without SCA application.

Treatment	Watershed	Mean	SD
Non-SCA	Fertilized	109.5	5.2
SCA	Fertilized	112.5	2.7
Non-SCA	Unfertilized	103.9	3.9
SCA	Unfertilized	106.3	0.6

Figures

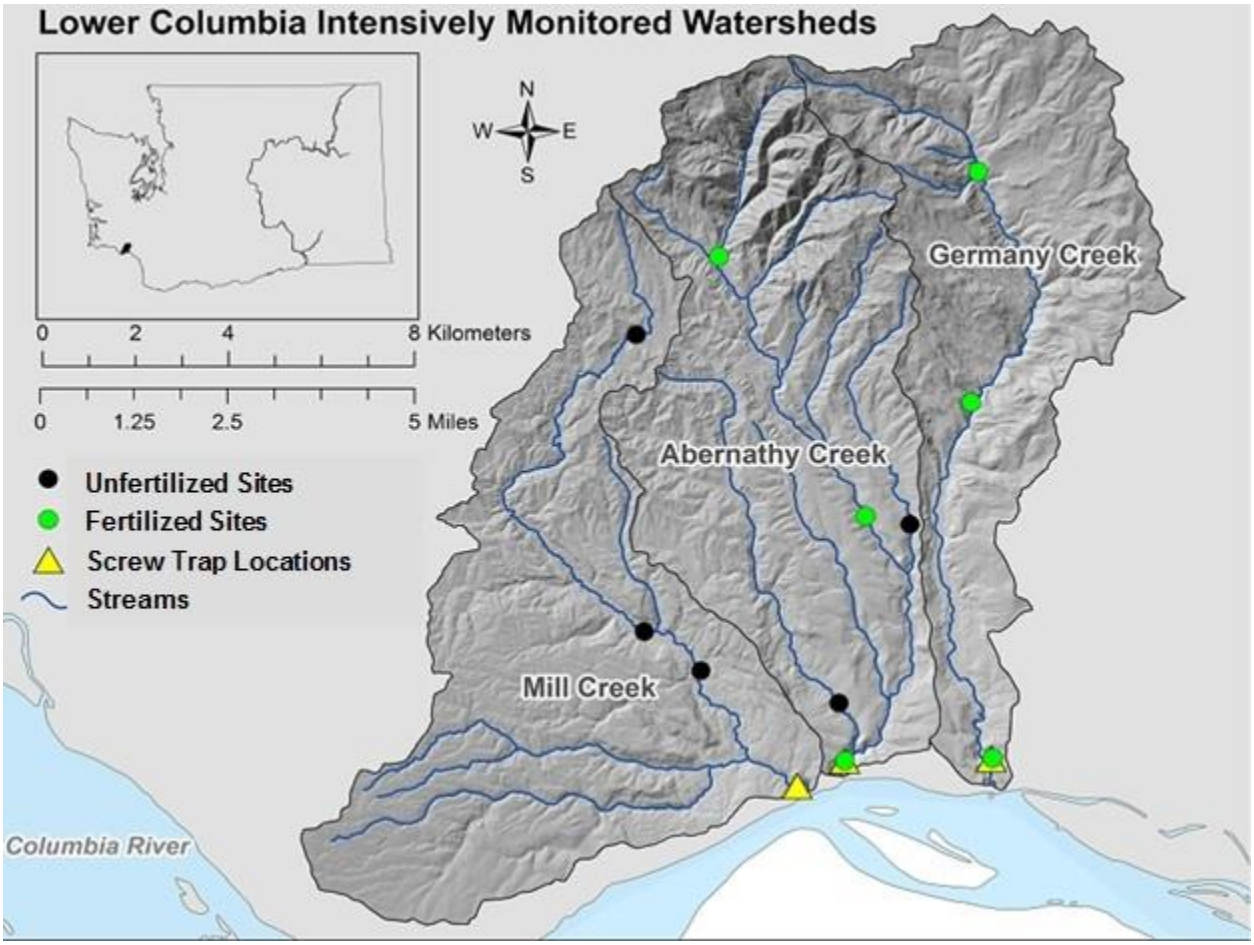

Figure 1. Study site map with watershed delineations and sampling site locations.

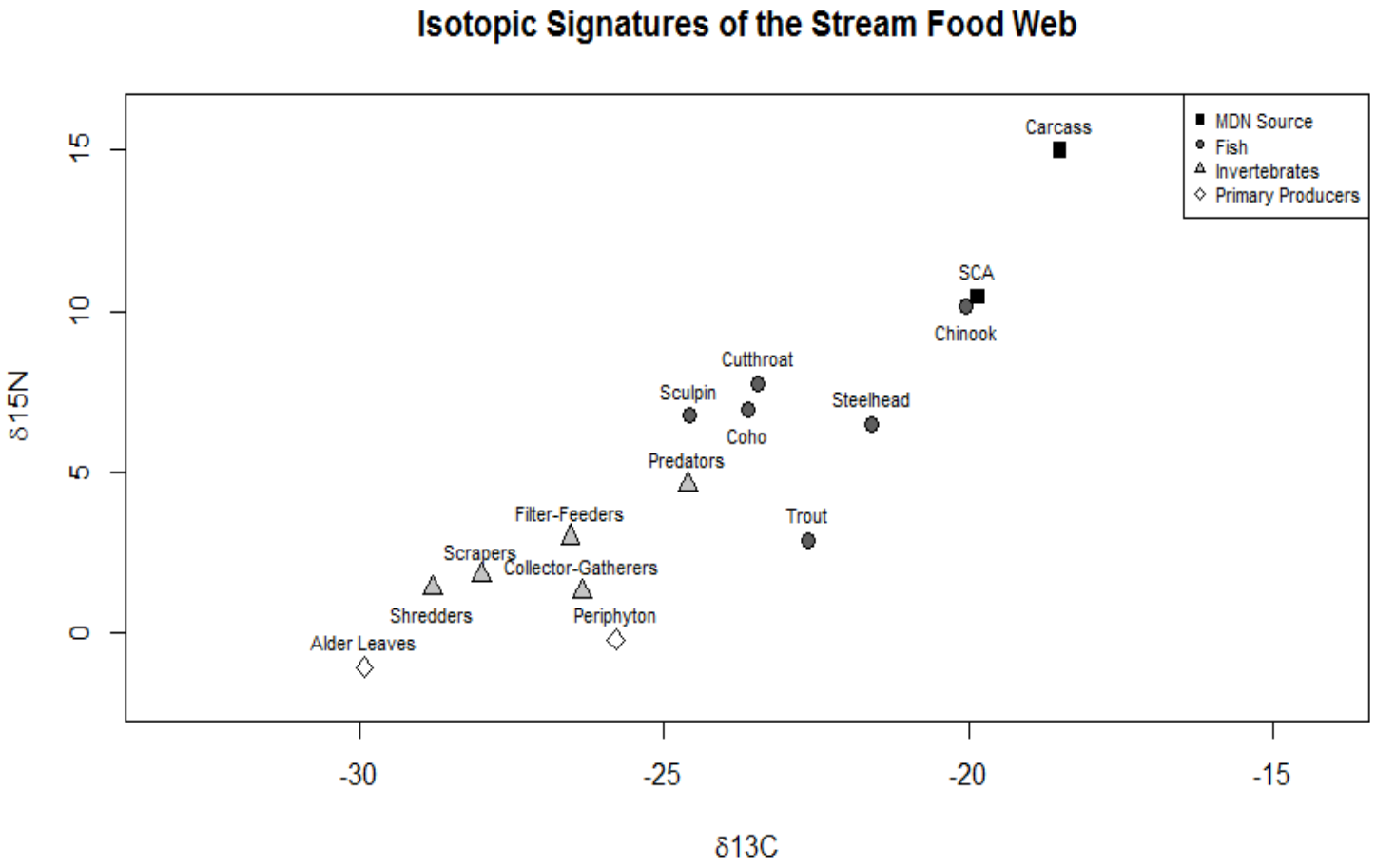

Figure 2. Stable isotope values plotted for each trophic level and each type of organism. Shading and shape denotes the trophic level as shown in the legend, individual organisms are labeled. Trout samples are from O. mykiss and O. clarkii less than 60 mm (could not be distinguished to species). All salmonid fish samples except the carcasses were fry or parr. Carcass samples were adult coho salmon. The y-axis represents average δ15N values, the x-axis represents average δ13C values.

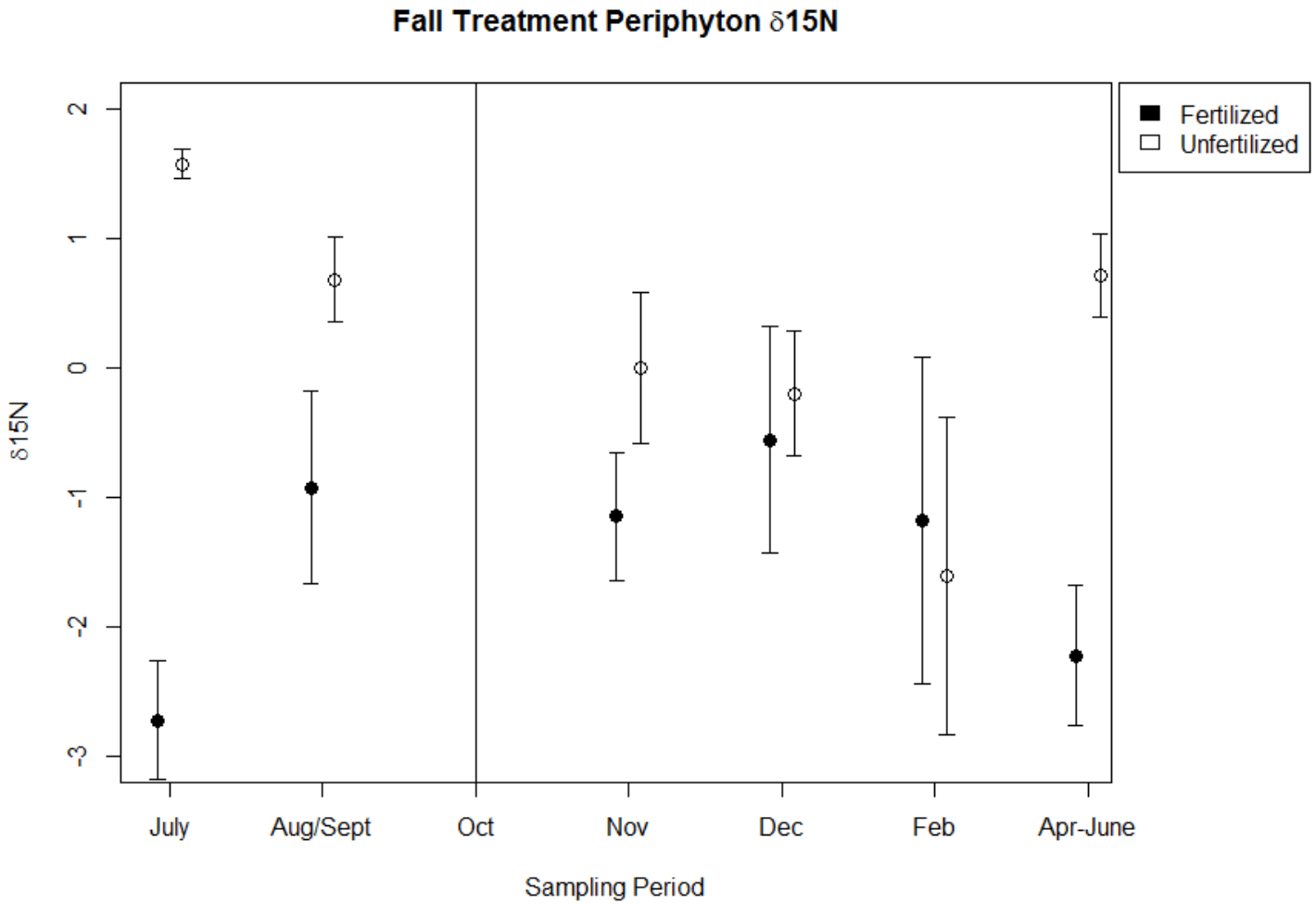

Figure 3. Means and standard errors of periphyton δ15N over all sampling periods associated with analysis of the fall SCA treatment, July 2010 to April-June 2014. Filled values represent samples taken from the fertilized watershed (Germany Creek), unfilled values represent samples taken from the unfertilized watershed (Mill Creek). The vertical line represents the timing of the fall SCA application in the fertilized watershed.

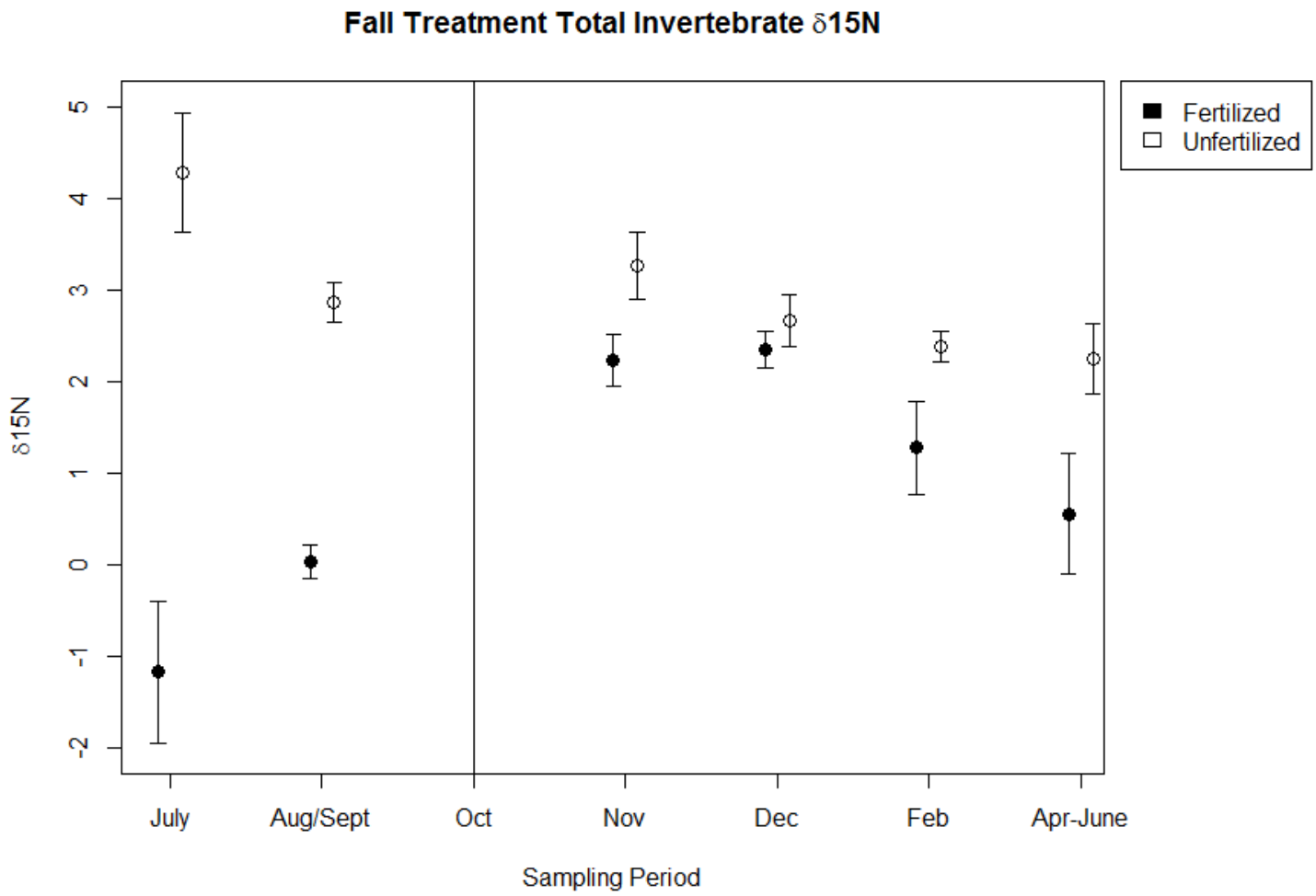

Figure 4.
Means and standard errors of macroinvertebrate δ15N over all sampling periods associated with analysis of the fall SCA treatment, July 2010 to April-June 2014. Filled values represent samples taken from the fertilized watershed (Germany Creek), unfilled values represent samples taken from the unfertilized watershed (Mill Creek). The vertical line represents the timing of the fall SCA application in the fertilized watershed.

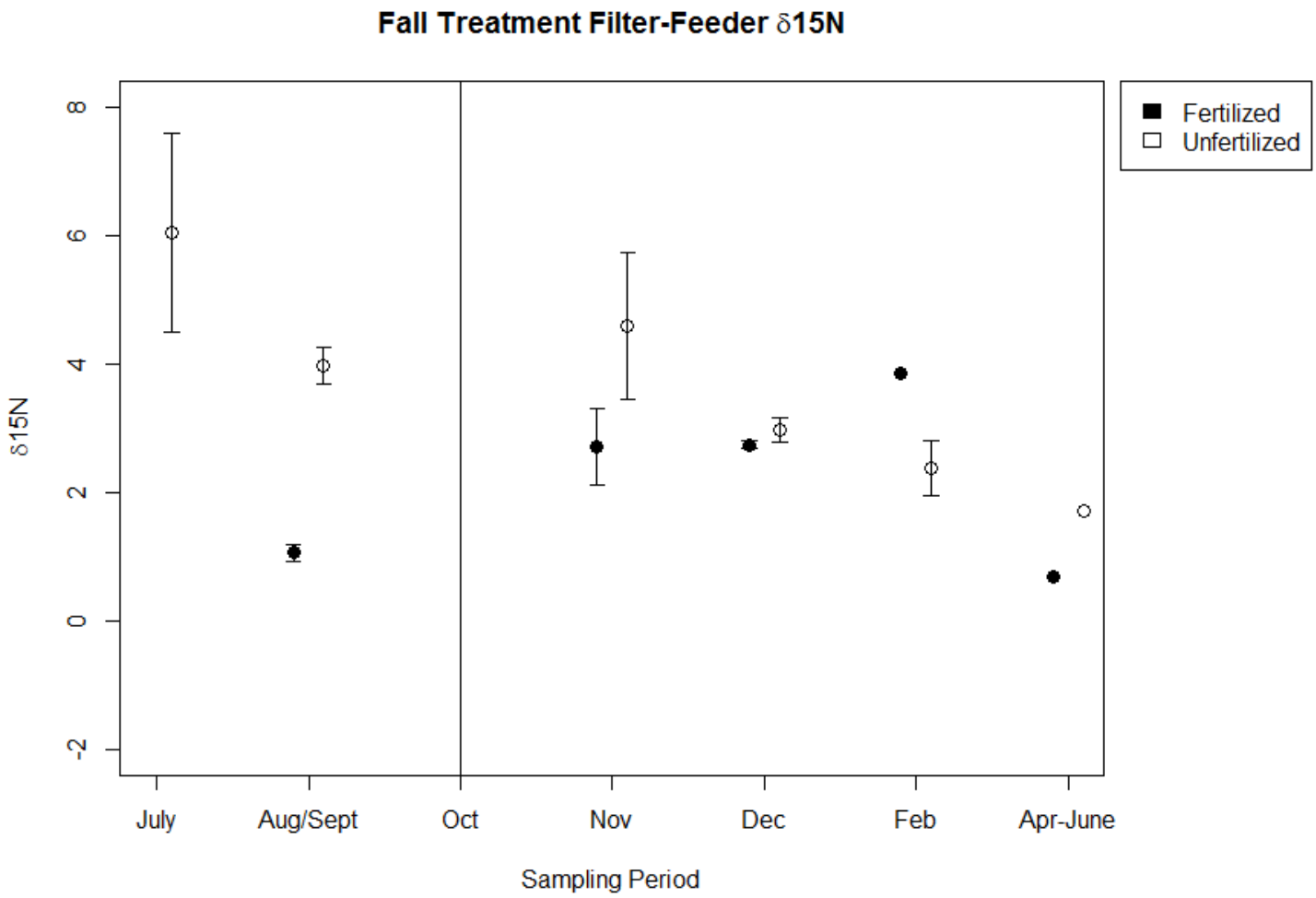

Figure 5. Means and standard errors of macroinvertebrate-filter-feeder δ15N over all sampling periods associated with analysis of the fall SCA treatment, July 2010 to April-June 2014. Filled values represent samples taken from the fertilized watershed (Germany Creek), unfilled values represent samples taken from the unfertilized watershed (Mill Creek). The vertical line represents the timing of the fall SCA application in the fertilized watershed.

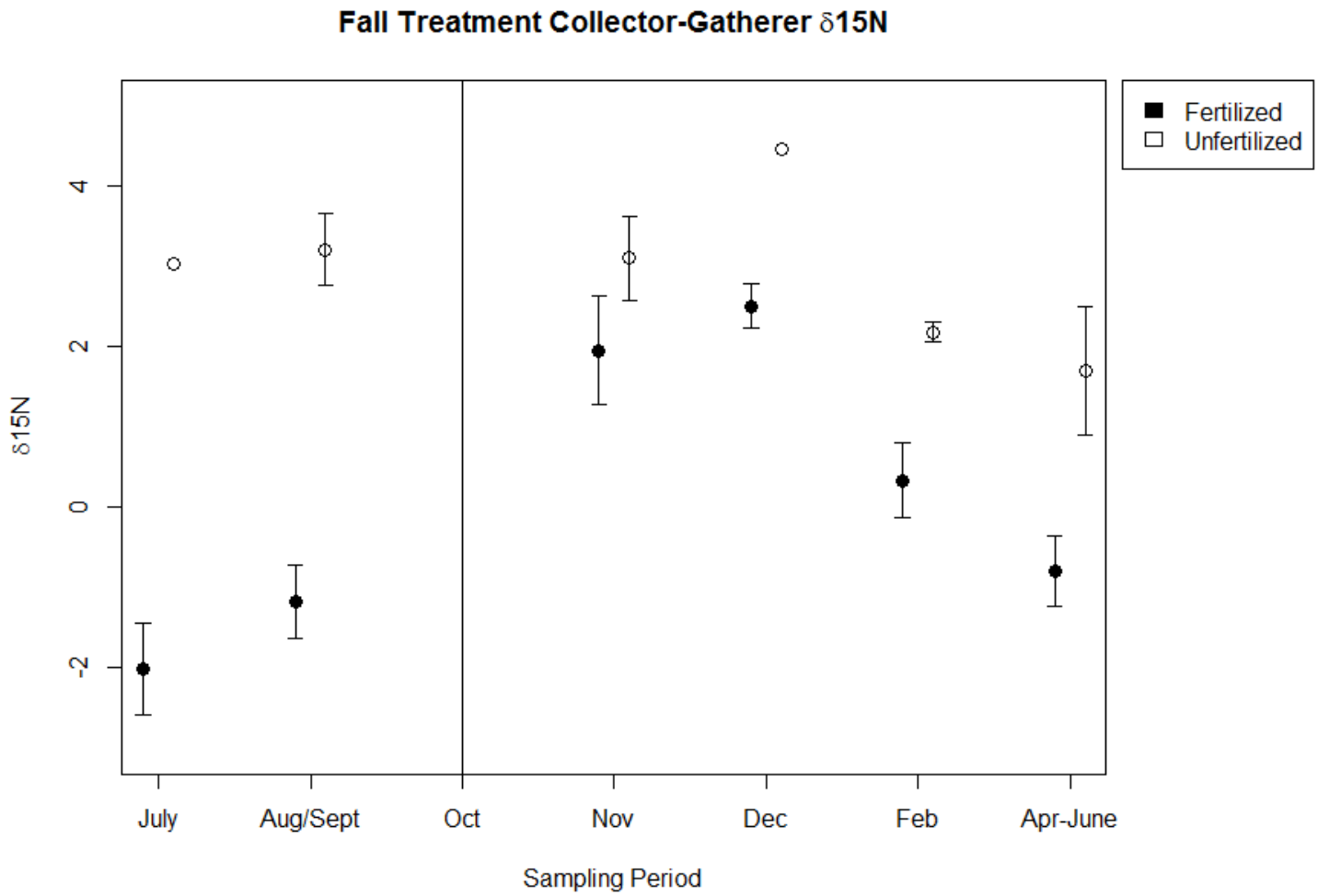

Figure 6. Means and standard errors of macroinvertebrate-collector-gatherer δ15N over all sampling periods associated with analysis of the fall SCA treatment, July 2010 to April-June 2014. Filled values represent samples taken from the fertilized watershed (Germany Creek), unfilled values represent samples taken from the unfertilized watershed (Mill Creek). The vertical line represents the timing of the fall SCA application in the fertilized watershed.

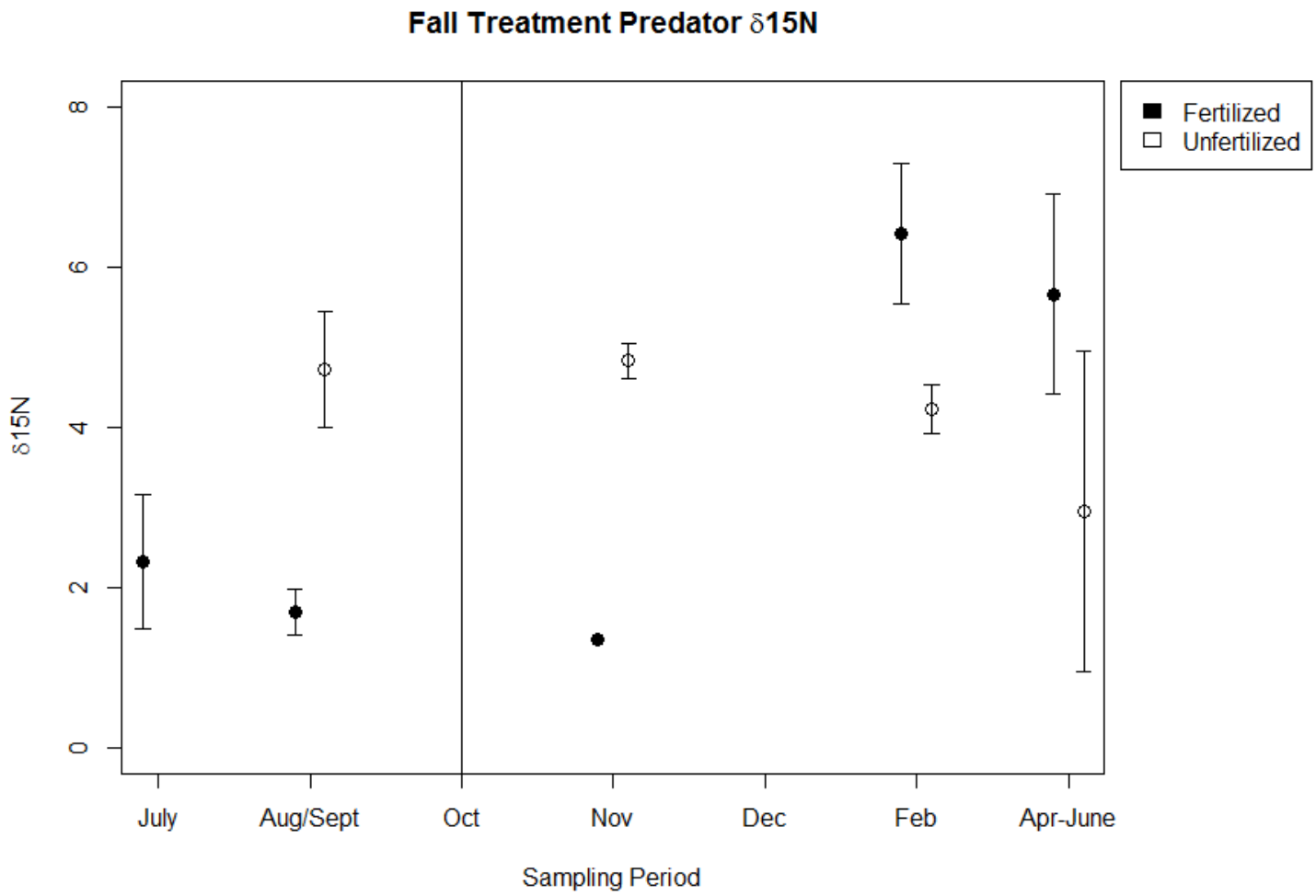

Figure 7. Means and standard errors of macroinvertebrate-predator δ15N over all sampling periods associated with analysis of the fall SCA treatment, July 2010 to April-June 2014. Filled values represent samples taken from the fertilized watershed (Germany Creek), unfilled values represent samples taken from the unfertilized watershed (Mill Creek). The vertical line represents the timing of the fall SCA application in the fertilized watershed.

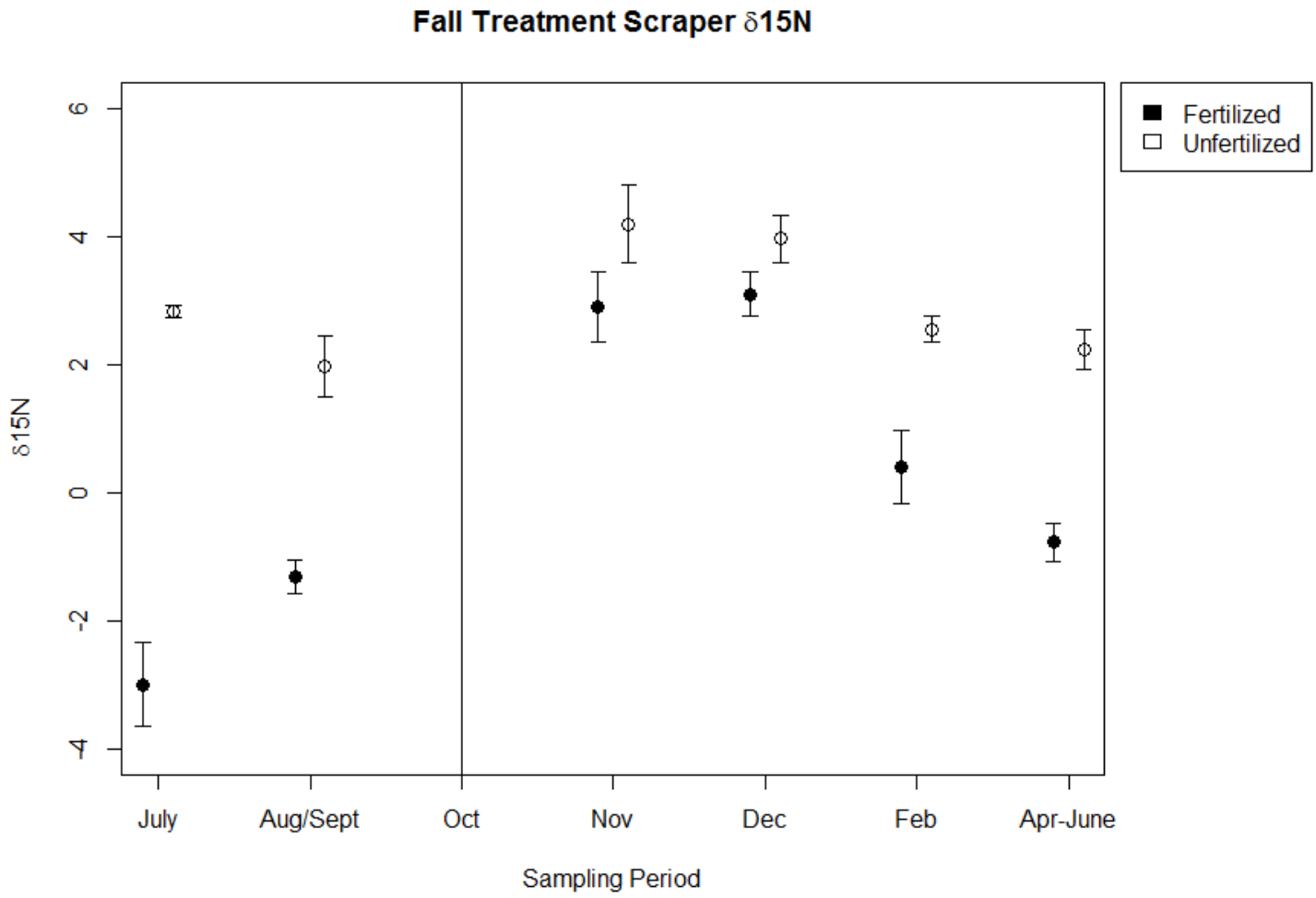

Figure 8. Means and standard errors of macroinvertebrate-scraper δ15N over all sampling periods associated with analysis of the fall SCA treatment, July 2010 to April-June 2014. Filled values represent samples taken from the fertilized watershed (Germany Creek), unfilled values represent samples taken from the unfertilized watershed (Mill Creek). The vertical line represents the timing of the fall SCA application in the fertilized watershed.

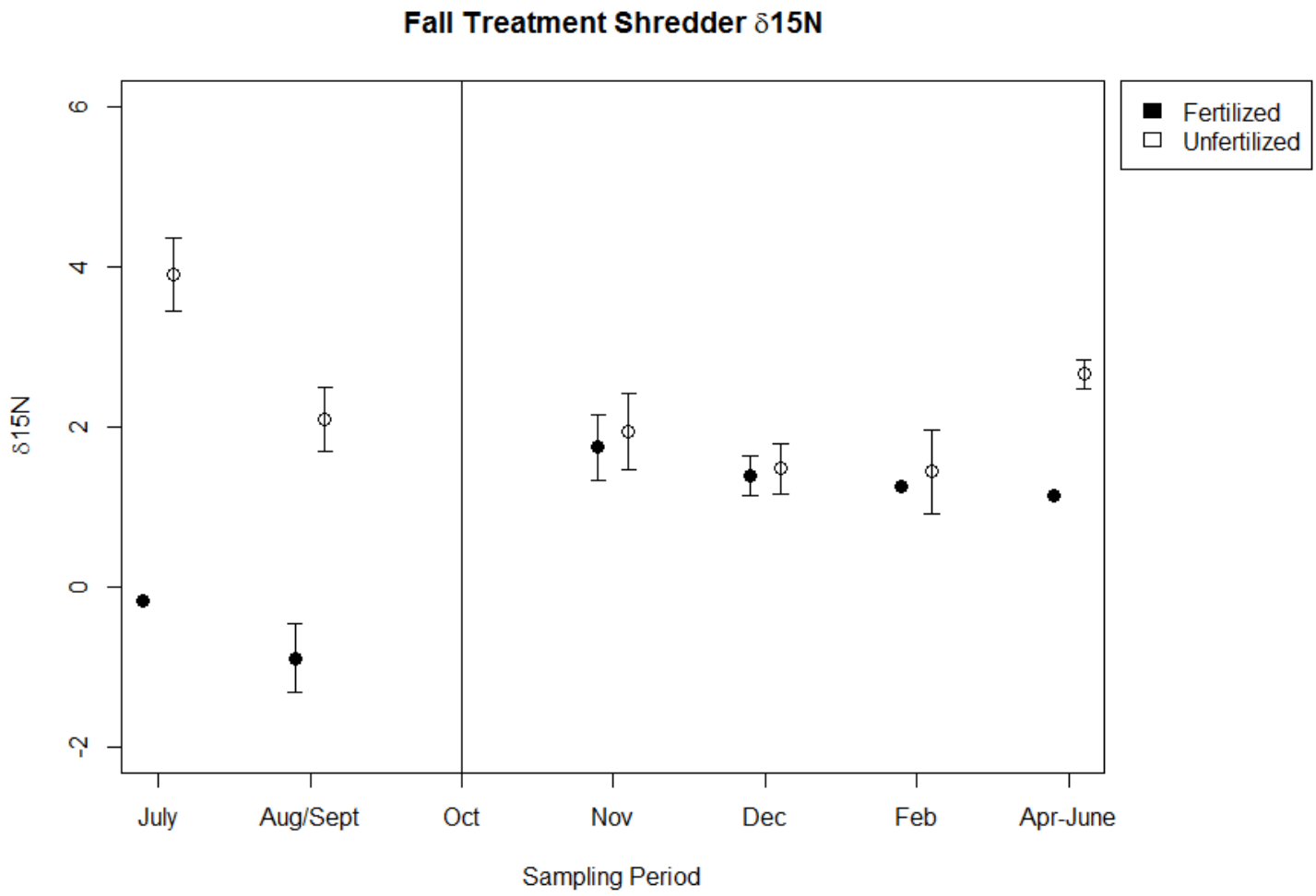

Figure 9. Means and standard errors of macroinvertebrate-shredder δ15N over all sampling periods associated with analysis of the fall SCA treatment, July 2010 to April-June 2014. Filled values represent samples taken from the fertilized watershed (Germany Creek), unfilled values represent samples taken from the unfertilized watershed (Mill Creek). The vertical line represents the timing of the fall SCA application in the fertilized watershed.

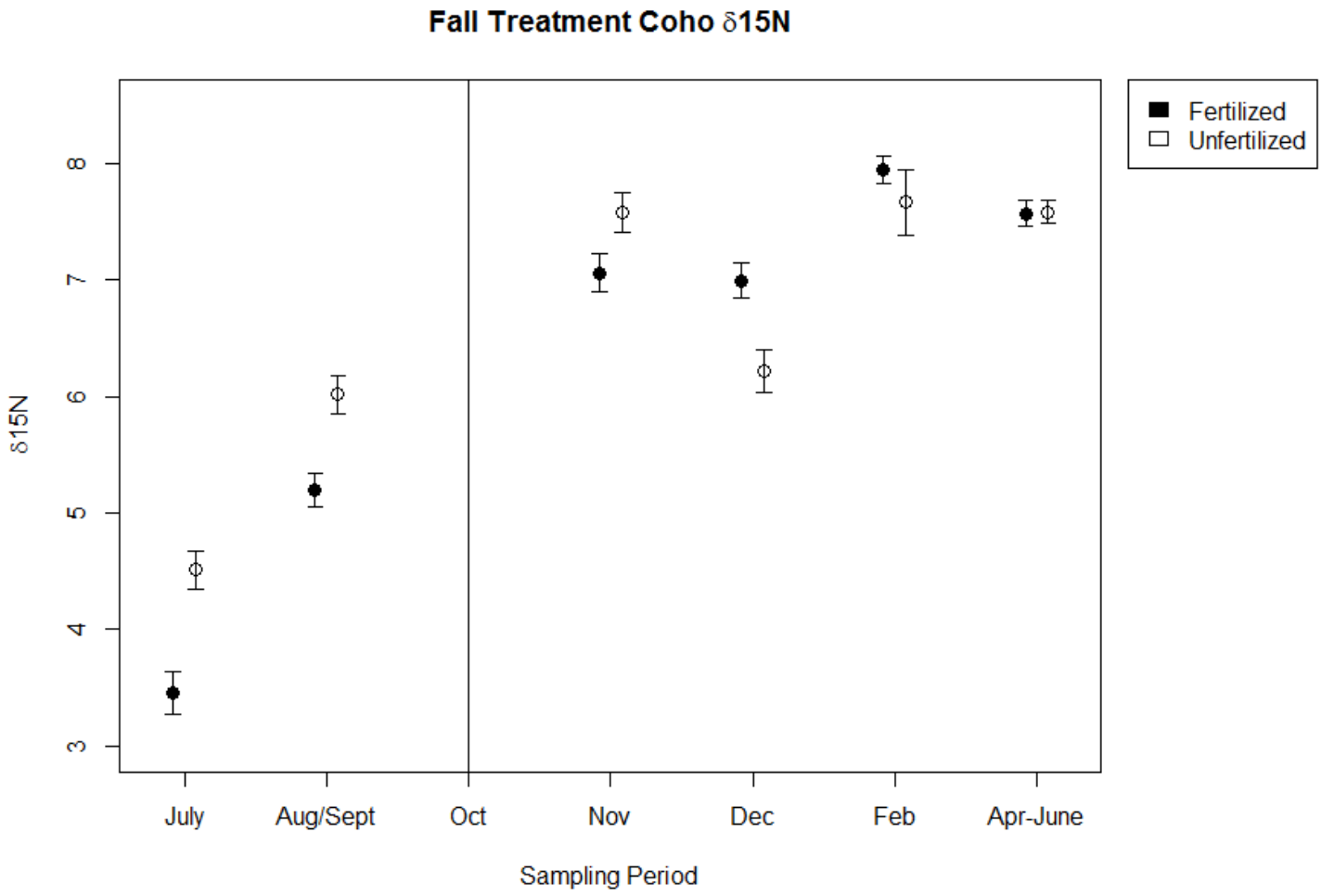

Figure 10. Means and standard errors of juvenile coho δ15N over all sampling periods associated with the analysis of the fall SCA treatment, July 2010 to April-June 2014. Filled values represent samples taken from the fertilized watershed (Germany Creek), unfilled values represent samples taken from the unfertilized watershed (Mill Creek). The vertical line represents the timing of the fall SCA application in the fertilized watershed.

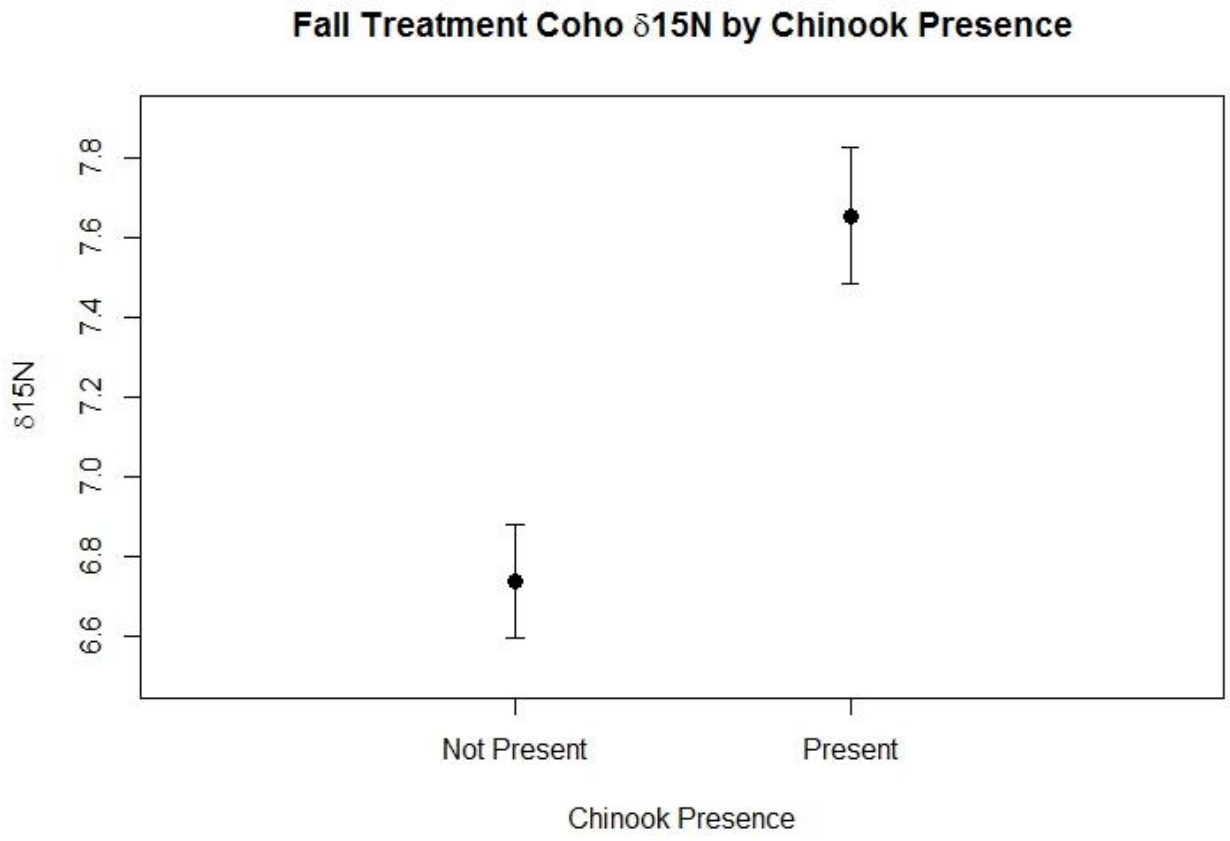

Figure 11. Mean and standard error of $\delta^{15}N$ values of juvenile coho in the month of November at sites where Chinook carcasses were present versus sites where Chinook carcasses were not present. Data are from the fall-fertilized (Germany Creek) and unfertilized (Mill Creek), 2010 to 2013.

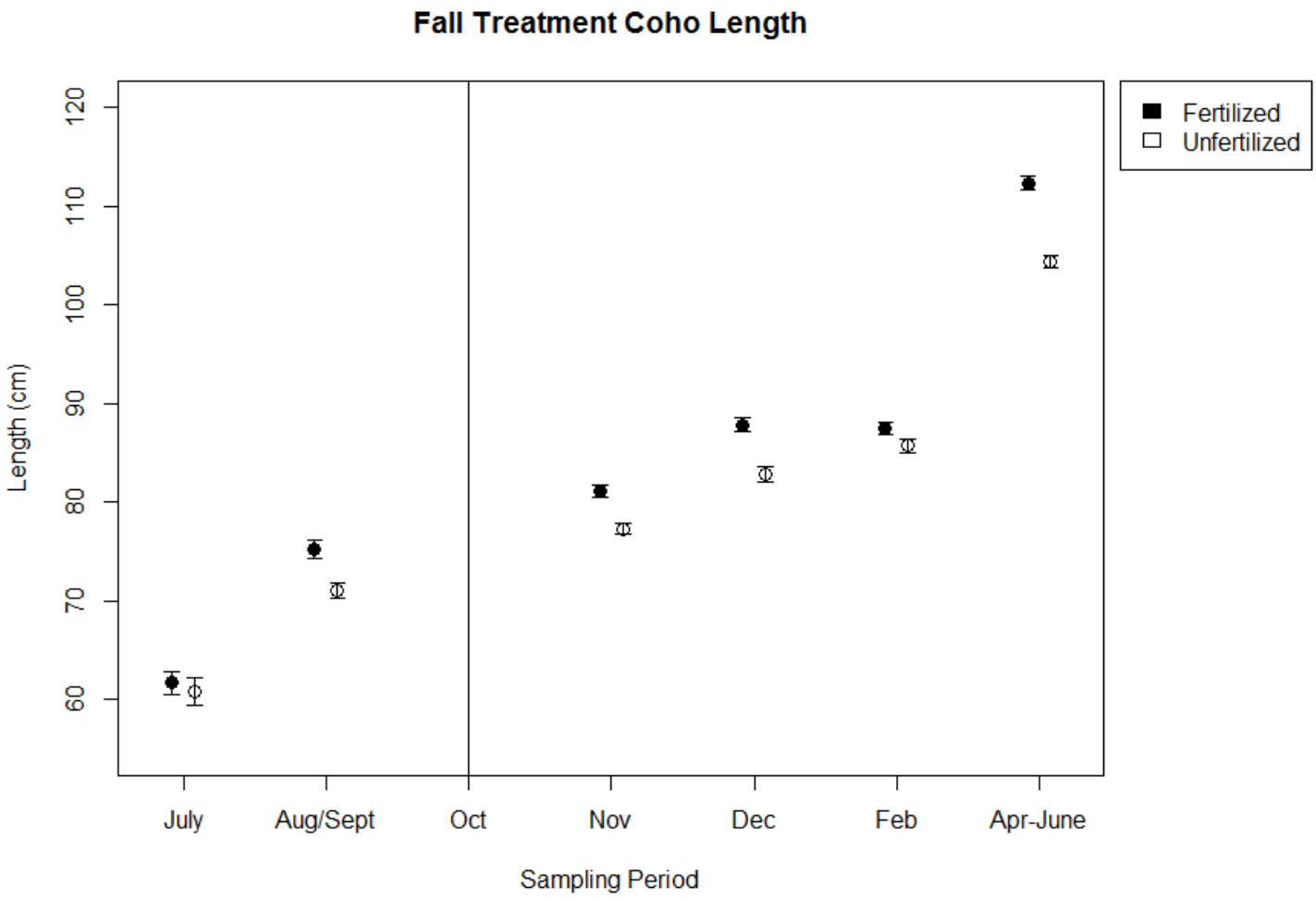

Figure 12. Means and standard errors of juvenile coho length over all sample periods associated with the analysis of the fall SCA treatment, July 2010 to April-June 2014. Filled values represent samples taken from the fertilized watershed (Germany Creek), unfilled values represent samples taken from the unfertilized watershed (Mill Creek). The vertical line represents the timing of the fall SCA application in the fertilized watershed.

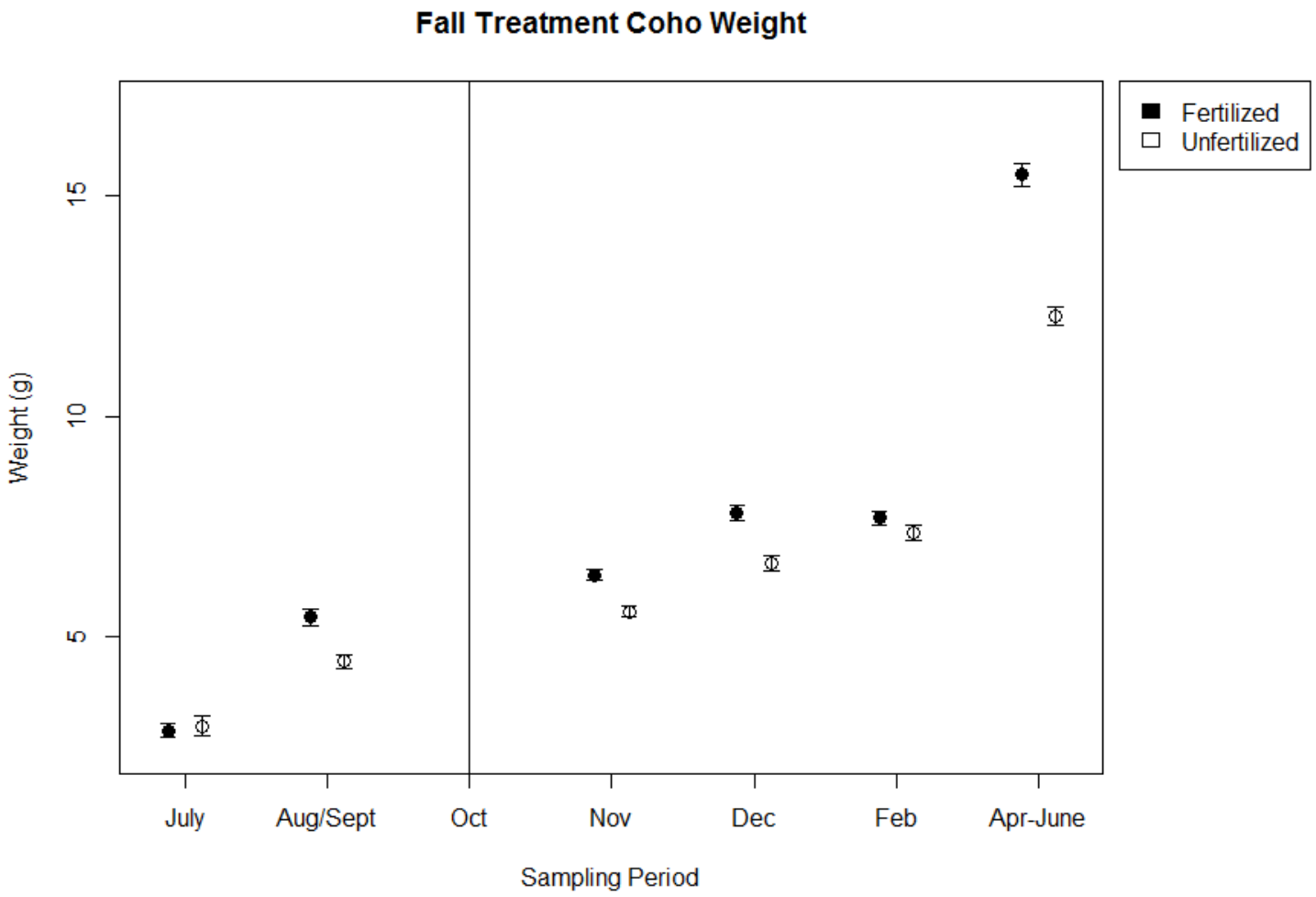

Figure 13. Means and standard errors of juvenile coho weight over all sample periods associated with the analysis of the fall SCA treatment, July 2010 to April-June 2014. Filled values represent samples taken from the fertilized watershed (Germany Creek), unfilled values represent samples taken from the unfertilized watershed (Mill Creek). The vertical line represents the timing of the fall SCA application in the fertilized watershed.

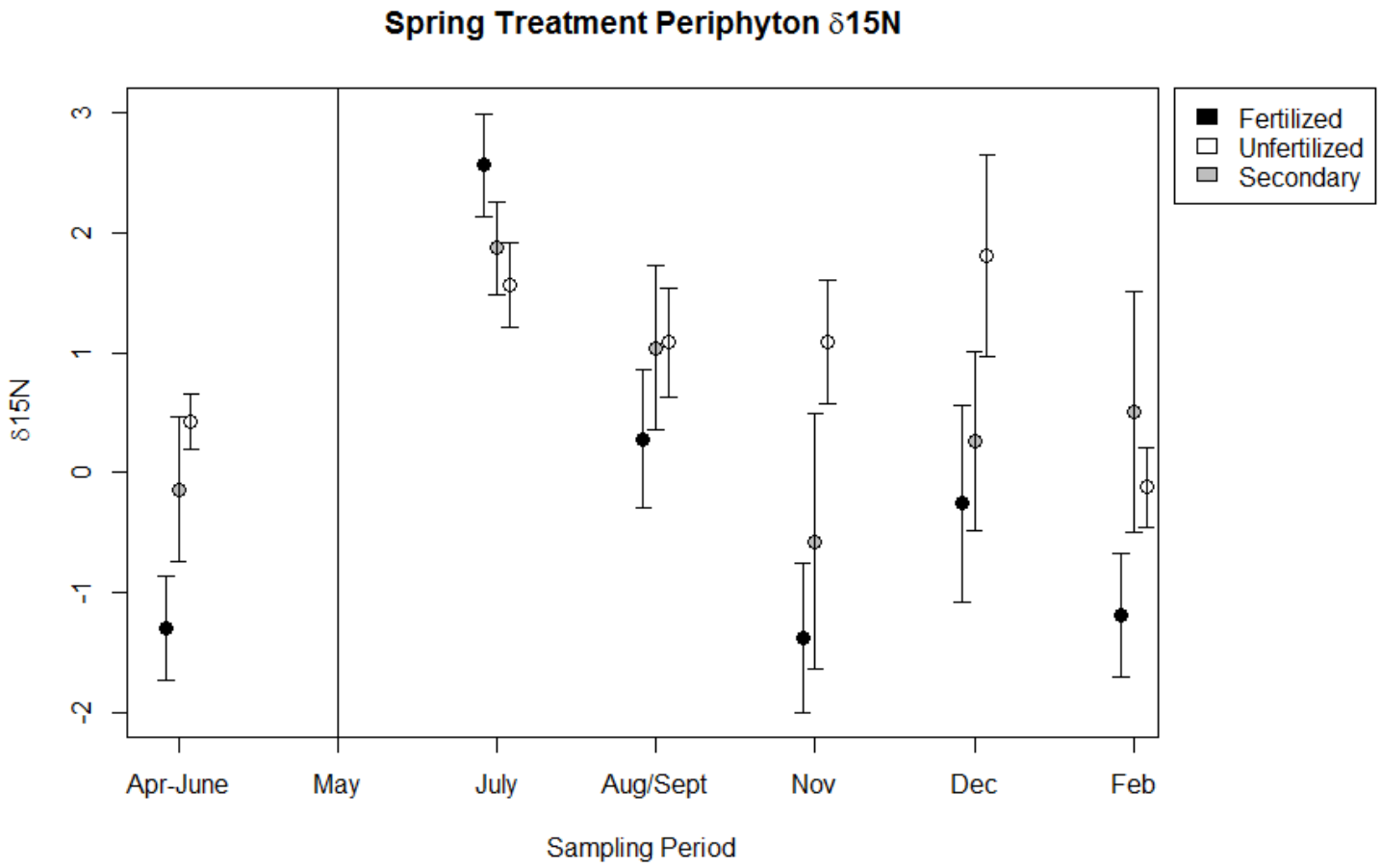

Figure 14. Means and standard errors of periphyton δ15N over all sample periods associated with the analysis of the spring SCA treatment, April-June 2013 to Feb 2016). Filled values represent samples taken from the fertilized watershed (Abernathy Creek), unfilled values represent samples taken from the unfertilized watershed (Mill Creek), and grey values represent samples taken from the secondary unfertilized tributaries (Cameron and Wiest creeks, tributaries to Abernathy Creek). The vertical line represents the timing of the spring SCA application in the fertilized watershed.

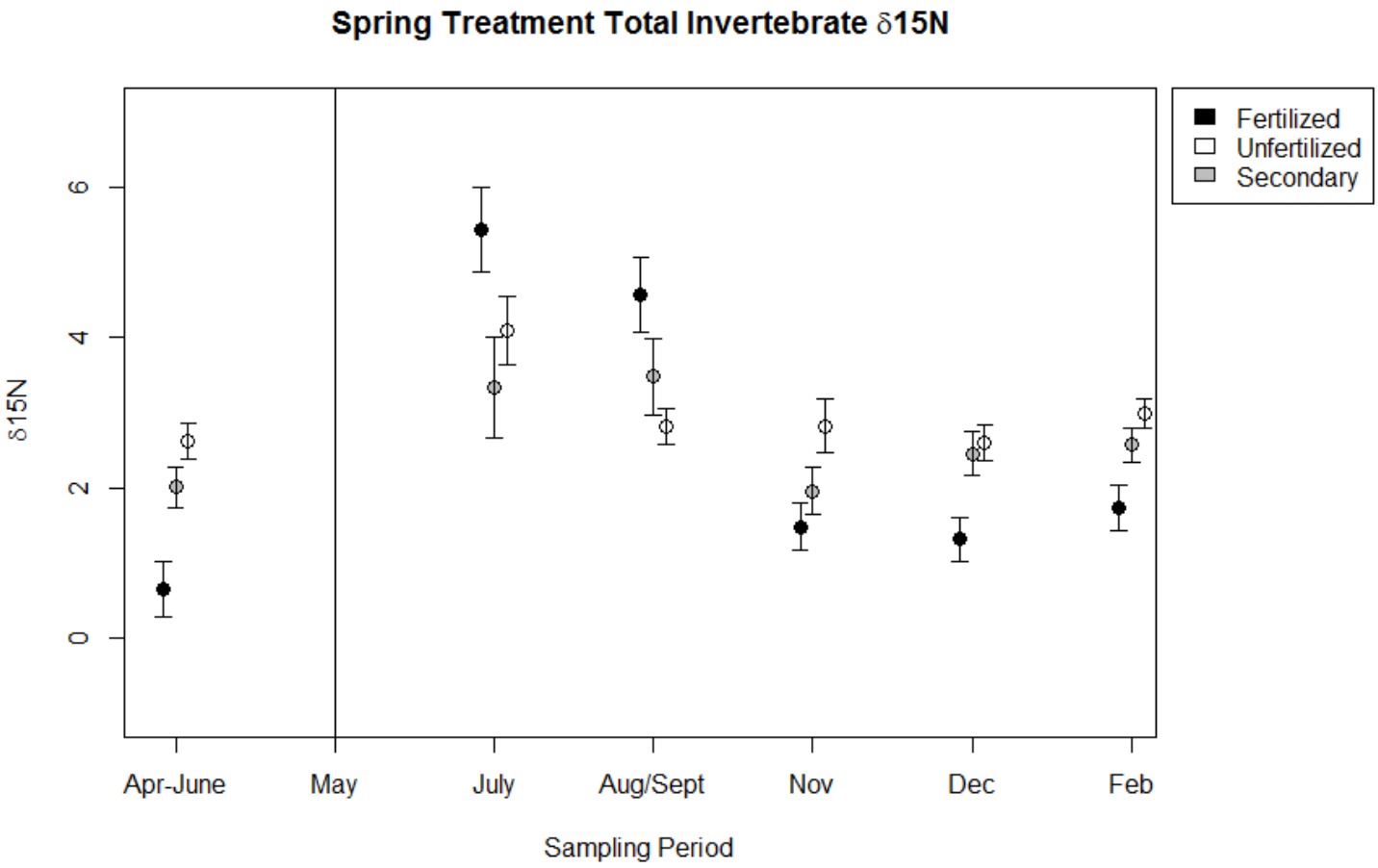

Figure 15. Means and standard errors of macroinvertebrate δ15N over all sample periods associated with the analysis of the spring SCA treatment, April-June 2013 to Feb 2016). Filled values represent samples taken from the fertilized watershed (Abernathy Creek), unfilled values represent samples taken from the unfertilized watershed (Mill Creek), and grey values represent samples taken from the secondary unfertilized tributaries (Cameron and Wiest creeks, tributaries to Abernathy Creek). The vertical line represents the timing of the spring SCA application in the fertilized watershed.

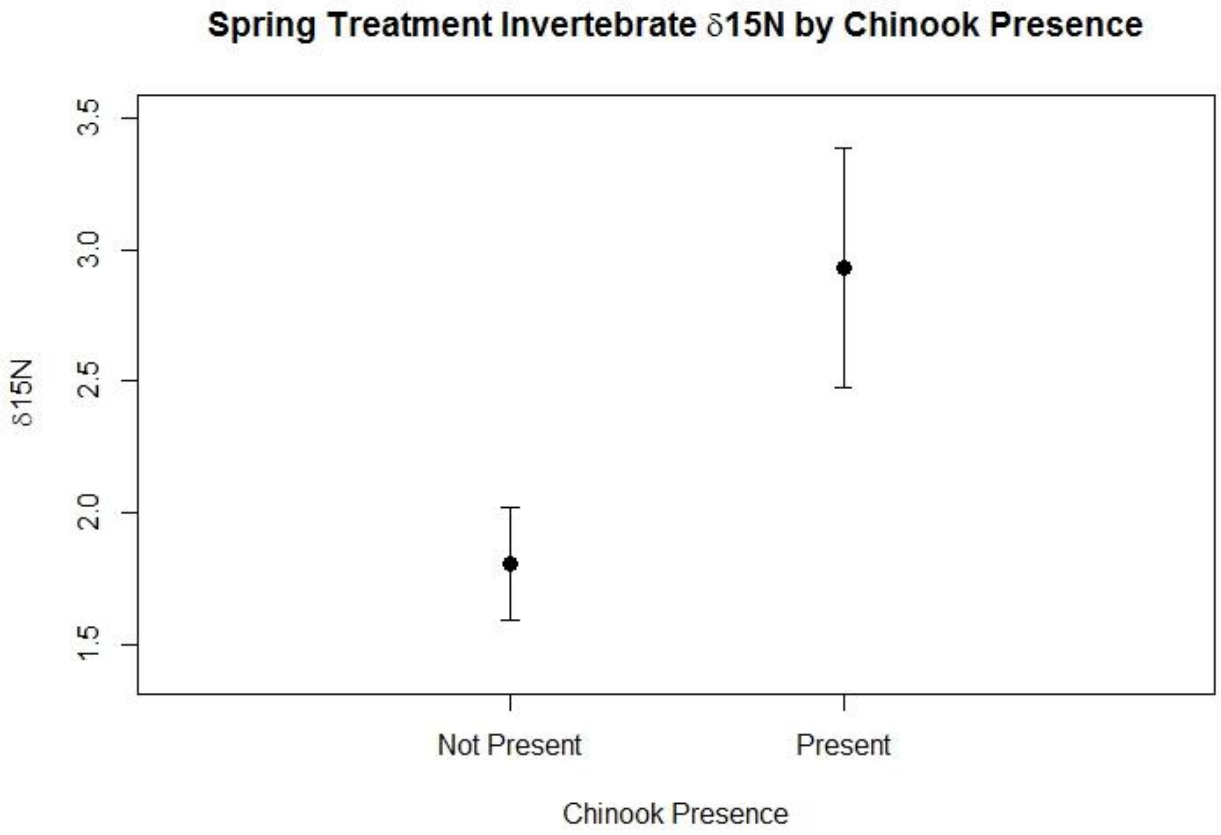

Figure 16. Mean and standard errors of $\delta^{15}N$ values of macroinvertebrates in the month of November at sites where Chinook carcasses were present versus sites where Chinook carcasses were not present. Data are from the spring-fertilized watershed (Abernathy Creek) and unfertilized watershed (Mill Creek), 2013 to 2015.

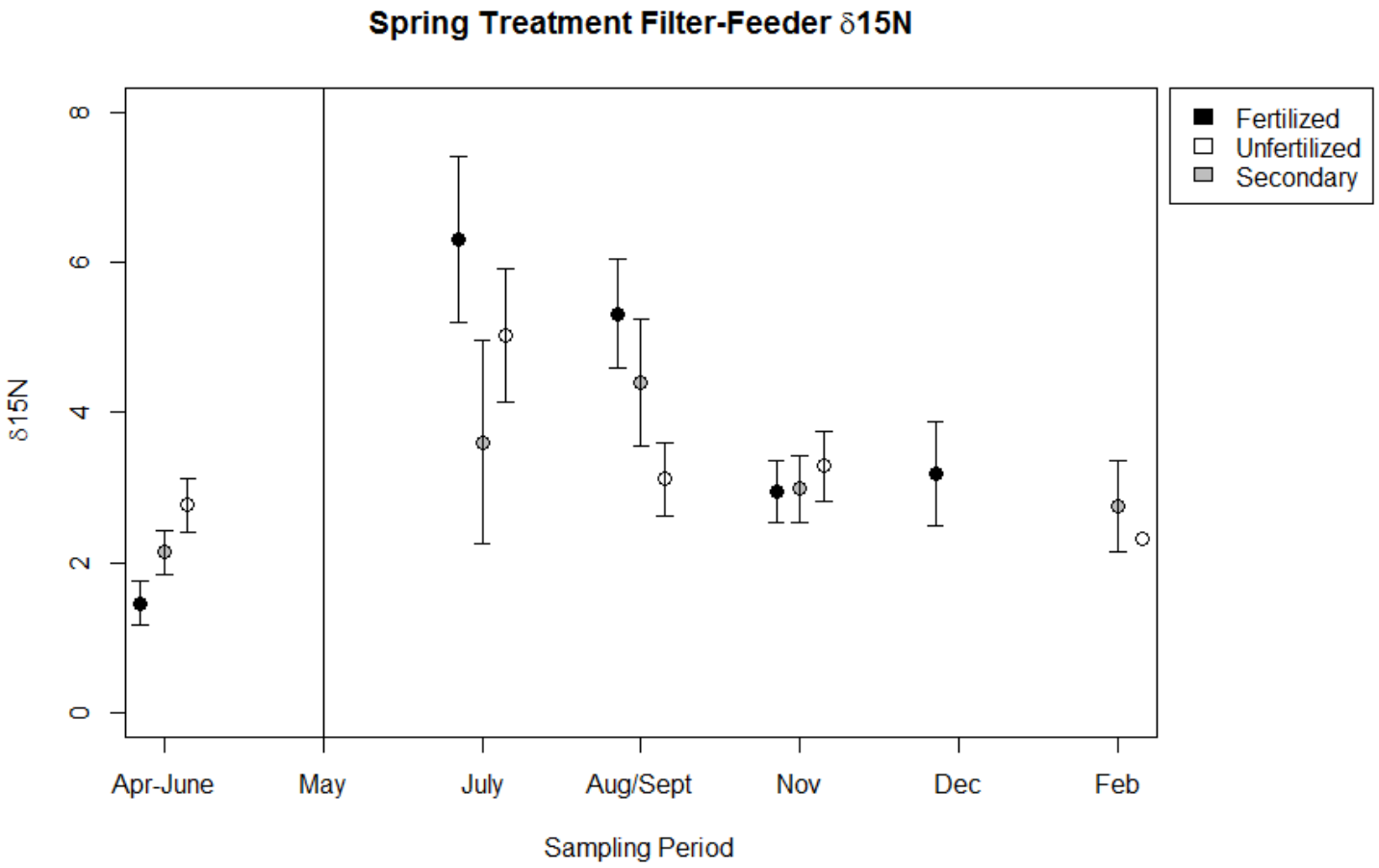

Figure 17. Means and standard errors of macroinvertebrate-filter-feeder δ15N over all sample periods associated with the analysis of the spring SCA treatment, April-June 2013 to Feb 2016). Filled values represent samples taken from the fertilized watershed (Abernathy Creek), unfilled values represent samples taken from the unfertilized watershed (Mill Creek), and grey values represent samples taken from the secondary unfertilized tributaries (Cameron and Wiest creeks, tributaries to Abernathy Creek). The vertical line represents the timing of the spring SCA application in the fertilized watershed.

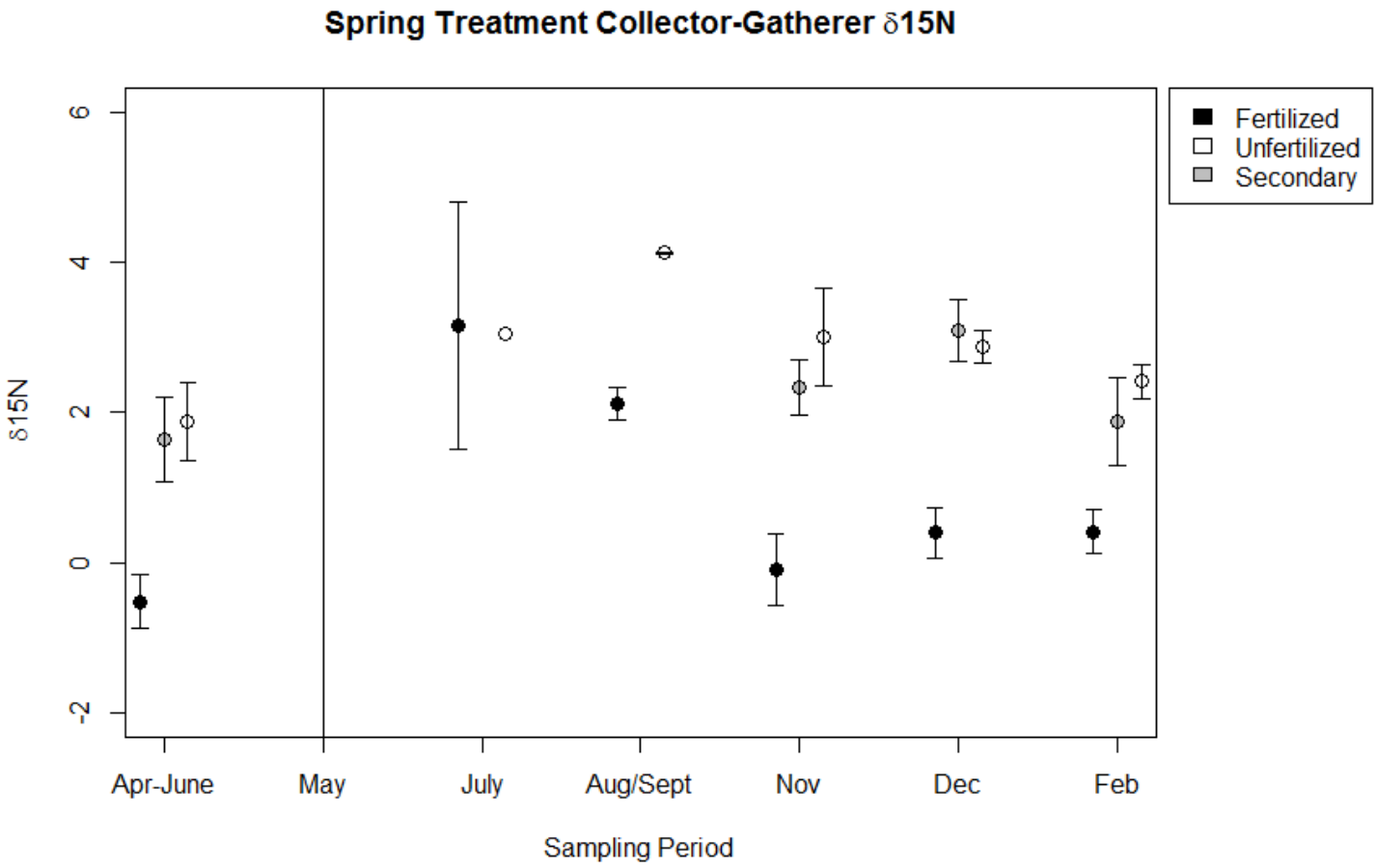

Figure 18. Means and standard errors of macroinvertebrate-collector-gatherer δ15N over all sample periods associated with the analysis of the spring SCA treatment, April-June 2013 to Feb 2016). Filled values represent samples taken from the fertilized watershed (Abernathy Creek), unfilled values represent samples taken from the unfertilized watershed (Mill Creek), and grey values represent samples taken from the secondary unfertilized tributaries (Cameron and Wiest creeks, tributaries to Abernathy Creek). The vertical line represents the timing of the spring SCA application in the fertilized watershed.

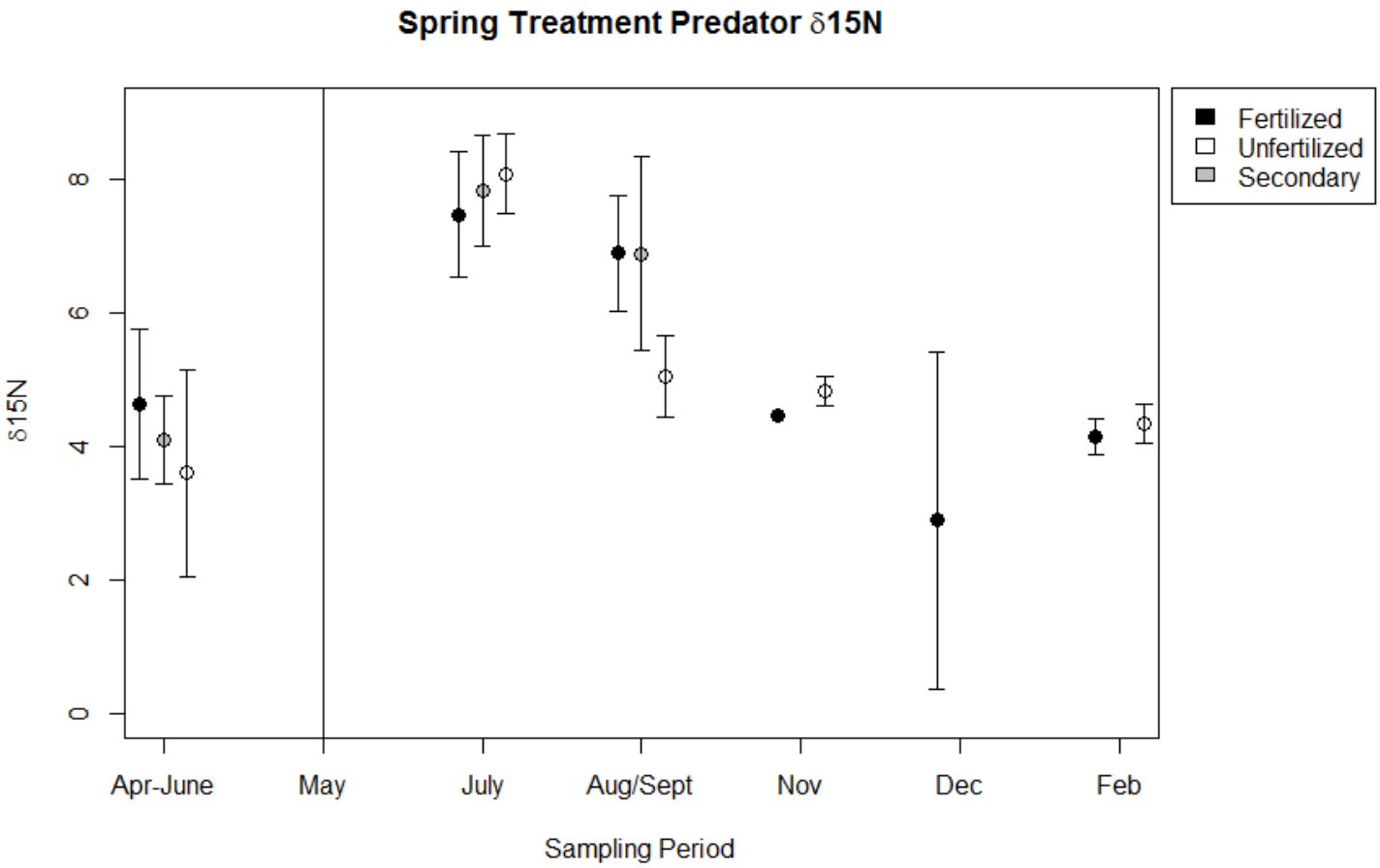

Figure 19. Means and standard errors of macroinvertebrate-predator δ15N over all sample periods associated with the analysis of the spring SCA treatment, April-June 2013 to Feb 2016). Filled values represent samples taken from the fertilized watershed (Abernathy Creek), unfilled values represent samples taken from the unfertilized watershed (Mill Creek), and grey values represent samples taken from the secondary unfertilized tributaries (Cameron and Wiest creeks, tributaries to Abernathy Creek). The vertical line represents the timing of the spring SCA application in the fertilized watershed.

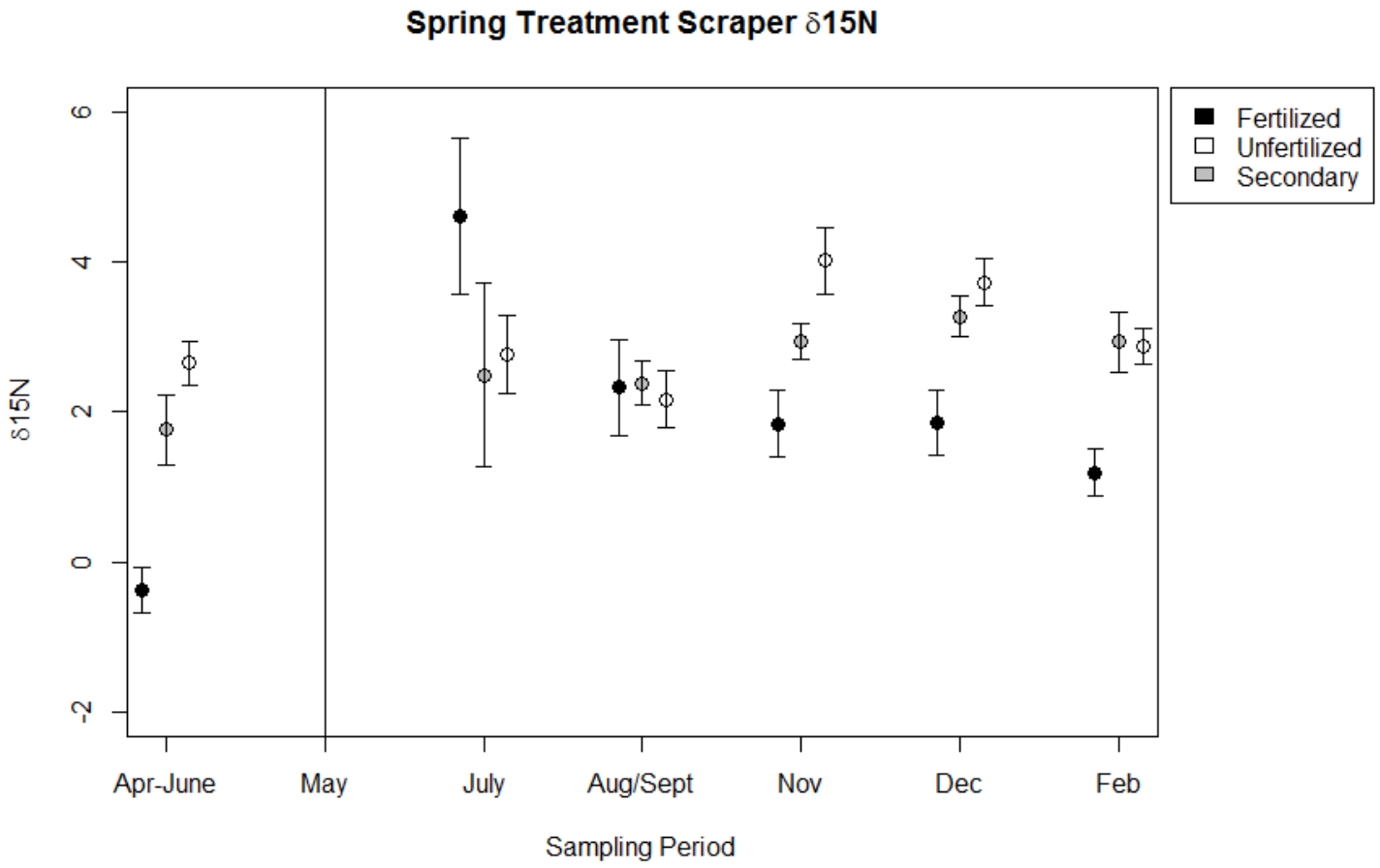

Figure 20. Means and standard errors of macroinvertebrate-scraper δ15N over all sample periods associated with the analysis of the spring SCA treatment, April-June 2013 to Feb 2016). Filled values represent samples taken from the fertilized watershed (Abernathy Creek), unfilled values represent samples taken from the unfertilized watershed (Mill Creek), and grey values represent samples taken from the secondary unfertilized tributaries (Cameron and Wiest creeks, tributaries to Abernathy Creek). The vertical line represents the timing of the spring SCA application in the fertilized watershed.

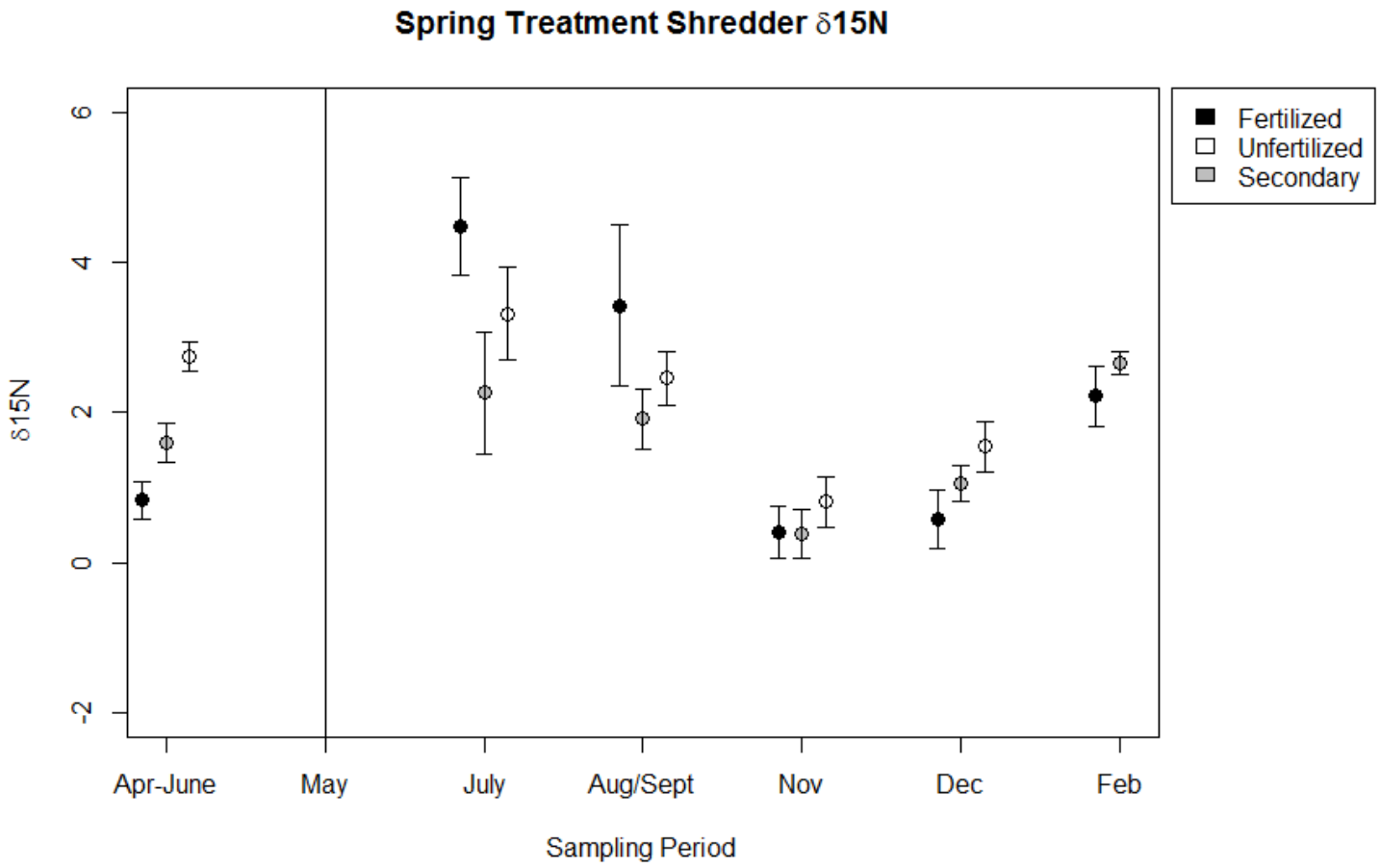

Figure 21. Means and standard errors of macroinvertebrate-shredder δ15N over all sample periods associated with the analysis of the spring SCA treatment, April-June 2013 to Feb 2016). Filled values represent samples taken from the fertilized watershed (Abernathy Creek), unfilled values represent samples taken from the unfertilized watershed (Mill Creek), and grey values represent samples taken from the secondary unfertilized tributaries (Cameron and Wiest creeks, tributaries to Abernathy Creek). The vertical line represents the timing of the spring SCA application in the fertilized watershed.

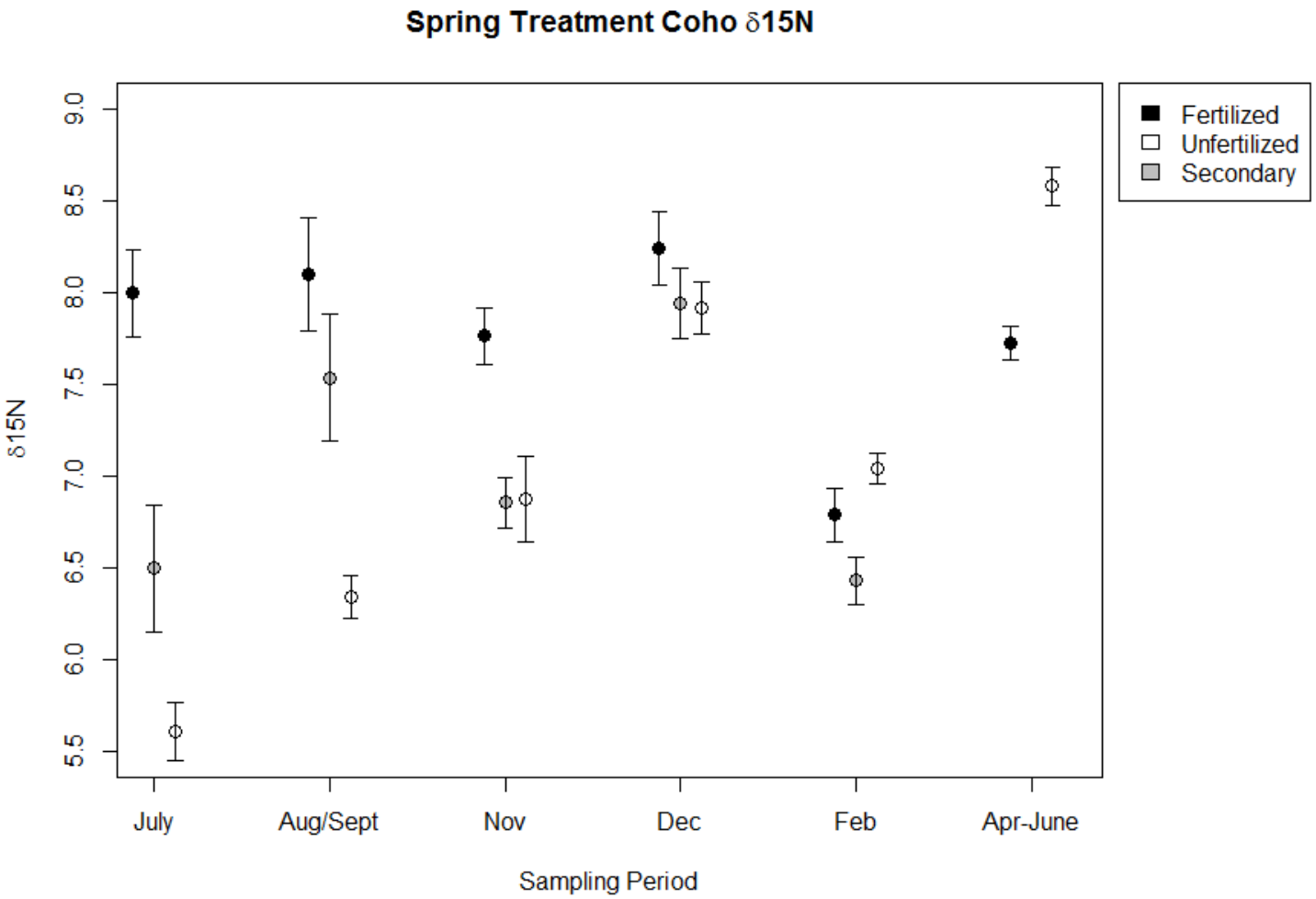

Figure 22. Means and standard errors of juvenile coho δ15N over all sample periods associated with the analysis of the spring SCA treatment, April-June 2013 to Feb 2016. Filled values represent samples taken from the fertilized watershed (Abernathy Creek), unfilled values represent samples taken from the unfertilized watershed (Mill Creek), and grey values represent samples taken from the secondary unfertilized tributaries (Cameron and Wiest creeks, tributaries to Abernathy Creek). The spring SCA applications occurred in May of each year.

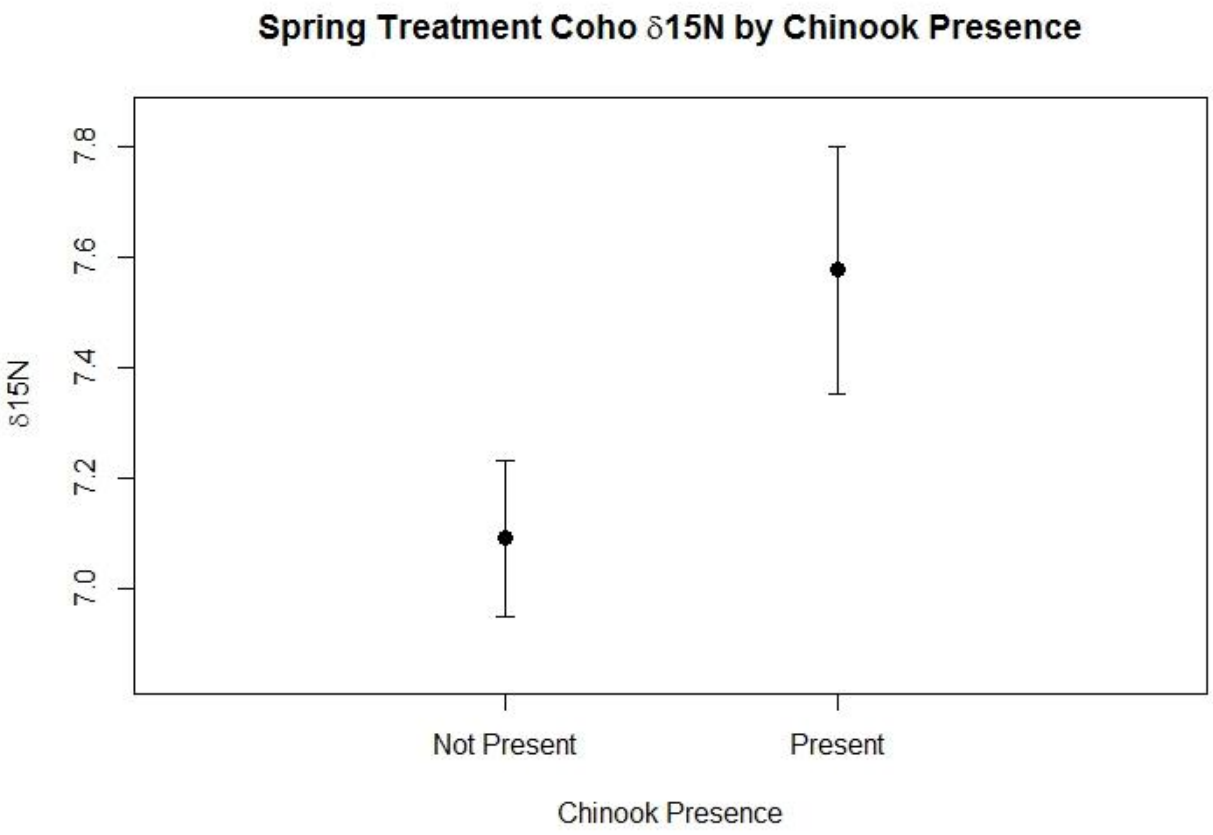

Figure 23. Mean and standard errors of $\delta^{15}N$ values of juvenile coho in the month of November at sites where Chinook carcasses were present versus sites where Chinook carcasses were not present. Data are from the spring-fertilized watershed (Abernathy Creek) and unfertilized watershed (Mill Creek), 2013 to 2015.

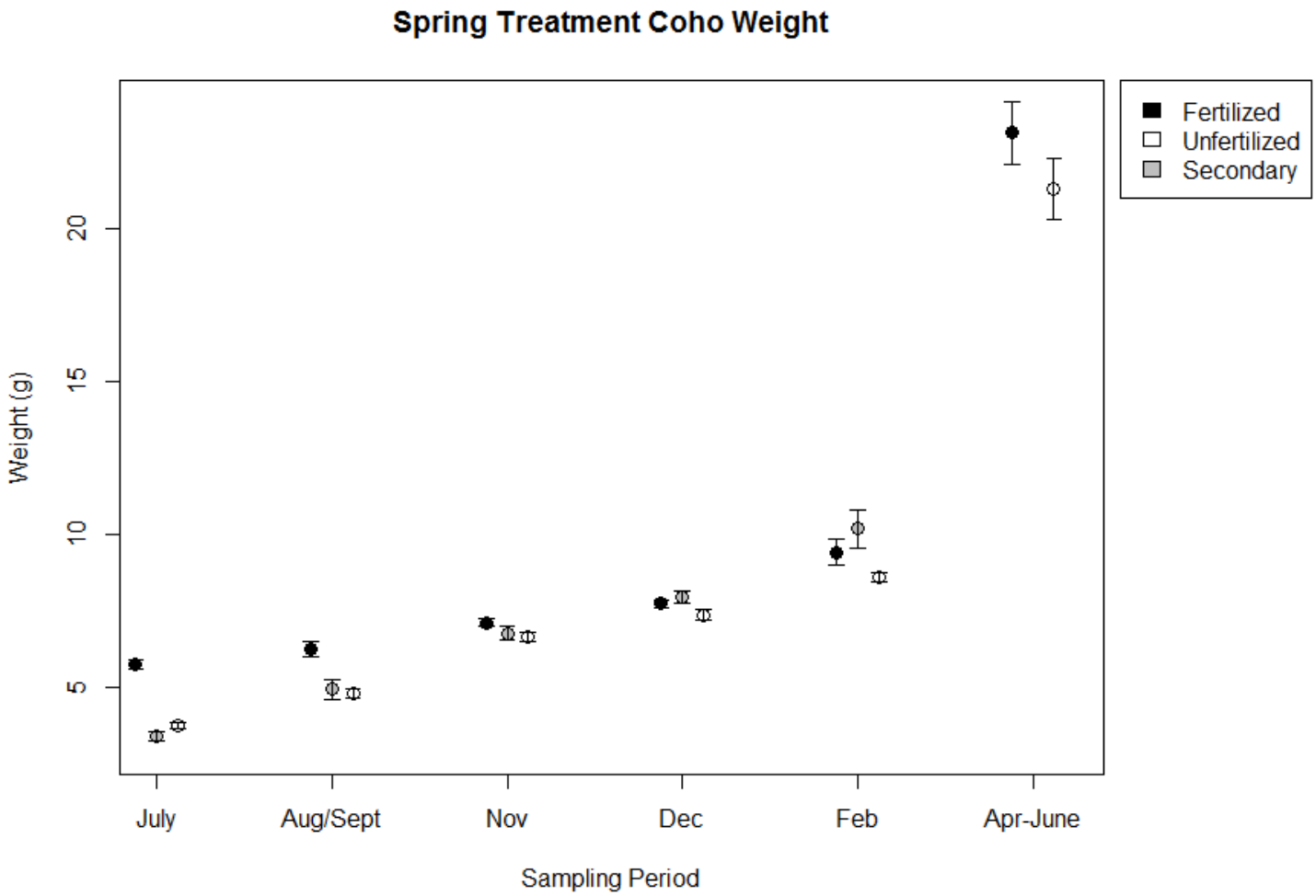

Figure 24. Means and standard errors of juvenile coho weights over all sample periods associated with the spring SCA treatment, April-June 2013 to Feb 2016. Filled values represent samples taken from the fertilized watershed (Abernathy Creek), unfilled values represent samples taken from the unfertilized watershed (Mill Creek), and grey values represent samples taken from the secondary unfertilized tributaries (Cameron and Wiest creeks, tributaries to Abernathy Creek). The spring SCA applications occurred in May of each year.

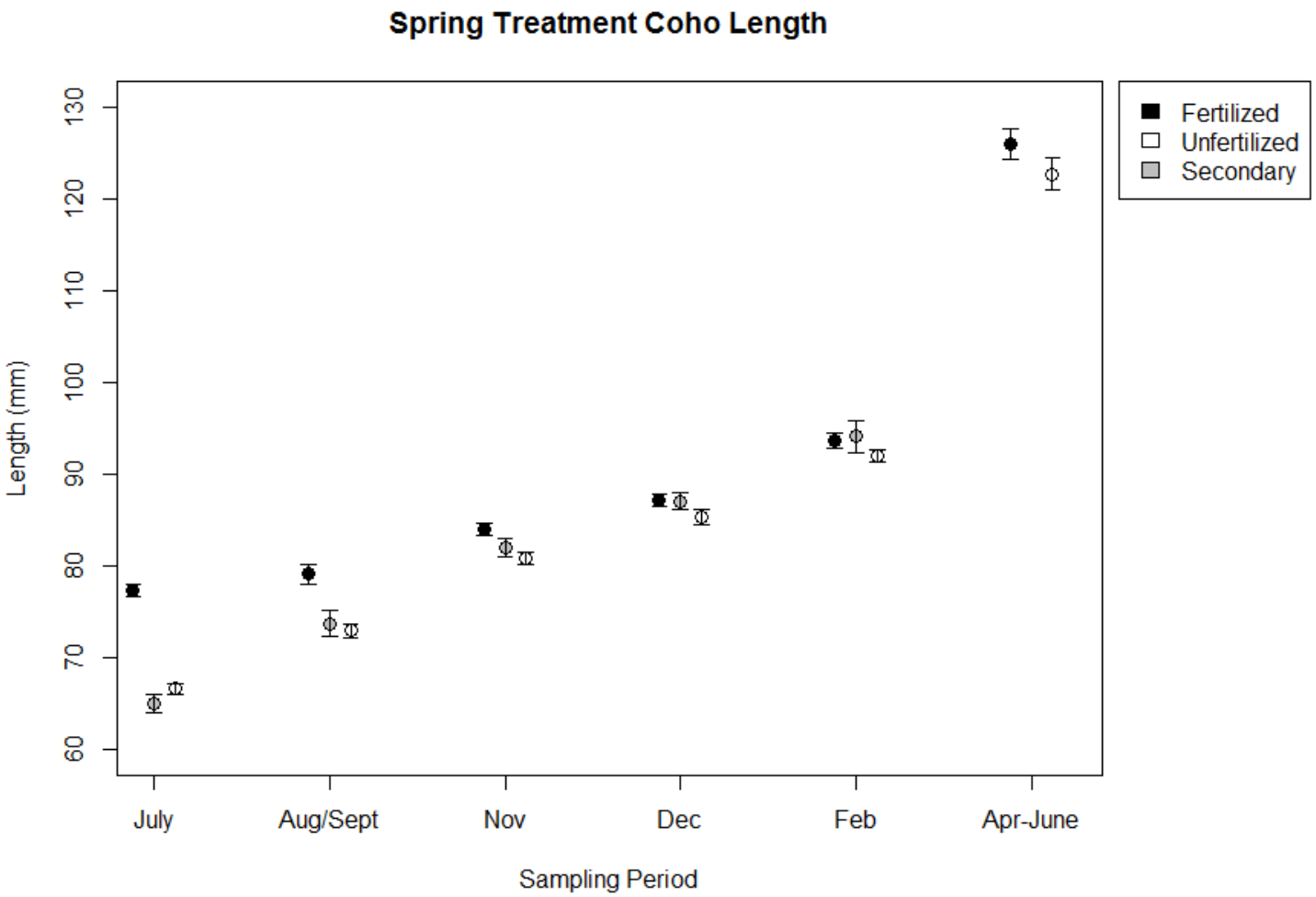

Figure 25. Means and standard errors of juvenile coho lengths over all sample periods associated with the spring SCA treatment, April-June 2013 to Feb 2016. Filled values represent samples taken from the fertilized watershed (Abernathy Creek), unfilled values represent samples taken from the unfertilized watershed (Mill Creek), and grey values represent samples taken from the secondary unfertilized tributaries (Cameron and Wiest creeks, tributaries to Abernathy Creek). The spring SCA applications occurred in May of each year.

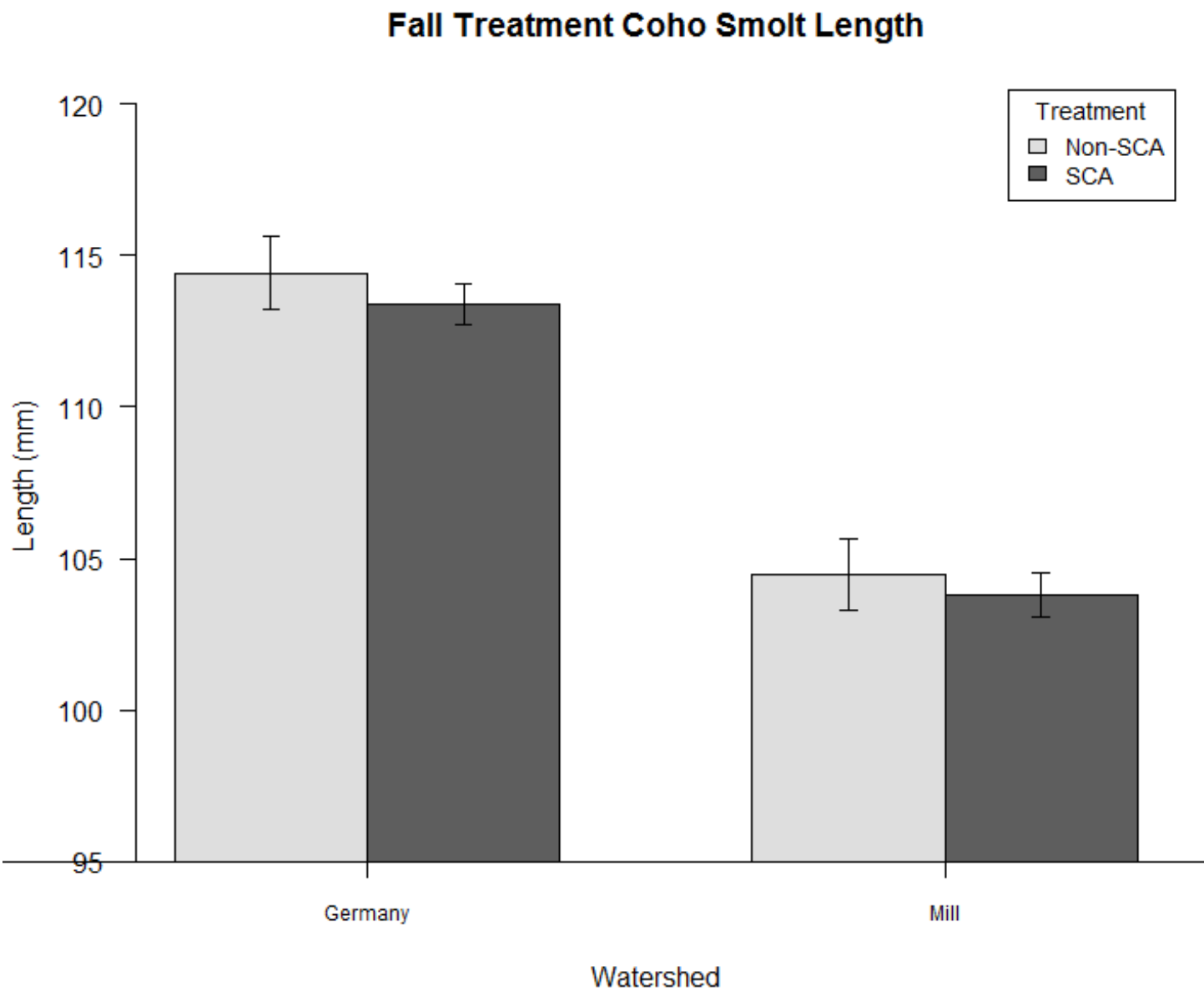

Figure 26. Mean lengths of coho smolts sampled during both SCA application years and non-SCA years for the fall treatment. Error bars represent the standard error. Germany Creek is the fertilized watershed and Mill Creek is the unfertilized watershed.

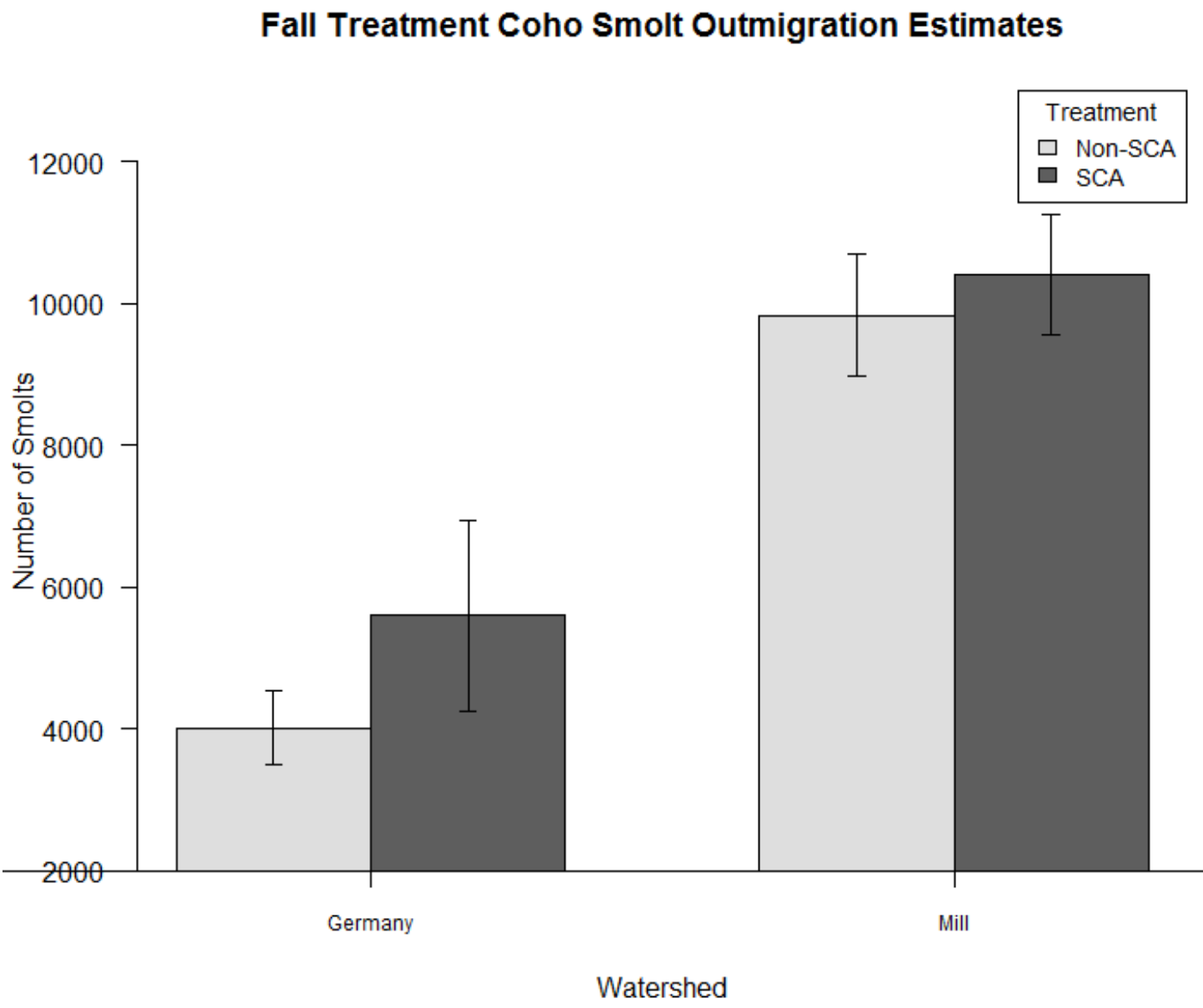

Figure 27. Mean outmigration estimates of coho smolts sampled during both SCA application years and non-SCA years for the fall treatment. Error bars represent the standard error. Germany Creek is the fertilized watershed and Mill Creek is the unfertilized watershed.

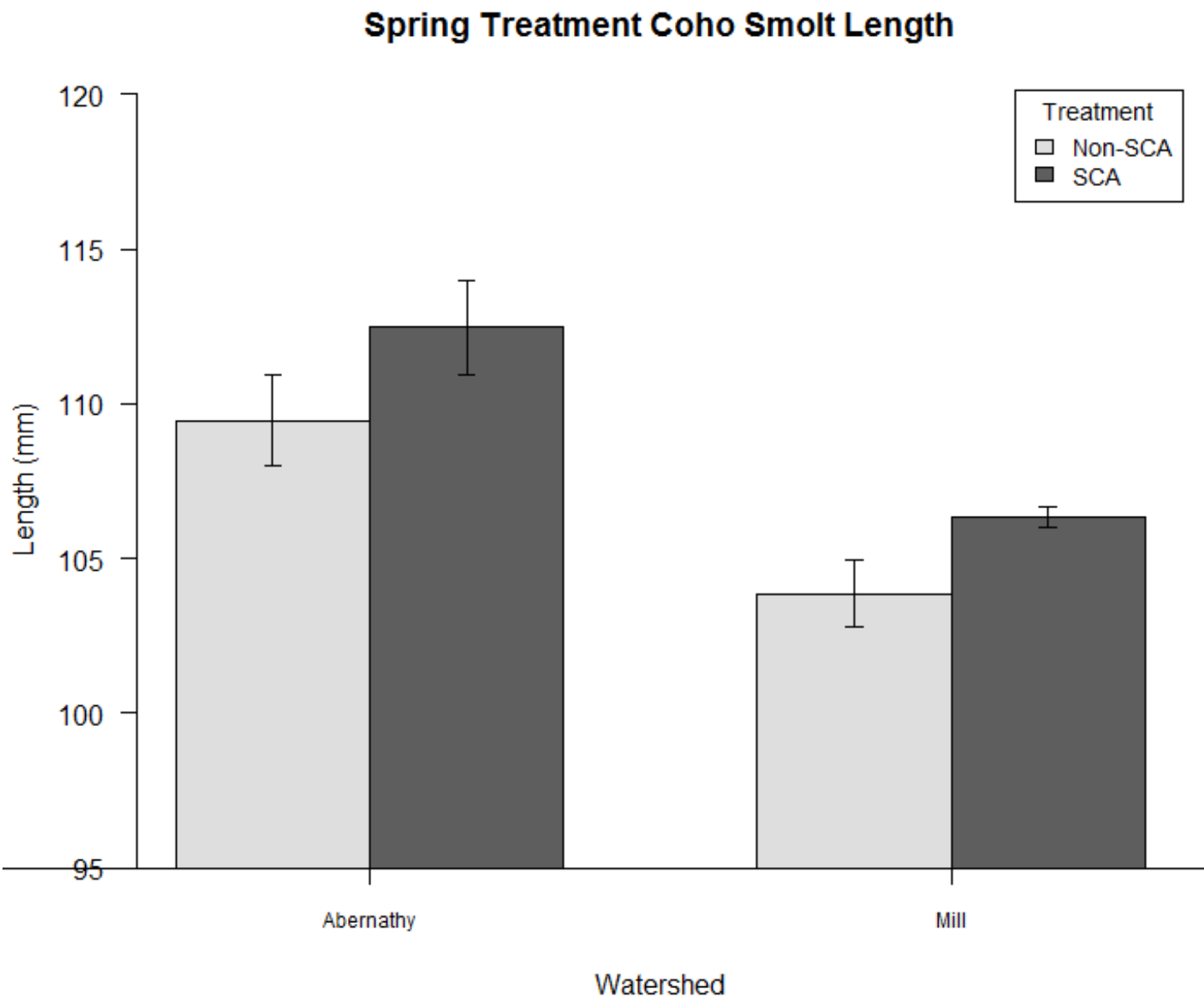

Figure 28. Mean lengths of coho smolts sampled during both SCA application years and non-SCA years for the spring treatment. Error bars represent the standard error. Abernathy Creek is the fertilized watershed and Mill Creek is the unfertilized watershed.

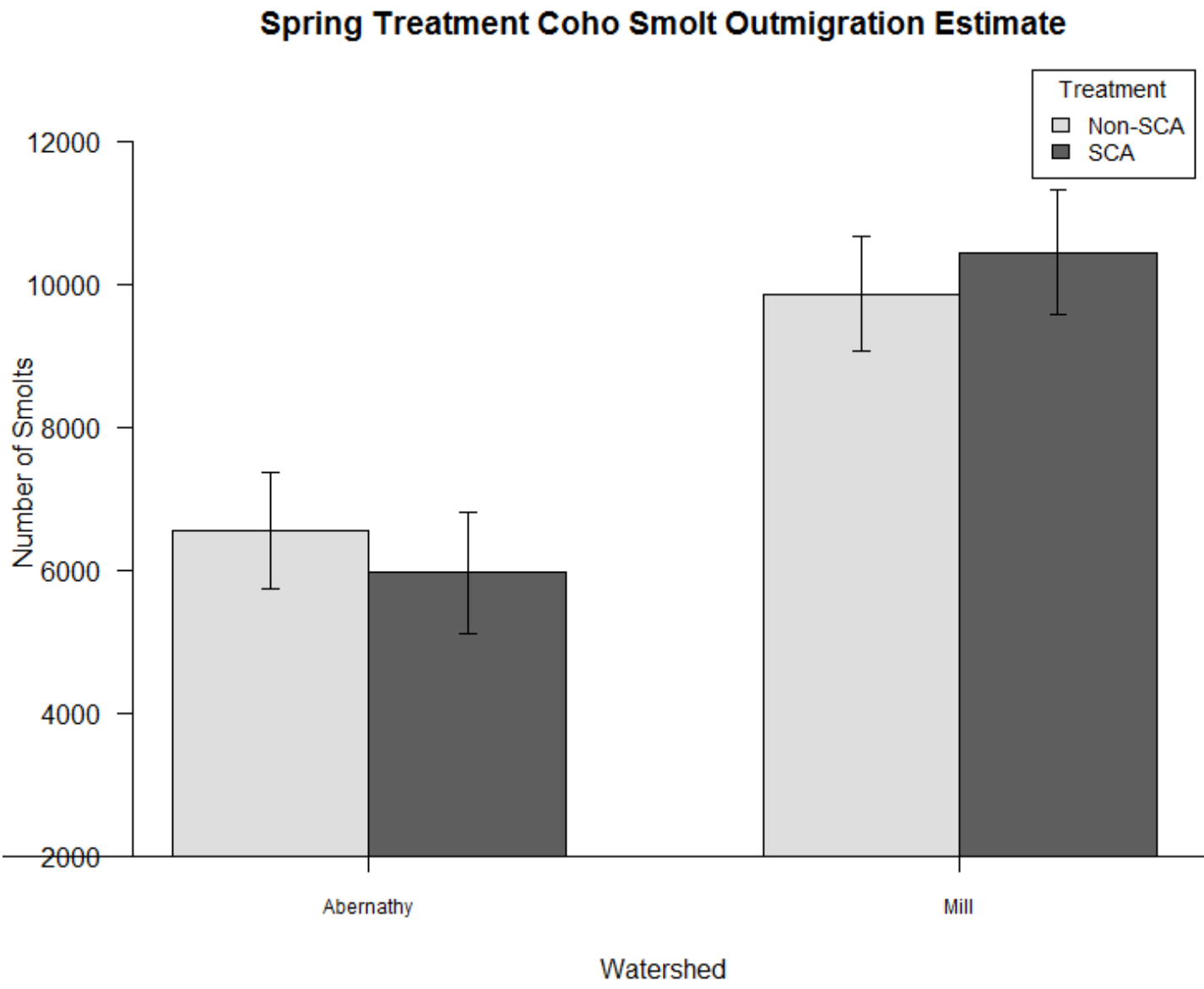

Figure 29. Mean outmigration estimates of coho smolts sampled during both SCA application years and non-SCA years for the spring treatment. Error bars represent the standard error. Abernathy Creek is the fertilized watershed and Mill Creek is the unfertilized watershed.

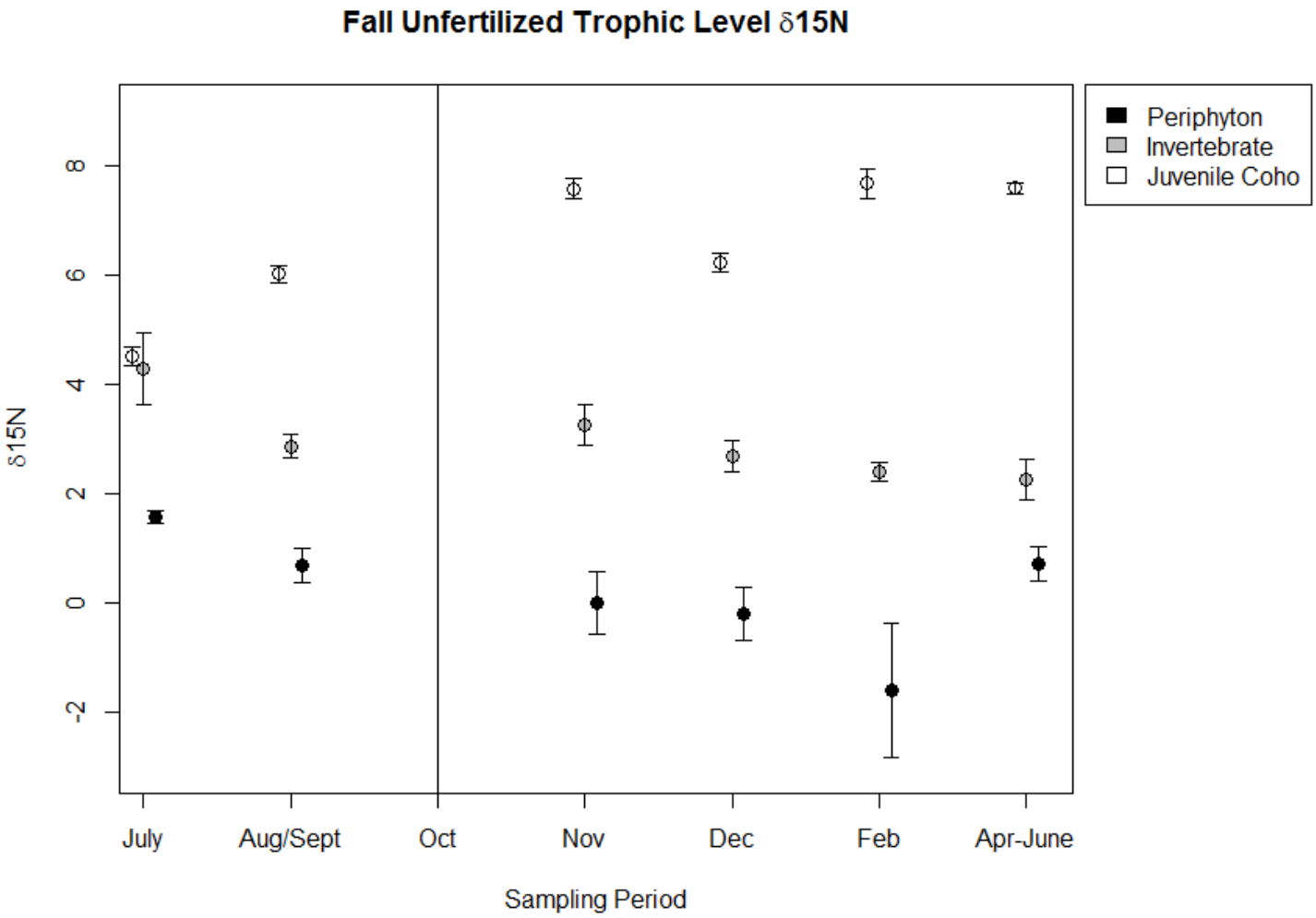

Figure 30. δ15N values summarized by three different trophic levels within the unfertilized watershed. Error bars represent standard errors. The vertical line in October represents the timing of the fall SCA application in the fertilized watershed.

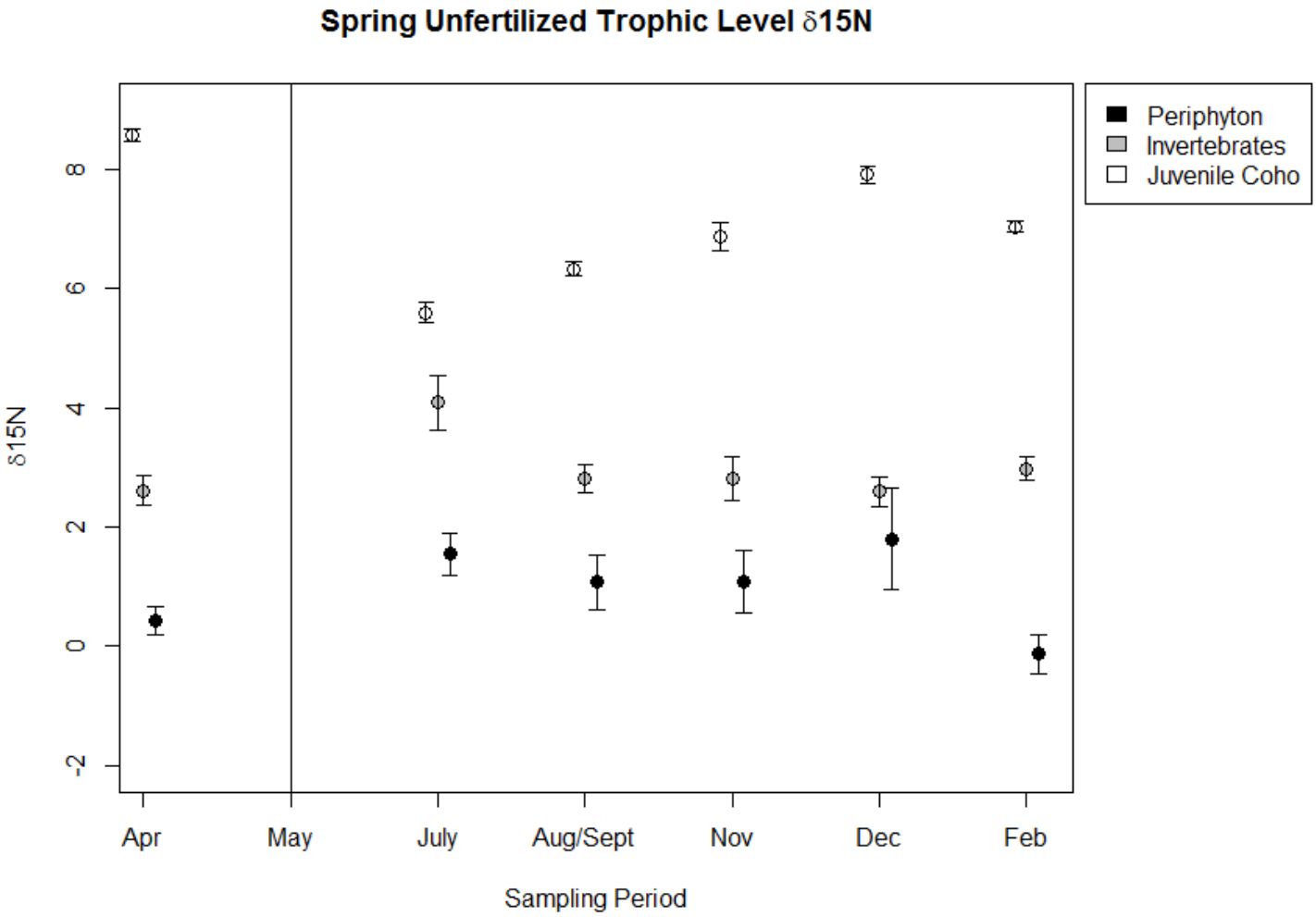

Figure 31. Spring treatment δ15N values for three different trophic levels within the unfertilized watershed. Error bars represent standard errors. The vertical line in October represents the time-period when SCA application took place. Juvenile coho samples taken during April represent the previous year's cohort.

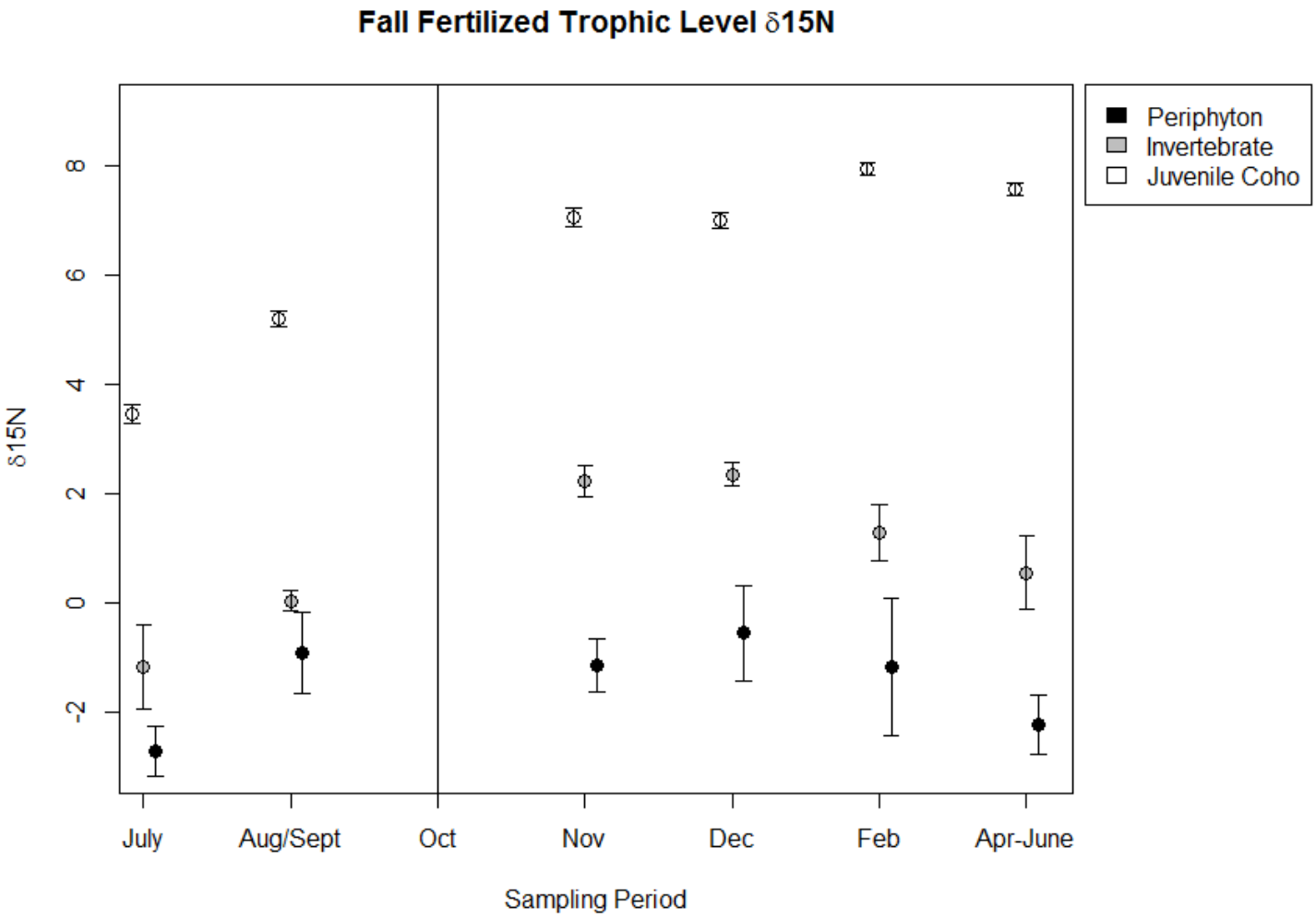

Figure 32. δ15N values summarized by three different trophic levels within the fall-fertilized watershed (Germany Creek). Error bars represent standard errors. The vertical line in October represents the time-period when fall SCA application took place.

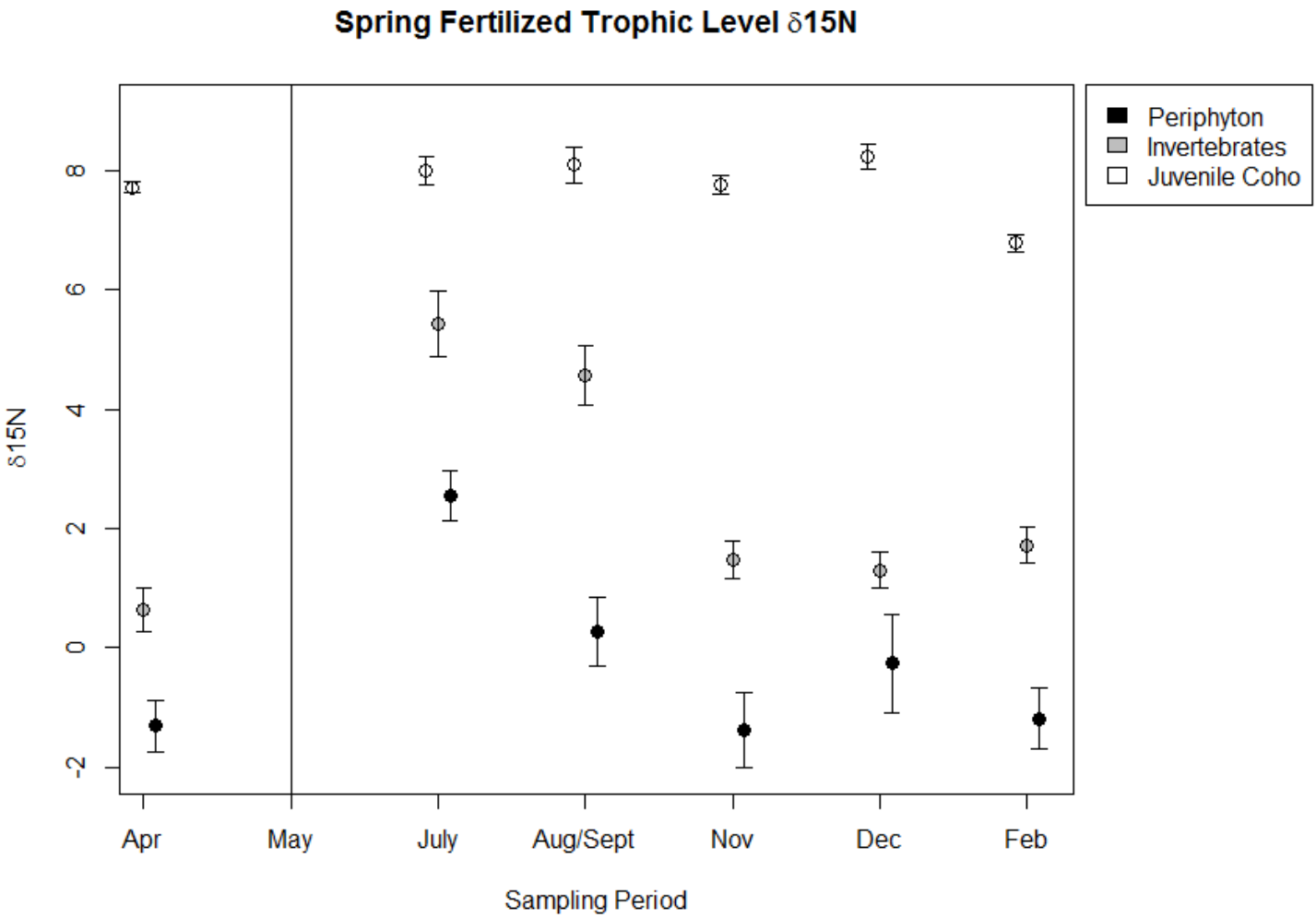

Figure 33. δ15N values for three different trophic levels within the spring-fertilized watershed (Abernathy Creek). Error bars represent standard errors. The vertical line in October represents the time-period when fall SCA application took place. Juvenile coho samples taken during April represent the previous year's cohort.

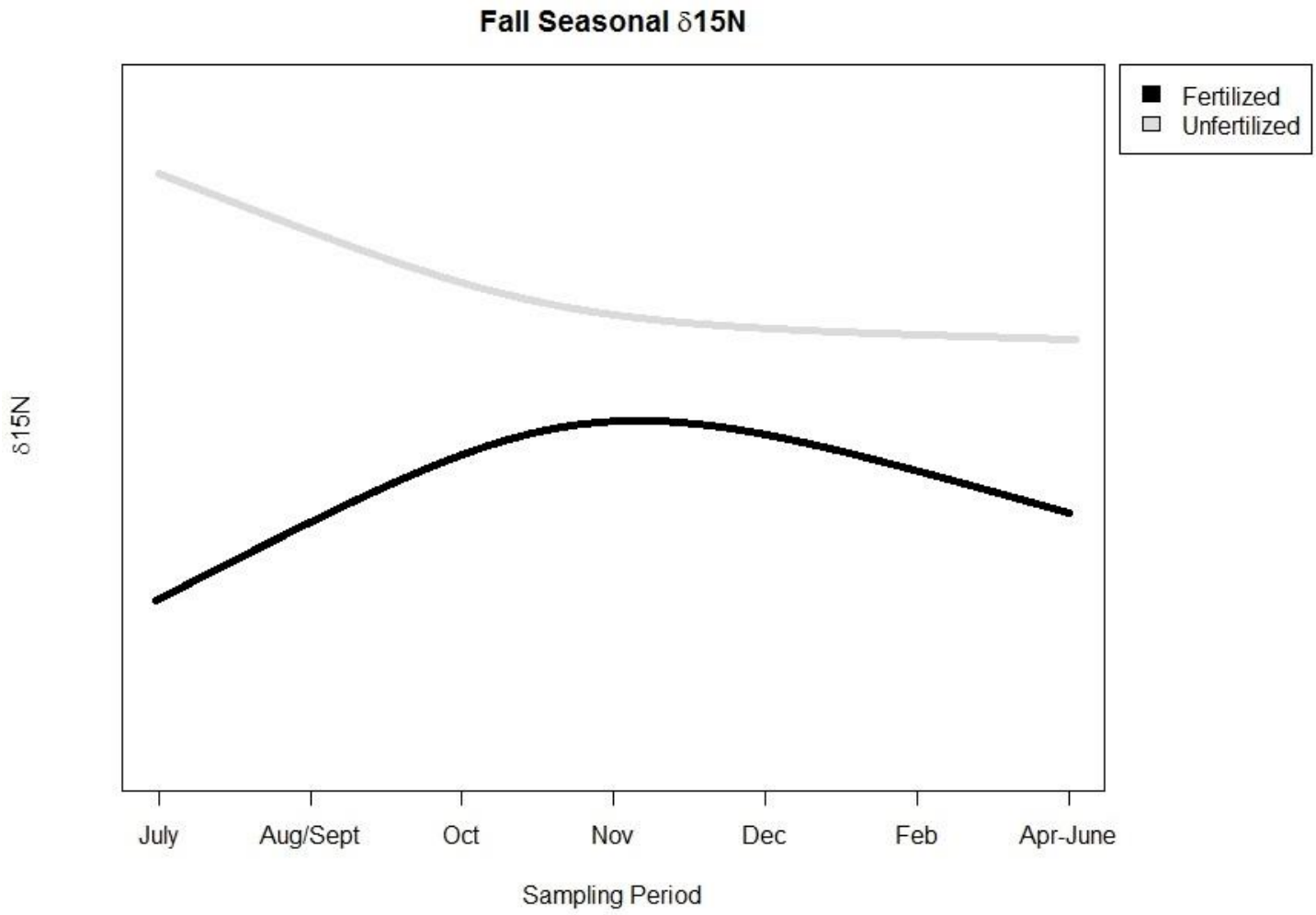

Figure 34. Diagram of the disruption effect that SCA application in the fall has on δ15N values of the food web.

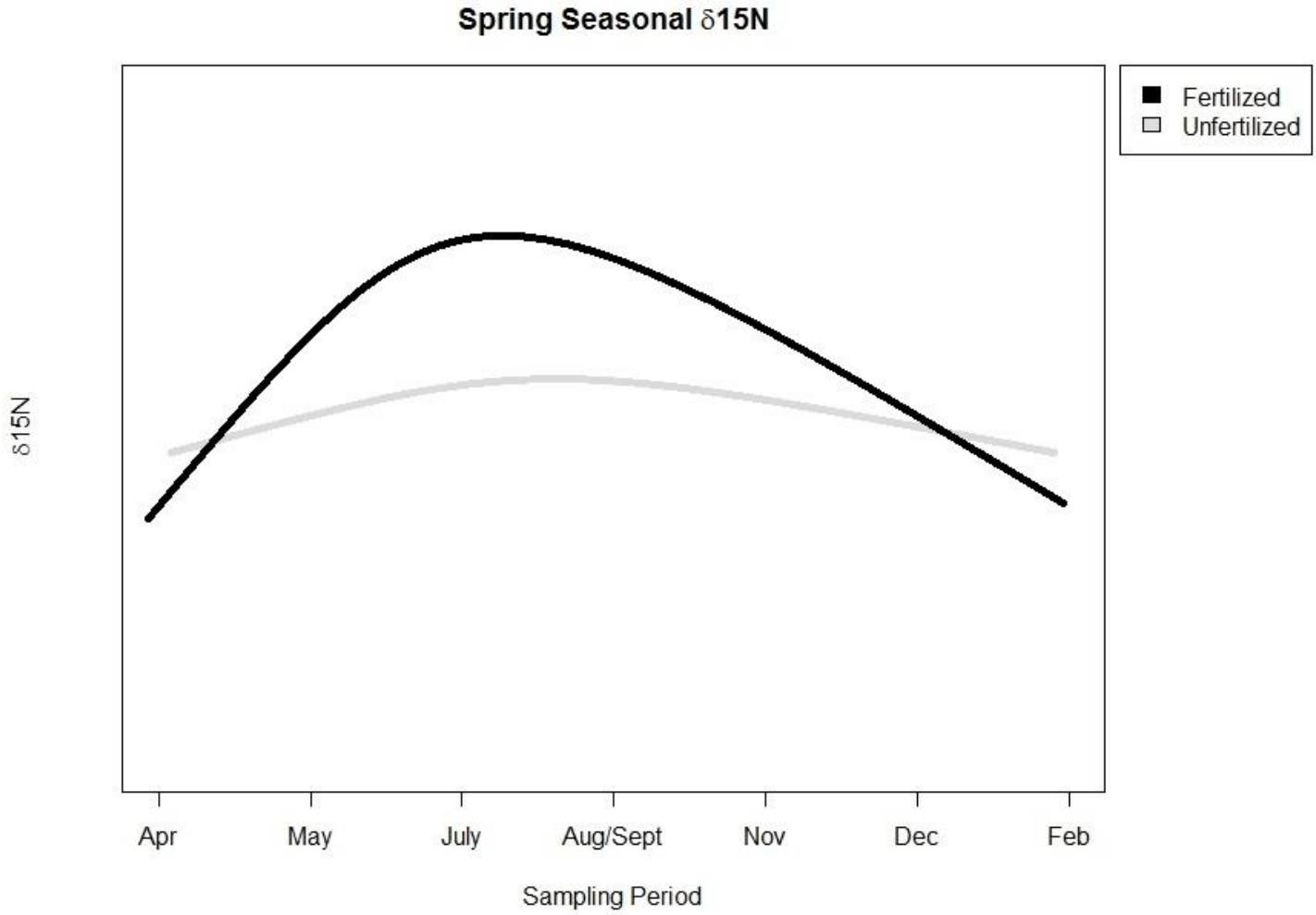

Figure 35. Diagram of the enhancement effect that SCA application in the spring has on δ15N values of the food web.

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