Links between fluctuations in sockeye salmon abundance and riparian forest productivity identified by remote sensing

Celeste N. Kieran [iD],[1],† Debora S. Obrist [iD],[1] Nicolas J. Muñoz [iD],[1]
Patrick J. Hanly [iD],[2] and John D. Reynolds[1]

[1]*Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby,
British Columbia V5A 1S6 Canada*
[2]*Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan 48824 USA*

Abstract. Pacific salmon (*Oncorhynchus* spp.) carcasses can fertilize riparian forests with marine-derived nutrients when populations make their annual return to natal streams to spawn; however, the strength of this cross-system linkage likely varies substantially among years due to the interannual fluctuations in abundance that characterize most salmon populations. Here, we used a 36-yr time series (1984–2019) of satellite imagery and salmon abundance estimates to assess spatiotemporal associations between forest greenness (a measure of plant productivity) and adult sockeye salmon (*Oncorhynchus nerka*) abundance in the lower Adams River, British Columbia, Canada. The Adams River sockeye population displays a quadrennial pattern of abundance, with a dominant cohort that spawns every four years in numbers that are typically two to three orders of magnitude larger than non-dominant cohorts. We found that variation in forest greenness was consistently explained best by models including dominant cohort year, whereas models lacking an index of salmon abundance were the lowest-ranked. Greenness of riparian vegetation increased by an average of 0.015 NDVI units (approximately 1%) in the summer after a dominant cohort return, and this effect on greenness persisted into the subsequent fall (11–13 months after spawning). The positive association between quadrennial pulses of salmon and riparian greenness occurred in plots both within 30 m of the stream and 95–125 m away from the stream, indicating that the spatial extent of fertilization may occur well beyond areas directly adjacent to the riverbank. These results suggest that forests respond to cyclical variation in salmon abundance and that overwinter storage of marine-derived nutrients within catchments allows plants to capitalize on these nutrients in the following growing season. Continued advances in remote sensing technology will enhance our understanding of cross-system resource linkages and can inform the ecosystem-based management of Pacific salmon.

Key words: ecosystem; fertilization effect; marine-derived nutrients; migratory species; NDVI; nitrogen; *Oncorhynchus*; Pacific Northwest; productivity; remote sensing; riparian vegetation; spatial subsidy.

† **E-mail:** celestekieran@gmail.com

Introduction

The salmon spawning migrations of Pacific North America offer a unique example of mass resource transport across ecosystem boundaries, with hundreds of metric tons of marine-derived nitrogen and phosphorus transported into inland freshwater systems and surrounding forest ecosystems each year (Gresh et al. 2000). Pacific salmon (*Oncorhynchus* spp.) accrue up to

99% of their body mass in the ocean before they return to freshwater ecosystems to spawn and die (Quinn 2005), delivering marine-derived nutrients to aquatic and riparian ecosystems in the form of gametes, excretion, and carcasses. These nutrients can reach the riparian zone through the activity of terrestrial salmon consumers such as bears, wolves, and scavenging birds (e.g., Hilderbrand et al. 1999, Reimchen 2000, Quinn et al. 2001, Harding et al. 2019), water movements that wash post-spawn carcasses out of streams (e.g., Ben-David et al. 1998, Dunkle et al. 2020), and subsurface water flow in the floodplain (e.g., O'Keefe and Edwards 2002). These pulses of nutrients influence the dynamics of riparian ecosystems, where salmon alter the composition of riparian plant assemblages (Hocking and Reynolds 2011, Morris and Stanford 2011), increase the growth rate of riparian trees (Helfield and Naiman 2001, Reimchen and Fox 2013, Quinn et al. 2018), are heavily consumed by terrestrial insects (Hocking and Reimchen 2006), and increase the density of forest birds (Field and Reynolds 2013, Wagner and Reynolds 2019).

Although most Pacific salmon populations spawn in the late summer or fall, a variety of mechanisms can cause salmon-derived nutrients to be retained in aquatic and riparian ecosystems year-round (Gende et al. 2002). For example, salmon-derived nitrogen and phosphorus can be microbially stored overwinter in the water beneath or beside the stream channel (i.e., the hyporheic zone) and made available to riparian plants in the growing season after spawning (O'Keefe and Edwards 2002, Pinay et al. 2009). Salmon-derived nutrients may also be stored in soil organic matter or in below-ground tree tissue before redistribution to stems and foliage in the following year (Drake et al. 2006), allowing plants to capitalize during the growing season on the nutrients delivered by salmon in the preceding fall. Over a longer timescale, soils can accumulate nitrogen after successive years of salmon spawning events (Morris and Stanford 2011; but see Feddern et al. 2019), suggesting that saturation of nitrogen in soils might limit the interannual response of riparian plants to fluctuations in salmon abundance. Given that growing season varies with latitude and that the response of riparian vegetation to salmon is likely mediated by local factors such as geomorphology and historical salmon returns, the degree to which plants respond to salmon between geographic locations and within and among years remains generally unclear.

Whereas many studies have tracked the ecological effects associated with variation in salmon abundance, these effects can be difficult to interpret due to the influence of complex and often confounding environmental and geographical factors. One method for tracing incorporation of marine-derived nutrients into terrestrial ecosystems is through stable isotope analysis (Peterson and Fry 1987). The heavy isotope of nitrogen (^{15}N) is generally more abundant in marine food webs than in freshwater and terrestrial food webs, allowing the use of ^{15}N as a tracer of salmon-derived nitrogen in streams and forests (Schindler et al. 2003). For example, riparian plants beside salmon streams have increased amounts of foliar ^{15}N compared to those beside streams without salmon (Bilby et al. 1996, Bartz and Naiman 2005, Nagasaka et al. 2006). This finding has been confirmed experimentally (Hocking and Reynolds 2012), with one study suggesting that as much as 36% of riparian foliar nitrogen can be derived from spawning salmon (Helfield and Naiman 2002). While stable isotopes can be helpful tracers of marine-derived nutrients, their interpretation can be complicated by biogeochemical and micro-topographical differences between study sites, as well as by isotope fractionation processes in soils (Feddern et al. 2019, Walsh et al. 2020). Additionally, collecting and processing samples for isotopic analysis can be costly and logistically challenging in remote areas, which generally restricts the spatial and temporal scale to which stable isotope analysis can be applied.

A spatially and temporally relevant method for studying effects of salmon on primary producers—while reducing the need for on-site data collection—is the use of satellite imagery (Brown et al. 2020), from which several indices that estimate plant productivity can be calculated. One such index is the Normalized Difference Vegetation Index (NDVI), which is a measure of vegetation "greenness" that is calculated as the difference between near-infrared and visible reflectance values, normalized over the sum of the two (Eidenshink and Faundeen 1994). NDVI

is strongly correlated to photosynthetic activity (Wang et al. 2004) and thus provides a sensitive indicator of canopy structure and productivity (Gamon et al. 1995) while being easily implemented from a variety of globally active airborne and satellite platforms. These factors make NDVI an efficient tool for monitoring ecosystem productivity over large spatial and temporal scales.

To date, only one other study has used NDVI to test for effects of salmon-derived nutrients on forest productivity (Brown et al. 2020). This study found a positive relationship between NDVI in summer months and the combined abundance of pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon among streams in the central coast of British Columbia (BC), Canada, as well as biennial increases in summer NDVI that corresponded with the two-year cycle of pink salmon returns to the lower Fraser River over an 18-yr time series. These results suggest that nutrient enrichment from pink and chum salmon positively influences riparian productivity in the summer after spawning and that this influence is detectable from space. However, given that plants can incorporate salmon-derived nutrients in as little as seven days (Drake et al. 2006), it remains unclear the degree to which fertilization occurs immediately after spawning events and whether this effect persists into the subsequent falls. Moreover, it is yet untested how other species and populations of Pacific salmon influence riparian productivity. Pink, chum, and sockeye (*Oncorhynchus nerka*) salmon are the three most abundant species of Pacific salmon (NPAFC 2017), but while pink and chum populations are generally stable in BC, many sockeye populations are in decline (COSEWIC 2017, Price et al. 2019). If interannual variation in sockeye abundance drives interannual variation in riparian productivity, this linkage could be an important consideration for ecosystem-based management responses to declining sockeye populations (Collin et al. 2015).

In this study, we sought to characterize the spatiotemporal association between salmon abundance and riparian productivity in a river dominated by sockeye salmon, the lower Adams River, which is home to the most productive population of sockeye salmon in Canada (Cal-Eco Consultants Ltd. 2006). This population displays an extreme, quadrennial cycle of abundance, with a dominant cohort that returns to spawn every four years in numbers that are two to three orders of magnitude greater than non-dominant cohorts (Levy and Wood 1992, White et al. 2014), making this an ideal system to study interannual associations between salmon abundance and riparian productivity.

We used a hierarchical modeling approach to test a series of hypotheses concerning drivers of forest greenness at the lower Adams River throughout a 36-yr time series. We predicted that quadrennial pulses of sockeye salmon abundance would increase riparian greenness both in the fall immediately after spawning and in the summer following spawning. We also predicted that this positive effect of dominant sockeye pulses would be strongest in areas directly adjacent to the river and those at low elevation gradients from the river.

Methods

Site description

We selected study sites along the north and south banks of the lower Adams River, British Columbia, Canada (Fig. 1). The lower Adams extends for roughly 11 km from the southern
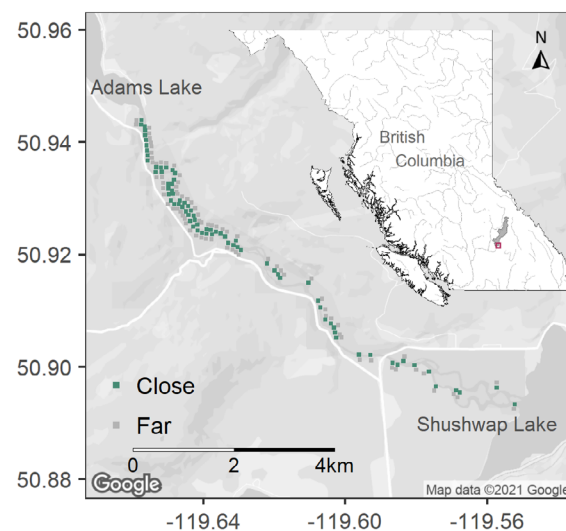

Fig. 1. Map of the lower Adams River study site and its location (marked by red square) in British Columbia, Canada. *Close* plots are marked in green and *far* plots in gray. The river flows in a southward direction.

end of the oligotrophic Adams Lake (50.946594°, −119.658075°) to the west side of Shuswap Lake (50.894728°, −119.548304°) where the river widens into a heavily braided alluvial fan in its final 3 km (Fig. 1). The Adams River is a tributary of the Thompson River, which itself is a tributary of the Fraser River that originates in the western slopes of the Canadian Rocky Mountains and reaches the Pacific Ocean through the city of Vancouver, BC.

The Adams River is part of the Montane Cordillera Ecozone and passes through a variety of micro-climate conditions which contribute to variation in riparian plant assemblages. Upper stretches of the lower Adams River are characterized by Douglas fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), and western redcedar (*Thuja plicata*). As the river nears Shuswap Lake, deciduous species such as trembling aspen (*Populus tremuloides*), black cottonwood (*Populus trichocarpa*), and paper birch (*Betula papyrifera*) dominate the forest, and there is an increased density of understory plants (Cal-Eco Consultants Ltd. 2006). The entire Adams River is territory of the Secwépemc Nation, and the lands on either side of the river from Adams Lake to the Shuswap lake are designated as part of Tsútswecw Provincial Park (formerly known as Roderick Haig-Brown Provincial Park). A moderately trafficked road runs along the upper west side of the river at varying distances from the bank (between 0 and 0.5 km) and a bridge crosses the river approximately 3 km from Shuswap Lake. Both Shuswap and Adams Lake have residential and commercial recreation activity throughout the year.

Adams River sockeye return annually to their natal river to spawn and die after four years of maturation (Larkin 1971), reaching their spawning grounds after traveling 484 km from the Pacific Ocean (Crossin et al. 2004). Within this population, there are four distinct cohorts, each displaying cyclical abundance: a dominant-year cohort, followed by a subdominant-year, and then two "off" (or non-dominant) years with low abundances (Collie and Walters 1987). The dominant cohort is especially pronounced, typically being two to three orders of magnitude larger than non-dominant cohorts and one order of magnitude larger than subdominant cohorts (Levy and Wood 1992, White et al. 2014). For example, the dominant cohort exceeded 3.5 million sockeye in 2010, whereas in the 2012 "off" year, only 12 spawning sockeye were recorded (Fig. 2, Appendix S1: Fig. S2). In addition to sockeye, populations of Chinook (*Oncorhynchus tshawytscha*), coho (*Oncorhynchus kisutch*), and pink salmon spawn in the lower Adams River; however, sockeye vastly outnumber these species in dominant years. During our study period, the yearly abundance of Chinook, coho, and pink salmon combined ranged from approximately 60 to 13,000 fish, whereas the yearly abundance of sockeye alone ranged from 0 to nearly 4 million fish (Appendix S1: Fig. S1).

Plot selection

To select plots and transects for image processing, we first visually examined Landsat imagery of the lower Adams River using Google Earth Pro and Google Earth Engine Timelapse and checked for large-scale disturbances in forest areas around the river such as deforestation or changes in riverbank morphology over time. We then used Google Earth Pro to place as many transects as possible along both north and south sides of the 11 km length of the river (perpendicular to the riverbank), avoiding locations with disturbances or areas closer than 30 m to roads or bridges. To account for spatial variation in salmon carcass deposition, we placed two plots within each transect, the first directly along the river's edge (where carcass deposition is more likely) and the second at a distance of 65 m behind the first, further from the river. These were designated as "*close*" and "*far*" plots, respectively (Fig. 1). The distance downstream for each transect was calculated as the distance along the lower Adams River between the transect and Adams Lake. Because Landsat pixels cover a 30 by 30 m area, we shaped our plots to cover approximately 30 by 30 m of vegetation and spaced them at least 65 m apart to reduce potential for pixel overlap between plots. Because salmon carcasses are less likely to be deposited on steeper slopes, we used Google Earth Pro to estimate the difference in elevation between the center of each plot and the elevation of the river at a point perpendicular to that plot.

Satellite image collection and filtering

To calculate NDVI for each of our plots, we used Google Earth Engine (Gorelick et al. 2017) to
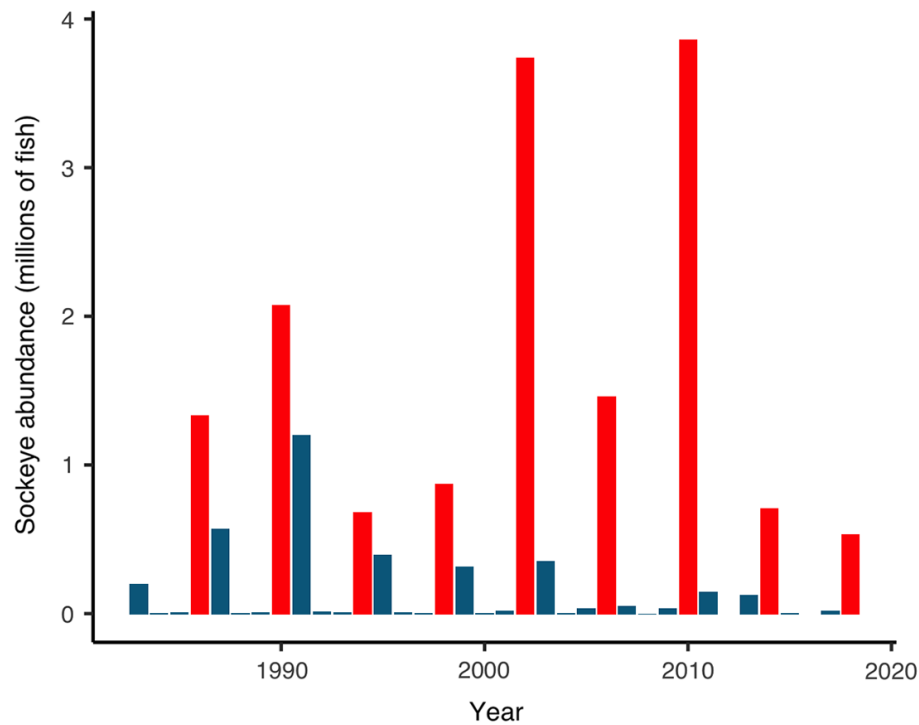
Fig. 2. Sockeye salmon (*Oncorhynchus nerka*) abundance at the lower Adams River from 1983 to 2019. Red bars represent dominant cohort years.

retrieve imagery from Landsat satellites 5 and 7 at 16-day intervals between 1984 and 2019 with a spatial resolution of 30 m pixels. We used U.S. Geological Survey LEDAPS atmospherically corrected Tier 1 surface reflectance with the pixel QA band to remove snow, cloud, and cloud shadow interference. In 2003, the Scan Line Corrector on Landsat 7 failed, resulting in missing data within scenes. Pixels with missing data due to the Scan Line Corrector failure are filtered out prior to analysis and do not contribute to our results. Because the scan line error location changes with each satellite pass, valid data can be extracted for plots, which we averaged by season across missing pixel data. We used imagery from Landsat 5 until Landsat 7 imagery became available in 1999 and then used Landsat 7 for the remaining duration of our study. NDVI was estimated from satellite images as:

$$NDVI = \frac{(NIR - Red)}{(NIR + Red)}$$

in which NIR is near infrared (band 4) and Red is red (band 3). If multiple Landsat images were available for the same day and location, NDVI was averaged between them. To filter for satellite interference and non-vegetative data, we removed individual NDVI observations that were lower than 0.3. To control for disturbances to vegetation undetected by our visual examination of historical satellite images, only blocks that we designated as consistently "densely vegetated" were retained (Zhou et al. 2003), with "densely vegetated" plots defined as having mean growing season NDVI values >0.5 in every year. After NDVI and vegetative density filters were applied, we retained 152 plots for use in NDVI satellite image collection.

We collected images from two time periods in each year: fall (September–November) and summer (July–September). The fall period coincided with the time during or immediately after salmon spawning, whereas the summer period coincided with the active growing season and avoided spring cloud cover.

Salmon abundance data

We obtained annual salmon abundance data for the lower Adams River from the Fisheries and

Oceans Canada New Salmon Escapement Database (DFO 2020), using data from 1983 to 2018 to coincide with the remote imagery data range available for the region. In addition to sockeye, abundance data were also obtained for Chinook, coho, and pink salmon. Salmon abundance was characterized in our models as either a numerical variable of abundance (all species) or a binary variable representing dominant sockeye cohort year (pulse year or non-pulse year).

Environmental covariates

Temperature and precipitation are key drivers of plant primary productivity (Grier et al. 1989) and were therefore used as environmental covariates in our analyses. We accessed historical temperature and precipitation data from two weather stations operated by the Government of Canada (Eagle Bay [50.93°, −119.22°] and Silver Creek [50.55°, −119.35°]) using the R package "*weathercan*" (LaZerte and Albers 2018). We selected these stations due to their proximity to the Adams River and because no individual station near our study site has continuous weather records throughout the duration of the study period. The Eagle Bay station has records from 1984 to 1994, and the Silver Creek station has records from 1989 to the present day. We tested for significant differences in weather data between these stations by comparing the mean daily temperature and total precipitation at each station between July and November for each of the overlapping years of station operation (1989–1994). Using a two-way ANOVA model with station ID and year as fixed effects as well as their interactions, we found no significant differences in weather between stations or interactions with year and station, allowing us to use both stations in our analyses. We calculated the average daily temperature and the total precipitation in each year from July and September (for the summer analysis) and from September to November (for the fall analysis).

Statistical analysis

Following Brown et al. (2020), we fit five generalized linear mixed effects models (GLMMs) to represent a suite of hypotheses about potential relationships between spawning salmon abundance and riparian forest greenness for each of our two seasons of interest. First, we tested for effects of salmon abundance on riparian NDVI in the growing season following salmon spawning (i.e., the next summer). All of our models included average daily temperature, total precipitation, distance downstream from the river's mouth, distance from the riverbank (either close or far), the elevation change between the plot and the river, and the random effect of plot ID nested within transect to account for naturally occurring spatial variability. In two of our models, we quantified the effect of salmon as total salmon abundance, calculated as the total number of returning salmon in the previous fall summed across all species. The first of these models tested the following additive effects: salmon abundance, elevation change, and distance from the river. The second model considered interactions between salmon abundance and elevation change as well as salmon abundance and distance from the river, as salmon nutrients may have disproportionately stronger effects on plots closer to the river and with minimal elevation change (i.e., shallower slopes).

In our third and fourth models, we quantified the effect of salmon as a binary variable indicating whether or not the previous fall saw the return of the dominant cohort of sockeye salmon (i.e., pulse year or non-pulse year). Such a binary characterization of salmon abundance should be a more parsimonious predictor of greenness than total salmon abundance if a large pulse of nutrients is required to stimulate vegetation productivity. This binary characterization also provided us with a continuous marker of salmon presence, as methods for estimating salmon abundance in British Columbia have changed over the time (Grant et al. 2014, Brown et al. 2020) and might slightly confound abundance estimates throughout our time series. Mirroring our first two models, the third model included additive effects of distance to the riverbank and elevation, whereas the fourth tested interactions between these variables and pulses of sockeye. Finally, we fit a null model without a salmon predictor to determine whether the inclusion of a salmon-derived nutrient parameter significantly improved the model fit.

To test whether the effects of salmon fertilization could be detected during and immediately after a fall-spawning event, we fit the same series of five models but with the NDVI values from the same fall season, instead of from the

following year's growing season. To aid interpretation of these models, we tested an additional fall model that evaluated salmon as a variable of specific cohort year (dominant, 1; subdominant, 2; and off, 3 and 4). This model was intended to be based on the top model from our fall analysis; however, we had to remove the interactions due to multicollinearity between predictors.

We fit all models from the beta regression class with a logit link function using the "*glmmTMB*" package in R (Brooks et al. 2017, R Core Team 2020). Beta regression models are a specific type of GLMM used for continuous proportional data bounded between 0 and 1 (Ferrari and Cribari-Neto 2004), which was appropriate because our NDVI values ranged from 0.5 to 0.9. All continuous variables in our models were scaled and centered. We used Akaike's information criterion (AIC) to evaluate our five hypotheses and to select top models from both summer and fall analyses (Harrison et al. 2018). We checked all models for multicollinearity among parameters using the "*performance*" package in R (Lüdecke et al. 2020) and validated the residual diagnostics of our top model using the "*DHARMa*" package in R (Hartig 2020).

RESULTS

We found evidence that the cyclical nature of sockeye salmon abundance affects riparian NDVI and can be detected through satellite imagery. In the summer, salmon effects were most detectable in years following returns of the dominant cohort of sockeye, with the most supported model including the binary presence or absence of a sockeye pulse in the preceding fall and the additive effects of distance from river and elevation (wAIC = 0.82; Table 1). Our second-highest ranked summer model (wAIC = 0.18) also measured salmon as a binary pulse but included interactions between pulse year and elevation change and between pulse year and distance from the riverbank. Our models testing effects of salmon as a measure of combined species abundance ranked third and fourth, and our model that did not include salmon effects at all had the lowest AIC ranking (Table 1).

Pulse years were associated with higher summer NDVI values than non-pulse years (Fig. 3) irrespective of distance from the riverbank, with

Table 1. AIC scores and AIC weights of five generalized linear mixed effects models testing the impacts of salmon on riparian growing season productivity of the following year.

Models	AIC	Delta AIC	AIC weight
Pulse year + distance from bank + elevation	−18,292.81	0.00	0.82
Pulse year × distance from bank + pulse year × elevation	−18,289.81	3.00	0.18
Salmon abundance + distance from bank + elevation	−18,196.25	96.56	0.00
Salmon abundance × distance from bank + salmon abundance × elevation	−18,192.48	100.32	0.00
Distance from bank + elevation	−18,172.22	120.59	0.00

Note: Salmon is measured as either the binary variable of pulse year (indicating presence or absence of a dominant sockeye cohort) or salmon abundance (indicating total number of salmon counted across all species). All models also include the additive effects of distance downstream, temperature, precipitation, and the nested random effect of plot within transect.

predicted mean NDVI increasing from 0.687 ± 0.008 to 0.703 ± 0.008 in close plots and from 0.762 ± 0.007 to 0.776 ± 0.007 in far plots. The effect of pulse years on NDVI was not clearly detectable when visually examining NDVI fluctuations over time (Fig. 4), likely due to effects of other extrinsic factors such as temperature and site-specific variation. The strongest predictor of NDVI was distance from the riverbank, with plots further from the river having a mean NDVI that was approximately 0.07 units higher than close plots following a dominant cohort return (estimated mean = 0.776 ± 0.007 in far plots, estimated mean = 0.703 ± 0.008 in close). Temperature also had a positive effect on greenness, with NDVI increasing by approximately 0.02 units for every 1°C increase in mean daily temperature. Higher levels of precipitation were negatively associated with greenness, and plots at a higher elevation away from the river were also less green. The distance between plots and the mouth of the river had no effect on NDVI (Fig. 3).

Unlike the analysis of summer NDVI, the top-ranking model for fall NDVI included interactive effects between sockeye pulse year and elevation and sockeye pulse year and distance from the riverbank (wAIC = 0.66). The second-highest ranking model included additive effects of pulse
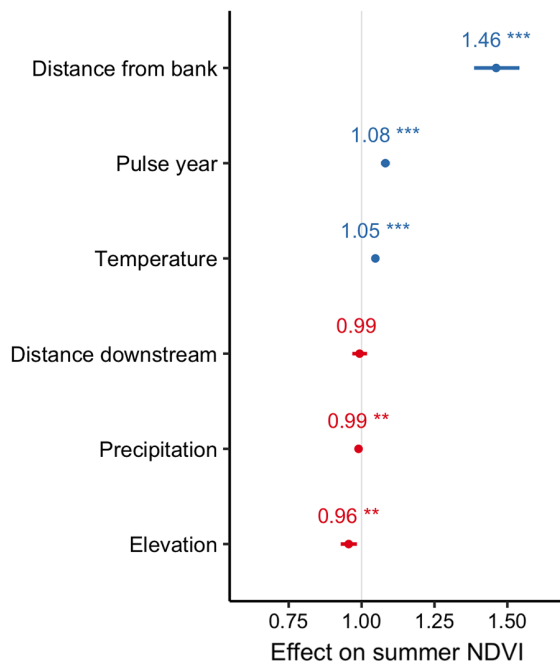
Fig. 3. Standardized coefficient plots from a generalized linear mixed effects model with beta-distribution testing the effects of dominant sockeye cohort presence on riparian forest Normalized Difference Vegetation Index (NDVI) of the following growing season at the lower Adams River, British Columbia. Model tested effects of distance from the riverbank, pulse year (dominant sockeye cohort year), summer mean temperature, summer total precipitation, and distance downstream. Values higher than 0 reflect a positive influence on NDVI, and values <0 reflect a negative influence; black bars represent 95% confidence intervals.

year (wAIC = 0.32), followed by models with salmon measured as total abundance. The null model with no salmon predictor was, again, the least supported model (Appendix S2: Table S1).

NDVI during or immediately after spawning in the fall was lower in years with a sockeye pulse compared to non-pulse years (Fig. 5a), decreasing by an average of 0.013 and 0.023 in close and far plots, respectively. Similar to our findings in the summer, fall NDVI was higher in plots further from the riverbank, was positively associated with mean daily temperature, and was negatively associated with precipitation (Fig. 5a). When assessing fall NDVI as a function of specific sockeye cohort year, we found that fall NDVI was lowest during the return of the

dominant cohort (year 1), was highest in the fall after dominant cohort returns (year 2), and reached intermediate values in years 3 and 4 (Fig. 5b). These results indicate that sockeye pulses increase forest greenness in the fall after the pulse, but not in the same fall season.

DISCUSSION

Using the longest time series to date to test for effects of spawning salmon on forest productivity, our study provides evidence that riparian forests respond to cyclical pulses of salmon-derived nutrients and that this response can be identified with remotely sensed data. We found that forests around the Adams River increase in greenness quadrennially in concert with the return of the dominant cohort of Adams River sockeye salmon. Importantly, increases in vegetative productivity occur in the growing season after the return of this cohort and persist for a full year after the cohort spawns. These results provide further evidence of linked productivity among marine and terrestrial ecosystems (Polis et al. 1997) and support the finding that salmon effects on riparian vegetation can be measured from space (Brown et al. 2020).

The temporal dynamics of plant uptake and use of salmon-derived nutrients are likely set by a suite of regional and local factors such as climate, vegetation, soil composition, stream geomorphology, and baseline nutrient regime (Gende et al. 2002, Naiman et al. 2002, Feddern et al. 2019). In the southern distribution of Pacific salmon in North America, most salmon populations spawn in the late summer or early fall, near the end of the active growing season. Across 36 yr at the Adams River, BC, we found that quadrennial pulses of sockeye salmon are associated with increased forest greenness during the subsequent summer growing season (i.e., 9–11 months after spawning). These pulses of sockeye do not increase forest greenness during or immediately after spawning in the fall; instead, these pulses are associated with increased greenness in the subsequent fall (i.e., 11–13 months after spawning). These results suggest that although there is a mismatch between salmon spawn timing and plant growing season, salmon-derived nutrients are retained in the watershed over the winter such that plants respond in the following year. Retention mechanisms likely include rapid uptake of nutrients within tree roots (Drake
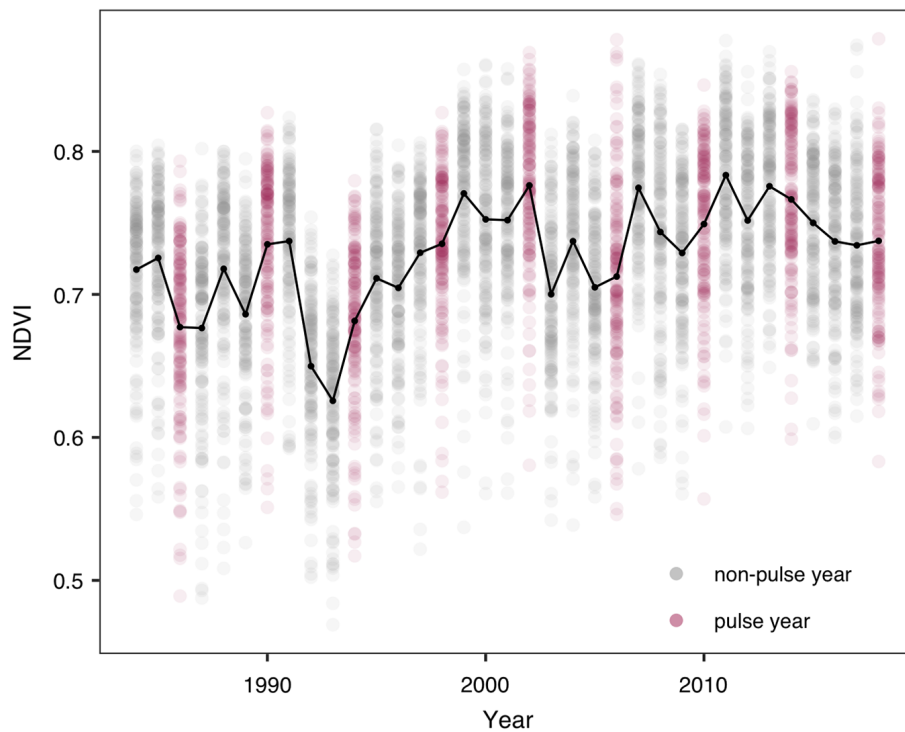
Fig. 4. Mean growing season riparian Normalized Difference Vegetation Index (NDVI) from 1984 to 2019 at the lower Adams River, British Columbia. Years with dominant sockeye cohort runs (pulse year) are marked in pink, and years with subdominant or "off year" runs (non-pulse year) are marked in gray. Black line indicates mean yearly NDVI trend.

et al. 2006), microbial storage of nutrients in subsurface waters (O'Keefe and Edwards 2002), slow decomposition of salmon skeletal remains, and storage as animal tissue within salmon predators and scavengers (Gende et al. 2002). Whereas our study provides support for overwinter storage and spring or summer use of salmon-derived nutrients, more research is needed to understand how variation in factors such as climate, soil composition, and stream geomorphology drives local and regional variation in riparian responses to salmon.

Although riparian greenness increased in years following a pulse of sockeye salmon spawning, the magnitude of this increase was moderate in comparison with spatiotemporal variability and the effect of other environmental factors. Following sockeye pulse years, during which the abundance of salmon typically increased by millions of fish, riparian greenness increased by an average of 0.015 NDVI units. In comparison, a 1°C increase in average daily temperature among years was associated with an increase of 0.02

NDVI units, and plots far from the riverbank were an average of 0.07 NDVI units higher than close plots. There was also considerable interplot variability in NDVI, with a standard deviation of 0.06 NDVI units. Although the return of the dominant sockeye cohort appears to add a nutrient pulse that boosts riparian greenness, these results indicate that forest productivity around the Adams River is largely influenced by other variables. Temperature is the main limiting factor for vegetative productivity in mid- and high latitudes (Churkina and Running 1998) and contributed to interannual variability in NDVI here. Extreme weather could also drive interannual variability in forest productivity by changing the prevalence of flooding events. Spatial variability in productivity could be explained by site-specific soil nutrient dynamics, canopy species composition, and other local factors. While salmon can influence the composition of riparian plant assemblages (Hocking and Reynolds 2011, Morris and Stanford 2011) and have a large,
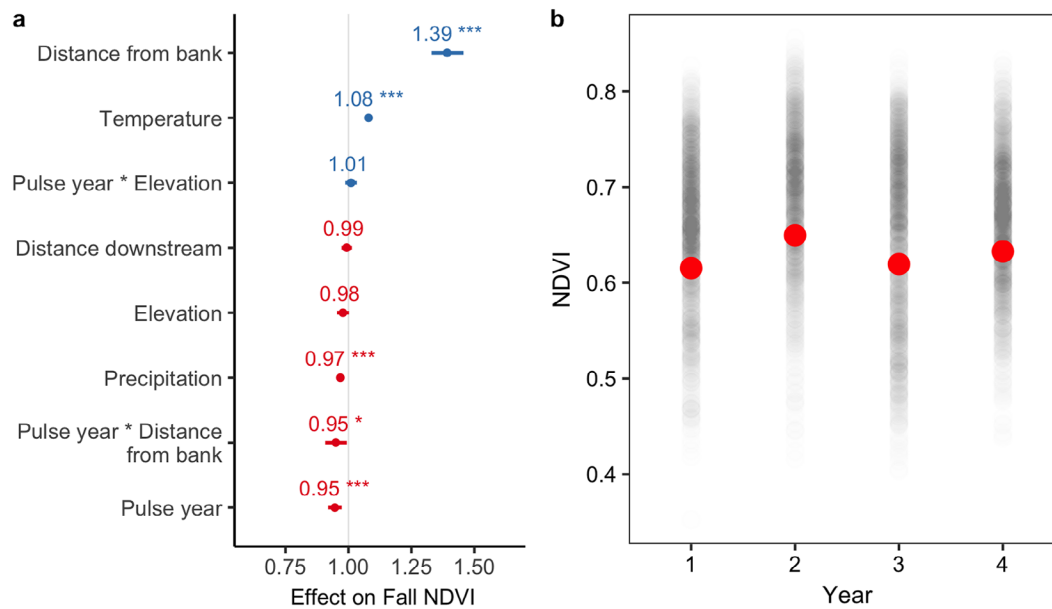
Fig. 5. Effects of sockeye salmon (*Oncorhynchus nerka*) cohort year on riparian Normalized Difference Vegetation Index (NDVI) of the fall same season at the Adams River, British Columbia, modeled by generalized linear mixed effects models with beta-distribution. Coefficient plot (a) visualizes a model testing interactive effects of distance from the riverbank, pulse year (dominant sockeye cohort year), fall mean temperature, fall total precipitation, and distance downstream. Values higher than 1 represent a positive influence on NDVI, and values <1 represent a negative influence, with bars representing 95% confidence intervals. Plot b shows predicted mean fall NDVI during each year of the four-year sockeye spawning cycle. Cycle year 1 is the dominant cycle year, 2 is subdominant, and 3 and 4 are "off" years.

positive effect on the biomass of many riparian animals (e.g., Hocking and Reimchen 2006, Wagner and Reynolds 2019), salmon appear to play a relatively minor role in interannual variation in overall productivity of riparian vegetation. However, comparisons of base fluctuations in riparian productivity between salmon bearing and non-salmon bearing streams would be helpful in clarifying these results, as salmon-derived nutrients may saturate the riparian zone overall, limiting the potential for between-year variation.

One of the most promising features of using remote sensing is the ability to better understand the spatial scale at which ecosystem processes occur. Several studies have predicted that the effects of salmon on riparian vegetation should be strongest in the area directly adjacent to streams, given that most carcasses are deposited within 20 m of the stream edge (Ben-David et al. 1998) and the input of inorganic nitrogen into soil is highly localized around individual carcasses (Holtgrieve et al. 2009). For example, Reimchen and Fox (2013) examined the influence of salmon on the growth of individual Sitka spruce (*Picea sitchensis*) trees located within 10 m of salmon spawning grounds (where there were high numbers of carcasses), between 50 and 90 m into the forest (where carcasses were either not present or much less abundant), and upstream of the spawning grounds (where salmon carcasses were not present). They expected the trees located 50–90 m away and trees located upstream of spawning grounds to be unaffected by salmon but found that the effect of salmon on tree growth was even more positive among trees 50–90 m into the forest than among trees adjacent to spawning grounds. Recently, Brown et al. (2020) examined the relationship between biennial returns of pink salmon and forest greenness as measured in plots at increasing distances from a stream, with the furthest plots being 273 m on average away from the stream. They

found that the positive effect of pink salmon on forest NDVI did not interact with distance away from the stream, suggesting that the effect of salmon may extend further away from the stream than expected. In our study, during the summer, the greenness of plots located further away from the stream edge (approximately 95–125 m) was similarly associated with pulses of sockeye salmon abundance as was that of plots within 30 m of the stream edge. Conversely, in the fall after a sockeye pulse, we found that the association between sockeye pulse and forest greenness was more positive in plots further away from the stream. Collectively, these studies suggest that the influence of salmon on vegetative productivity extends beyond the areas directly adjacent to spawning grounds. This may be due to highly mobile bears spreading salmon-derived nutrients throughout the forest via urine (Hilderbrand et al. 1999), secondary dispersal of carcass materials by mobile scavengers such as corvids (Reimchen 1994), nutrient storage within subsurface waters that can extend hundreds of meters into riparian floodplains (Clinton et al. 2002, O'Keefe and Edwards 2002), translocation of minerals by soil mycorrhizal networks (Simard et al. 2012), or historic accumulation of salmon-derived nutrients along the riverbank causing plants there to be less nutrient-limited and thus less responsive to salmon pulses relative to plants further from the river (Lu et al. 2011). Additionally, increased deciduous canopy species near the riverbank could suggest the presence of nitrogen-fixing alders (*Alnus* spp.), which confound the effects of marine-derived nitrogen (Helfield and Naiman 2002). Indeed, without data related to the spatial distribution of salmon-derived nutrients and canopy composition, it is difficult to fully explain the spatial patterns of greenness that were observed here. This highlights a key limitation of remote sensing techniques: On-the-ground data can often enhance the potential inference of remotely sensed data.

The interannual response of vegetation to pulses of nutrients can be modulated by historical nutrient inputs and baseline dynamics of nutrient cycling in soils (Lu et al. 2011, Feddern et al. 2019). In general, additions of nitrogen fertilizer increase the availability and accumulation of nitrogen in soils, but concurrent increases in rates of nitrogen emission and leaching limit the benefits of fertilization to plant uptake over time (Lu et al. 2011). In our study, variation in forest greenness was consistently explained best by whether or not there was a quadrennial pulse of sockeye salmon (i.e., pulse or no pulse), with models containing quantitative variation in salmon abundance being less parsimonious. This result suggests that salmon might only stimulate vegetative productivity to an extent discernable by remote sensing after some threshold of nutrients is added, a threshold that is only reached after pulse years. Additionally, given that forest greenness is highly variable, and that the positive effect of sockeye pulses was modest (0.014–0.016 mean growing season increase in NDVI compared to non-pulse years) despite pulse years involving orders of magnitude more fish, it is likely that any effect of salmon in non-pulse years would be difficult to detect using our remote sensing approach. Whereas the Landsat program provides the longest record of satellite imagery available, newer satellites with higher pixel resolution or finer-resolution imagery in which individual tree species are distinguishable may provide a more fine-scale understanding of vegetative responses to marine nutrient inputs.

CONCLUSION

The spatiotemporal association between salmon and riparian productivity described here is relevant to ecosystem-based management of Pacific salmon. Our results suggest that declines in sockeye salmon abundance could lead to declines in riparian productivity. However, given that quadrennial pulses of sockeye have only a minor effect on the overall productivity of riparian vegetation, declines in sockeye abundance should be expected to cause only minor declines in riparian productivity in the short term. This effect may become more severe over the longer (multidecade) term if historic salmon inputs mediate the annual effect of present-day inputs.

In future studies, matching satellite overpasses with on-the-ground measurements of ecosystem processes could improve the utility of remotely sensed data. With ongoing improvements in technology and processing, remote sensing could aid large-scale assessments of ecosystem

processes and enhance the effectiveness of management actions.

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DATA AVAILABILITY

Data and code are available at Figshare: main script for analysis of the effects of salmon on riparian NDVI at the Adams River, British Columbia, https://doi.org/10.6084/m9.figshare.14794206; main dataset used for the analysis of salmon effects on riparian NDVI of the following growing season, https://doi.org/10.6084/m9.figshare.14794425; main dataset used for the analysis of salmon effects on riparian NDVI of the same fall season, https://doi.org/10.6084/m9.figshare.14794434; and metadata for Adams River, https://doi.org/10.6084/m9.figshare.14794443.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3699/full