# Spawning salmon density influences fruit production of salmonberry (*Rubus spectabilis*)

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**Abstract.** Annual spawning migrations by Pacific salmon can provide substantial subsidies to nutrient-limited freshwater and riparian ecosystems, which can affect the abundance, diversity, and physical characteristics of plant and animal species in these habitats. Here, we provide the first investigation of how salmon subsidies affect reproductive output in plants, focusing on a common riparian shrub, salmonberry (*Rubus spectabilis*). We studied 14 streams with a range of spawning salmon densities on the central coast of British Columbia, Canada. We determined the effects of chum (*Oncorhynchus keta*), pink (*O. gorbuscha*), and total salmon spawning density on the number of fruits per shrub, number of seeds per fruit, fruit weight, and estimated sugar content (° Brix) of salmonberry fruits. We found that the number of fruits per salmonberry shrub increased with increasing salmon density. However, we found no effect of salmon density on the number of seeds per fruit, fruit weight, or sugar content. The effect of salmon density was species-dependent; the number of fruits per shrub increased with chum salmon density but was not affected by pink salmon density. This could be because chum salmon occur at higher densities and are transferred from water to land at higher rates than pink salmon in our study area. Higher salmonberry fruit production could lead to a larger input of salmonberry fruits to coastal food webs. These results demonstrate how salmon can cross ecological boundaries and influence reproductive output of terrestrial species.

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## INTRODUCTION

Nutrients, detritus, and organisms can move across ecological boundaries and heavily influence the biota in neighboring ecosystems (Polis et al. 1997). Once transferred to recipient sites, these subsidies can influence ecosystem productivity (Polis et al. 1997, Anderson and Polis 1999, Childress et al. 2014), function (Cocks et al. 1998), and composition (Hocking and Reynolds 2011, Wagner and Reynolds 2019). Subsidies are common in nutrient-limited systems; for example, nomadic grazers increase rates of nutrient flow through herbivory action in the Serengeti desert (Mcnaughton 1985), and seabird guano, sea wrack, and carrion provide relatively high energy inputs to nutrient-poor islands in the Sea of Cortez (Polis and Hurd 1996).

The anadromous life history of Pacific salmon allows them to provide a significant subsidy to coastal freshwater and riparian ecosystems. Nutrients typically flow from freshwater systems towards the ocean; however, salmon reverse this process by creating a nutrient flux upstream during spawning migrations. During this process, salmon carcasses and eggs are transferred from

streams to riparian areas by predators, scavengers, and water flow (Ben-David et al. 1998, Gende et al. 2002). Salmon-derived nutrients have been identified in soils, plants, and invertebrates in riparian areas through stable isotope analysis, showing that these nutrients cycle through terrestrial ecosystems (Reimchen et al. 2002, Bartz and Naiman 2005). Furthermore, a salmon carcass transfer experiment found direct effects of salmon-derived nutrients on the isotopic composition of terrestrial plants (Hocking and Reynolds 2012). Examples of salmon subsidy linkages include increased growth rates of riparian trees (Helfield and Naiman 2001, Reimchen and Fox 2013, Quinn et al. 2018), increased bird abundance and diversity (Wagner and Reynolds 2019), and shifts in riparian plant community composition toward lower diversity and higher densities of nitrophilic species (Hocking and Reynolds 2011). Relationships between salmon and freshwater and terrestrial plants and animals have recently been quantified by Walsh et al. (2020).

There is limited research investigating how salmon subsidies can affect plant traits in natural environments. Studies have shown that salmon-derived nutrients correlate with increased conifer tree growth (Helfield and Naiman 2001, Reimchen and Fox 2013, Quinn et al. 2018) and stomatal density of nitrophilic plants (van den Top et al. 2018). However, there is a lack of research on how salmon subsidies may influence the reproductive output of plants. In agricultural settings, nutrient additions can increase both fruit yield (Percival and Sanderson 2004, Buskien and Uselis 2008, Stojanov et al. 2019) and seed yield (Thies et al. 1995, Ham et al. 2010). Nutrient addition can also lead to increased fruit size (Buskien and Uselis 2008, Stojanov et al. 2019) and estimated sugar content (° Brix; Cao et al. 2015). However, these results are not universal, as other studies have found no effect of nutrient fertilizers on these characteristics (Alleyne and Clark 1997, Naraguma et al. 1999). Evaluating these traits in a natural environment may help explain the increase in salmonberry abundance seen on streams with higher salmon densities when controlling for other physical and biotic differences among streams (Hocking and Reynolds 2011).

Fruit yield, seed yield, and seed germination are a few of the many traits related to plant reproductive success. Higher fruit or seed yield could increase potential for successful reproduction by providing more germination opportunities. Additionally, some frugivores prefer sweeter (Levey 1987, Koike et al. 2008) or larger (Sallabanks 1993) fruits, and since the passage of salmonberry seeds through a vertebrate digestive system can improve germination rates (Traveset and Wilson 1997), both fruit weight and sugar content could potentially be important for plant reproductive success.

To examine links between salmon subsidies and plant traits related to reproductive output, we studied salmonberry (*Rubus spectabilis*) shrubs on the central coast of British Columbia, Canada, along 14 streams with a range of spawning salmon densities. Salmonberry is a nitrophilic species that grows competitively in areas with high nutrient availability (Hocking and Reynolds 2011). At each stream, we observed salmonberry traits at two levels: the number of fruits per shrub, and the characteristics of these fruits—weight, seed count, and estimated sugar content (° Brix). Higher spawning salmon densities result in increased carcass deposition in riparian areas (Harding et al. 2019), where carcasses can have a fertilizing effect. As such, we predicted a positive correlation between salmon density and each of the shrub and fruit-level traits that we evaluated. Specifically, we expected that higher salmon densities would correlate with more fruits, which would also be larger, sweeter, and have more seeds. We also predicted that chum salmon (*Oncorhynchus keta*) would have a greater effect than pink salmon (*O. gorbuscha*), since they are transferred to riparian areas at higher rates in our study area (Hocking and Reimchen 2006, Harding et al. 2019).

## Methods

### Study sites

We studied salmonberry plants and Pacific salmon at 14 streams in Haíɫzaqv (Heiltsuk) territory on the central coast of British Columbia, near the town of Bella Bella (Fig. 1, 52°02′33″ N to 52°30′54″ N and 128°05′42″ W to 127° 49′56″ W). This region is located within the Coastal Western Hemlock Biogeoclimatic Zone (Pojar et al. 1987), and experiences a maritime climate with heavy rainfall—over 3 m annually. We chose streams that span a wide range of salmon
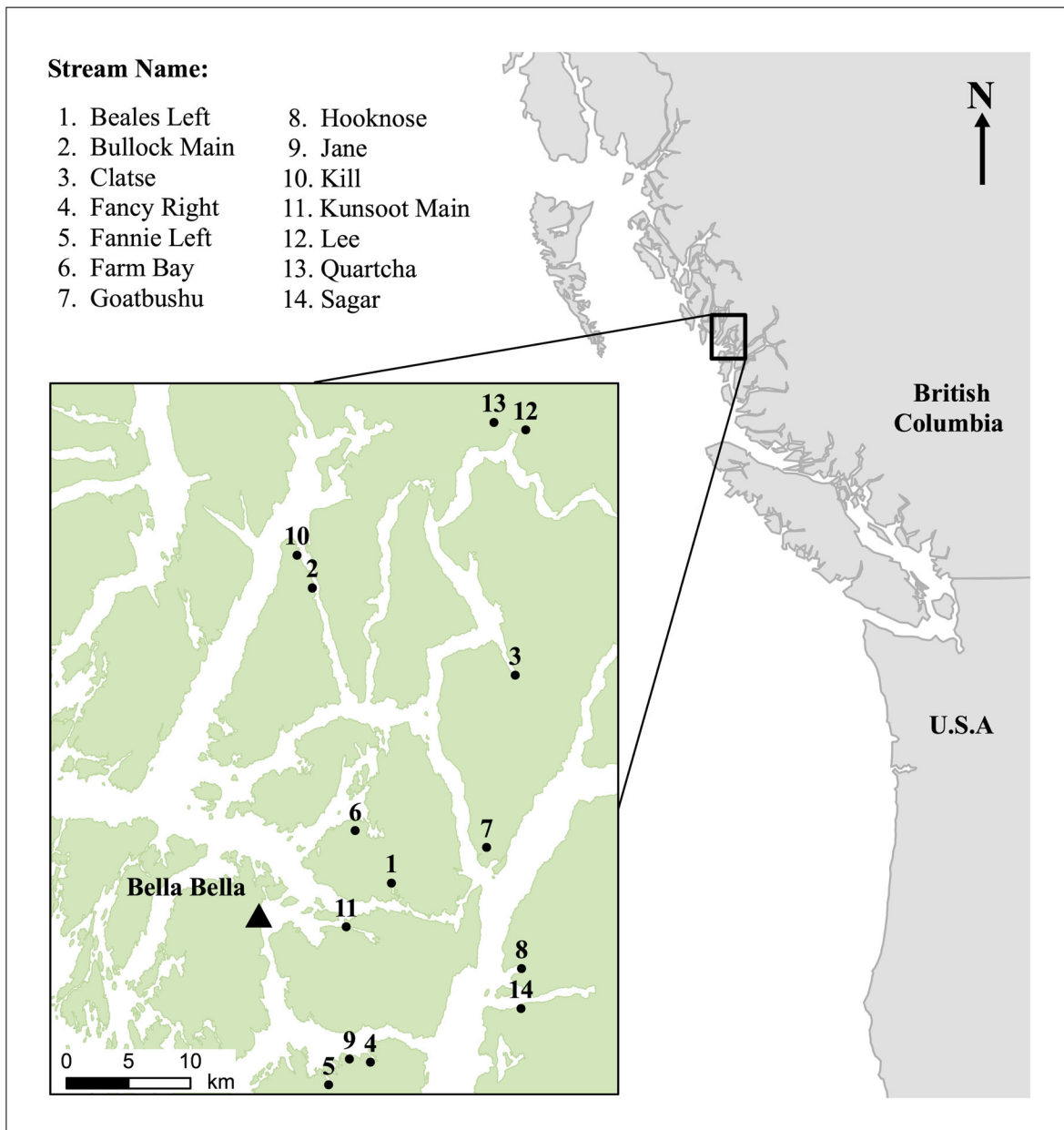
Fig. 1. Location of our 14 study streams on the central coast of British Columbia, Canada.

spawning densities and experience minimal impacts from recent human activity; streams are accessible only by boat and have had minimal logging activity (Fig. 2).

Although multiple types of bedrock exist in our study area, soil properties tend to be similar throughout the region due to the influence of similar climate and vegetative inputs (Heilman and Gass 1974, Kranabetter and Banner 2000). Nutrient cycling in coastal western hemlock forests is primarily confined to the upper soil horizons, which has limited influence from parent materials because of high accumulations of organic matter, high rainfall, and shallow rooting

Fig. 2. A typical stream on the central coast of British Columbia. The photo shows the mouth of Quartcha Creek (52°30′52″ N 127°50′26″ W) opening into the estuary (Credit: Allison M. Dennert).

of vegetation (Heilman and Gass 1974). In this region, including some of the same streams that we studied, streams with higher densities of spawning salmon tend to have higher levels of compounds associated with soil fertility, such as ammonium and nitrate (A. Larocque, *unpublished data*). Nitrate is a known limiting nutrient for plants that have associations with arbuscular mycorrhizae, such as salmonberry. In addition, there tends to be a negative correlation with spawning salmon densities and both aluminum and iron, which are associated with decreases in soil fertility (A. Larocque, *unpublished data*). Although soil microbiota have been shown to absorb up to 64% of salmon-derived nutrients within 14 d (Drake et al. 2006), plants may not show signs of benefits from these subsidies until the following spring due to a seasonal mismatch in salmon run timing and the plant growing season. In our study area, peak chum and pink salmon runs occur in September and October every year.

### Salmonberry characteristics

Salmonberry is a common deciduous shrub in coastal forests of western North America, ranging from northern California to southern Alaska. It is a culturally important plant to many First Nations people and is known as ĜúI̓áli by the Haíɫzaqv (Heiltsuk) First Nation. It prefers moist, nutrient-rich soils near streambanks, habitat edges, and disturbed areas (Klinka et al. 1989). Reproduction occurs both by seed dispersal and vegetative regeneration. Salmonberry fruits are composed of an aggregate of druplets surrounding the receptacle, with each druplet containing one seed. The fruits are dimorphic, but both red and orange color morphs have similar weight, seed load, and nutrient composition (Traveset and Willson 1998).

### Salmon density

We derived salmon densities for each of the 14 streams using multiple years of count data from JDR's research group, Fisheries and Oceans

Canada, and the Haíɫzaqv (Heiltsuk) First Nation. Survey teams visited each stream up to three times during spawning season and counted all live and dead salmon between the river mouth and the end of the spawning reach, which was defined by a physical barrier, a lake, or the absence of salmon. Counts for streams that were visited 3 times per season were calculated by using the area under the curve method, while streams visited only once or twice used the peak live or dead method. Both methods yield similar estimates (Hocking and Reynolds 2011). Since the presence of other salmon adults was negligible, we focused on chum and pink salmon inputs within these streams. To account for the variable life history and stochastic variation between years seen in salmon abundance on the central coast of British Columbia, we used an average of the most recent 3 yr of data (2016–2018) and the following equation to calculate salmon spawning densities:

$$\text{Salmon Density (kg/m)} = \frac{\sum (N_i \times W_i)}{L}$$

where $N$ = average number of salmon per year, $i$ = salmon species (chum or pink), $W$ = average weight of salmon (chum = 3.1 kg, pink = 1.05 kg), and $L$ = spawning length (Hocking and Reynolds 2011). Chum and pink salmon spawning densities were also calculated separately. Total salmon density ranged from 0 to 31 kg/m, chum density ranged from 0 to 22 kg/m, and pink density ranged from 0 to 9 kg/m (Appendix S1: Table S1).

*Salmonberry survey and collection*

We conducted riparian surveys on each stream between July 16 and July 31, 2019. The length sampled (reach length) ranged from 80 to 560 m and was proportional to the bank-full width at the start of the stream (e.g., Hocking and Reynolds 2011). Following a stratified random sampling design, we divided the reach length into 4 equal sections and randomly selected 4 distances from the stream mouth per section. We placed a 1 × 1 m quadrat around the stems of the nearest fruiting salmonberry shrub at each distance, alternating between right and left sides of the stream. Shrubs were sampled within 10 m of the streambank, avoiding those with roots submerged in water. Since salmonberry clones in similar forests are typically <5 m in diameter (Tappeiner et al. 1991), we avoided sampling shrubs within 10 m of each other to reduce the chance of sampling genetic clones (e.g., van den Top et al. 2018). This design allowed us to sample 16 shrubs per stream, where possible.

At each shrub, we collected fruit samples and recorded fruit counts, soil moisture, exposure direction, canopy cover, and salmonberry stem density. We randomly collected up to 5 ripe fruits per shrub for analysis. Fruits were considered ripe if they detached easily from the receptacle but were not shriveled or moldy. Fruit counts included the number of fruits and empty receptacles per shrub. Since we observed salmonberry fruits to take longer than 1 month to develop from a bud into ripe fruit, and buds were no longer developing during our survey, fruits missed in our count due to timing were assumed to be negligible. We measured soil moisture using a handheld soil moisture meter (Fieldscout TDR 300; Spectrum Technologies, Aurora, Illinois, USA) at four locations within each quadrat and averaged the readings. To account for temporal variation in soil moisture, we calculated the relative soil moisture for each quadrat by subtracting a reference site reading for that day from the readings obtained at each quadrat. We measured the main direction of sun exposure at each shrub by using a compass to determine either the aspect of the most prominent slope, or the orientation to the stream's open canopy if the slope was zero. Since compass readings provide circular data, we took the cosine and sine of the exposure direction to transform it into northness and eastness, respectively. Canopy cover (%) was estimated using a densiometer by averaging 4 readings per quadrat. We used stem density as a proxy for plant size by counting the number of salmonberry stems produced per shrub.

*Salmonberry fruit measurements*

We recorded seed count (#/fruit), fruit weight (g), and estimated sugar content (° Brix) for each fruit collected. Fruits were analyzed on the same day they were collected and were allowed to acclimatize to laboratory temperatures for a minimum of one hour before processing. Using an electronic scale, we measured the wet weight rather than dry weight of each fruit since we found wet and dry weight of salmonberry fruits

to be highly correlated ($R^2 = 0.82$; Appendix S1: Fig. S1) and dry weight would hinder subsequent data collection. Soluble solids in juices are primarily made up of sugars (Cao et al. 2015) and can be measured by refractometry in units of ° Brix (Tolman and Smith 1906). Since sugar content and soluble solids are highly correlated in fruit (Lott and Barrett 1967), we used the Brix value to represent sugar content. To measure the sugar content (° Brix) of each fruit, we wrapped the fruit in tulle fabric to act as a filter, extracted the juice using a garlic press, then used a handheld refractometer (Master-20M, Atago, Japan) to obtain the Brix value of the juice. The refractometer was recalibrated daily, following manufacturer guidelines for temperature compensation. Lastly, we removed the seeds and pulp from the tulle and used forceps to manually separate and count the seeds. Each task was performed by the same person for every fruit to maintain consistency.

### Statistical analysis

*Shrub-level analysis.*—We recorded the number of fruits produced per shrub from 166 shrubs. Using the lme4 package in R (Bates et al. 2015, R Core Team 2019), we developed a global generalized linear mixed model (GLMM) to determine the relationship between salmon density and fruit count, while accounting for canopy cover, soil moisture, stem density, distance upstream, distance from streambank, and direction of exposure (i.e., northness and eastness). To determine if one salmon species had more of an effect on fruit count than the other, we fit a second global GLMM using chum and pink salmon densities as separate covariates in place of salmon density. In both models, we classified stream as a random effect to account for similarities between shrubs sampled on the same stream. This random effect also accounts for variation among streams in the rate of transfer of salmon carcasses to riparian areas. All variables were standardized (scaled and centered) for analysis. To assure the fit of these models, we used the DHARMA package in R to perform GLMM diagnostic tests (Hartig 2019, R Core Team 2019). We then fit all possible subsets of parameters from both global models and averaged across each resulting model set to estimate parameter coefficients

and to determine the relative importance of each variable (RVI).

We recorded the weight, estimated sugar content (° Brix), and number of seeds per fruit of 439, 426, and 441 fruits, respectively. We used these data to fit three global linear mixed effects models (LMMs) to examine the relationship between salmon density and each of these fruit-level response variables. For these models, we used the same standardized explanatory variables as our shrub-level models—salmon density, canopy cover, soil moisture, stem density, distance upstream, distance from streambank, and direction of exposure (i.e., northness and eastness). We also fit a second LMM where we separated chum and pink salmon densities to explore whether the effects were dependent on the species of salmon. To account for sampling multiple fruits per plant, and multiple shrubs per stream, we nested shrub within stream as a random effect in each fruit-level model. As with the shrub-level analysis, we fit all possible subsets of our global models, then used model averaging to calculate parameter estimates and RVIs.

## RESULTS

### Shrub-level results

Spawning salmon density ranged from 0 to 31 kg/m across the 14 streams. Fruit counts ranged from 1 to 180 fruits per shrub. As predicted, we found a significant positive relationship between the number of fruits produced per shrub and salmon density (Fig. 3A). We also found that stem density and distance from streambank had significant relationships with fruit count—fruit count increased with higher stem density (Fig. 3B) and decreased with distance from the streambank (Appendix S1: Fig. S2). Stem density was the most important predictor of fruit count (RVI = 0.97), followed by distance from streambank (RVI = 0.79), then salmon density (RVI = 0.68). All other variables were not important (RVI < 0.50). However, the effect of salmon density was approximately 1.3 × stronger than stem density and 2 × stronger than distance from streambank (Fig. 3C). We estimate that an increase in salmon density by one standard deviation above the average (8.8 kg salmon per meter of stream) would amount to approximately 23% more salmonberry fruits per shrub.
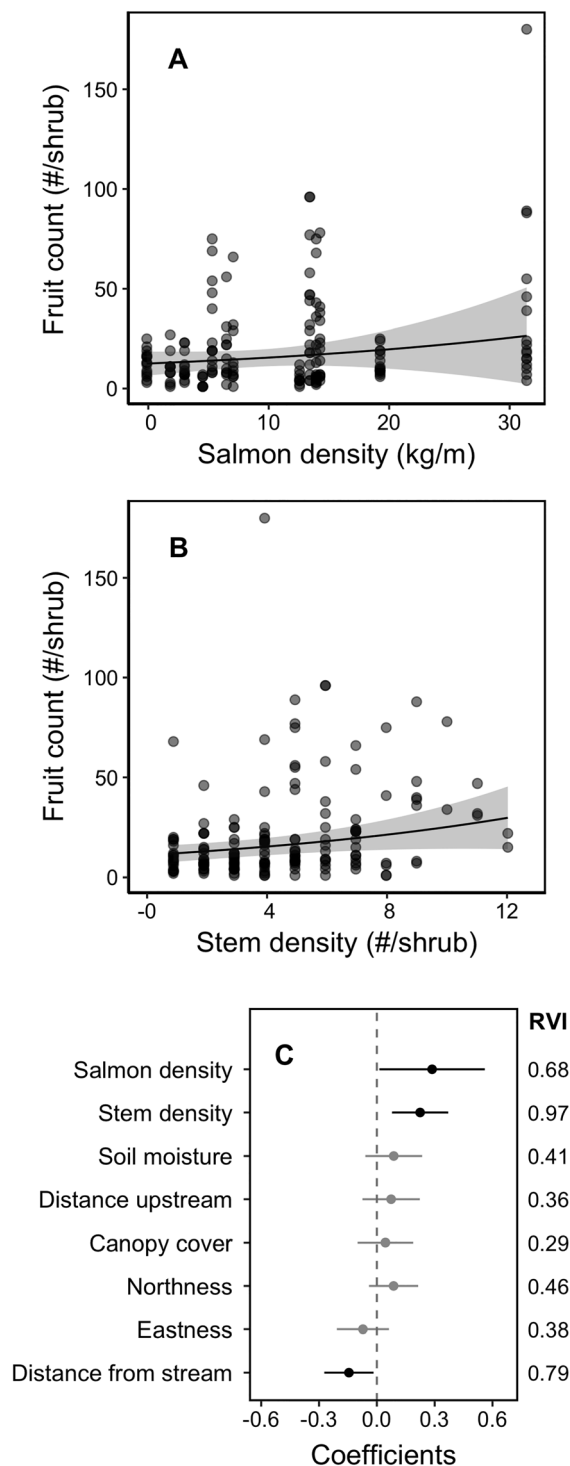
Chum salmon density had a strong, positive relationship with the number of fruits produced per shrub, while pink salmon density showed no effect (Fig. 4A, B). Likewise, chum density was a moderately important predictor of fruit count (RVI = 0.76), while pink salmon was not important (RVI = 0.30). However, stem density and distance from streambank were still the most important predictors (RVI = 0.97 and 0.80). All other variables had an RVI of less than 0.50. Despite a lower RVI, the coefficients show that the effect of chum density was approximately 1.5 × stronger than stem density and 2.3 × stronger than distance from streambank (Fig. 4C). We estimate that an increase in chum salmon density by one standard deviation above the average (6.8 kg chum per meter of stream) would amount to approximately 31% more salmonberry fruits per shrub.

### Fruit-level results

Contrary to our predictions, we did not find any evidence of a relationship between salmon density and the fruit-level traits—seed count, fruit weight, and sugar content estimated by Brix value (Fig. 5A-C). The other explanatory variables in each model also had no strong effects on any of these fruit-level traits. Our sugar content model had no important predictors (all RVI < 0.50), while our fruit weight and seed count models showed weak negative effects of distance upstream (RVI = 0.64, 0.57, respectively), though neither relationship was significant (Appendix S1: Fig. S3). The remaining predictor variables for both fruit weight and seed count models were not important (RVIs < 0.50). These relationships did not change when we considered chum and pink salmon density separately in each fruit-level model.

(Fig. 3. *Continued*)

the other variables in the model. Shaded areas represent 95% confidence intervals, and darker points indicate overlapping data. The standardized coefficient plot for the fruit count model (C) displays model-averaged data, with the error bar displaying the 95% confidence interval and black points highlighting coefficients that do not cross zero. Relative variable importance (RVI) is listed for each variable.
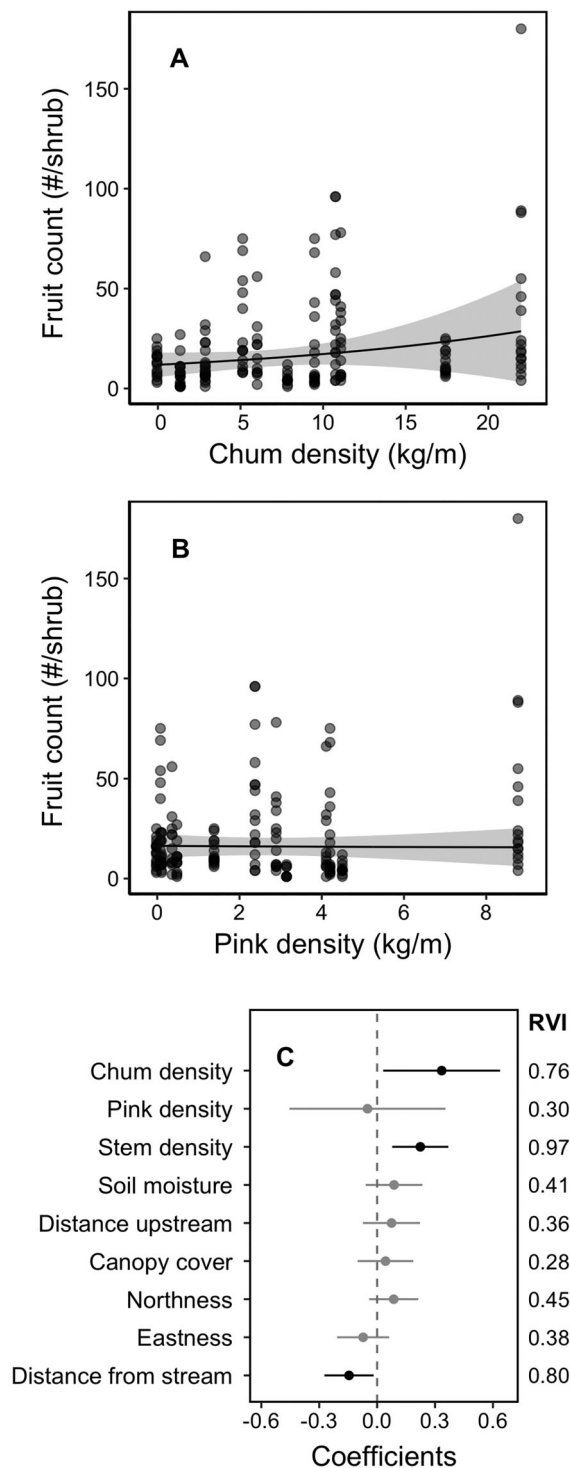
Fig. 3. Number of fruits per shrub in relation to (A) salmon spawning density and (B) stem density per shrub. The line in each graph represents the output from model-averaged predictions, and accounts for

## DISCUSSION

In this analysis of 14 streams on the central coast of British Columbia, Canada, we showed that spawning salmon density correlated with the number of fruits produced per shrub, but not the number of seeds per fruit, fruit weight, or estimated sugar content (° Brix) of the fruit. We also found that the effect of salmon density on the number of fruits per shrub is species-dependent—chum salmon were better predictors than pink salmon. The number of fruits per shrub increased with chum density but was not affected by pink salmon density. Shrubs that had higher stem density or were closer to the stream-bank also had more fruits, while shrubs further upstream had slightly lighter fruits with fewer seeds.

We found a positive relationship between salmon spawning densities and the number of fruits produced by salmonberry shrubs. This is consistent with previous studies, where increases in salmon density resulted in greater percent cover of nitrophilic species including salmonberry (Hocking and Reynolds 2011) and higher stomatal density in salmonberry leaves (van den Top et al. 2018). The former study also showed increased 15N in plant species along streams with more salmon, while accounting for an index of soil moisture. Our finding is also consistent with agricultural studies that have found a positive relationship between fertilizer additions and fruit yield of other *Rubus* species (e.g., Stojanov et al. 2019).

While salmon carcass deposition is highly heterogeneous (Gende et al. 2007), the clonal nature of salmonberry plants may mediate this patchiness by allowing them to integrate nutrients over large areas. Salmonberry plants can

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(Fig. 4. *Continued*)

accounts for the other variables in the model. Shaded areas represent 95% confidence intervals, and darker points indicate overlapping data. The standardized coefficient plot for the fruit count model with chum and pink salmon as covariates (C) displays model-averaged data, with the error bar displaying the 95% confidence interval and black points highlighting coefficients that do not cross zero. Relative variable importance (RVI) is listed for each variable.

Fig. 4. Number of fruits per shrub in relation to (A) chum salmon spawning density and (B) pink salmon spawning density. The line in each graph represents the output from model-averaged predictions and
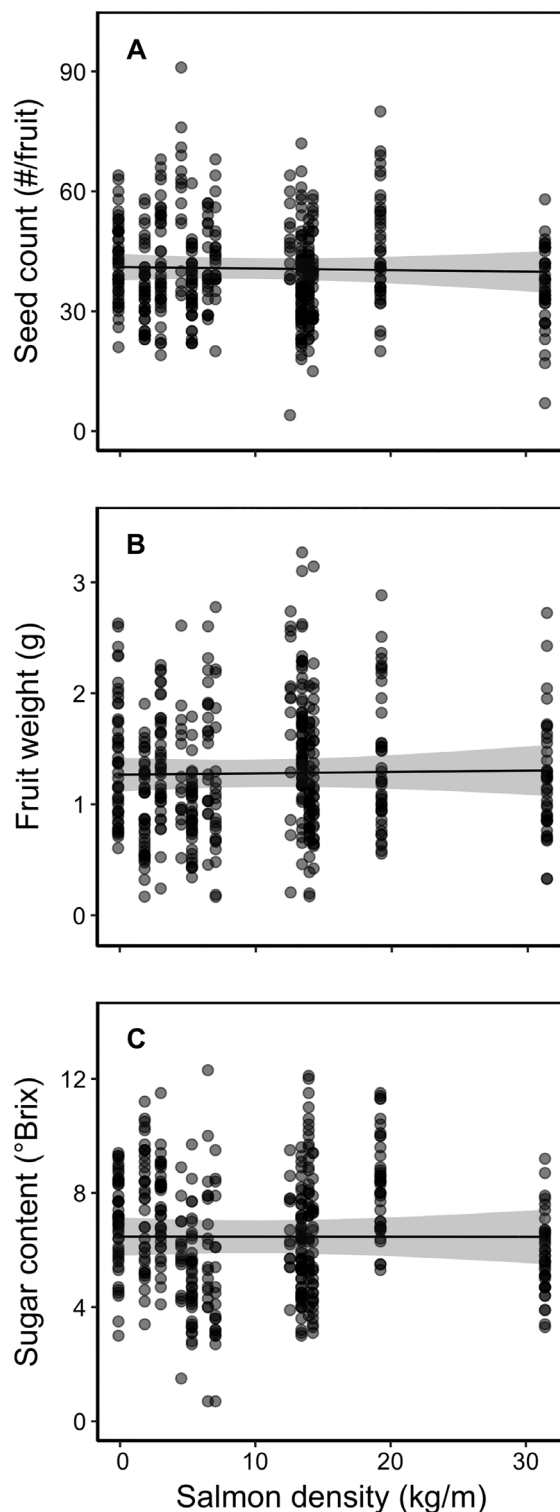
Fig. 5. Salmon spawning density in relation to (A) seed count per fruit, (B) fruit weight, and (C) sugar

have rhizomes as long as 5 to 18 m, depending on the forest type (Tappeiner et al. 1991). Furthermore, previous research has demonstrated that nutrient availability in riparian areas can be highly variable within a watershed, regardless of the presence of salmon-derived nutrients (Feddern et al. 2019). In salmon-bearing streams, bears are primary drivers of changes in nutrient cycling, while adding to the spatial inequality of carcass deposition (Holtgrieve et al. 2009). Although this within-watershed variation adds to the uncertainty around our estimates, the cross-watershed variation we observed was sufficient to find a relatively strong relationship between salmon density and salmonberry reproductive output (Figs. 3A, C and 4A-C). In fact, we estimate that on an average stream, an increase of 8.8 kg salmon per meter of stream would amount to approximately 23% more salmonberry fruits per shrub. While this only amounts to a handful of fruits per shrub, on the watershed level these additions could be substantial, especially considering that there is generally a greater abundance of salmonberry shrubs near streams with higher salmon densities (Hocking and Reynolds 2011).

We found that chum salmon were a better predictor of the number of fruits per shrub than pink salmon. This unequal effect has been observed in previous studies, where chum salmon were better predictors of juvenile coho salmon body size (Nelson et al. 2015) and the level of marine-derived nutrients detected in riparian vegetation and invertebrates (Hocking and Reimchen 2009). In our study streams, chum salmon were observed at much greater densities than pink salmon, with the highest density of each species being 22 and 9 kg/m, respectively. Chum salmon are also transferred to terrestrial ecosystems at a higher rate than pink salmon (Reimchen 2000, Hocking and Reimchen 2006). Bears are

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(Fig. 5. *Continued*)
content (° Brix), which is estimated using soluble solid content. The line in each graph represents the output from model-averaged predictions and accounts for the other variables in the model. Shaded areas represent 95% confidence intervals, and darker points indicate overlapping data.

responsible for approximately 75% of the salmon transfer from water to land in coastal British Columbia (Reimchen 2000) and they prefer chum over pink salmon (Andersson and Reynolds 2018, Harding et al. 2019). This is thought to be because chum salmon are larger than pink salmon (3.1 and 1.05 kg, respectively), making it easier for bears to access energy-rich parts and providing a greater reward (Andersson and Reynolds 2018). The combination of higher chum densities and higher transfer rates from water to land could help explain why chum were much better predictors than pink salmon for fruit count in our system.

Factors other than nutrient availability can also influence the number of fruits produced per shrub. In our study, the number of fruits increased with increasing stem density, which was expected since plants with more stems produced more fruits per row of shrubs in other *Rubus* species (Sonsteby et al. 2019). We also found a decrease in fruit count with increasing distance from the streambank. However, other salmonberry studies found no effect of distance from stream on plant traits (van den Top et al. 2018) and marine-derived nutrient levels (Ben-David et al. 1998). We took the majority of our samples in close proximity to the stream, and we limited our collection sites to be within 10 m of the streambank, where salmon carcass density is highest in riparian areas (Reimchen 2017). For these reasons, the association between fruit number per shrub and the distance from streambank should be interpreted cautiously. Soil moisture and canopy cover were not related to the number of fruits produced per shrub; however, these values were very consistent among the streams in our study. It is worth noting that some members of the Haíɫzaqv (Heiltsuk) First Nation considered the year of the study (2019) to be a particularly poor year for salmonberry, with less fruit than normal near Bella Bella, B.C. (S. Humchitt, *personal communication*). Fruit development also depends on other factors, including weather conditions and pollinator activity. For example, desirable weather conditions during pollination can lead to more successful pollination of flowers by bees and higher fruit numbers (Tuell and Isaacs 2010), plants experiencing drought conditions can have reduced fruit yields in the same year (Milošević et al. 2018, Stojanov et al. 2019)

and the following year (Morales et al. 2013), and raspberry plants growing in cooler temperatures have higher fruit yields in the following year (Woznicki et al. 2016).

Contrary to our expectations, we found no evidence of a relationship between salmon density and the number of seeds per fruit, fruit weight, or estimated sugar content (° Brix) of salmonberry fruits. However, shrubs on streams with higher spawning densities produce more seeds per shrub, since there are more fruits per shrub and a similar number of seeds per fruit. Fruit traits can be strongly influenced by factors other than nutrient availability such as weather conditions (Morales et al. 2013, Woznicki et al. 2016, Stojanov et al. 2019), genetics (Mezzetti et al. 2004), phenology (Thies et al. 1995), soil properties (Li et al. 2015), and the rate and timing of fertilizer applications (Lovatt 2001). Biological trade-offs such as seed count vs. seed size and vegetative growth vs. reproductive output could also help explain the lack of response of these traits to salmon subsidies.

An increase in salmonberry fruits could contribute to greater plant reproductive success and provide a larger input of salmonberry fruits into the food web. This could lead to benefits for consumers; for example, food availability affects songbird reproductive success and survival (Martin 1987). Additionally, since the number of seeds that were produced per fruit was not statistically different between our study streams, higher numbers of fruits per shrub would provide a higher potential for seed dispersal. Therefore, our research may help explain our previous finding that there is a higher density of salmonberry near streams with more spawning salmon in these watersheds (Hocking and Reynolds 2011), though additional factors such as enhanced survival or clonal growth could also be involved.

## Conclusion

Spawning salmon have substantial impacts on freshwater and riparian ecosystems (Walsh et al. 2020). We found that spawning salmon densities correlate with the number of fruits produced per salmonberry shrub but not the number of seeds per fruit, fruit weight, or sugar content (° Brix) of the fruit. This pattern appears to be driven by chum salmon rather than pink salmon. Our

findings imply that salmon can affect fruit production of a common plant in the coastal forests of western North America, even though spawning and fruiting events are seasonally mismatched. Increased fruit availability may also provide additional food resources to consumers and potentially contribute to shifts in salmonberry abundance. This research provides the first evidence of marine productivity having the potential to influence the reproductive output of a riparian plant species, demonstrating the extent to which salmon subsidies can influence terrestrial ecosystems.

## ACKNOWLEDGMENTS

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## DATA AVAILABILITY

Our data and code for analysis are accessible from github.com/SiemensLisa/salmon-subsidy-research-2020.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3282/full