

Juvenile Chum Salmon and Pink Salmon use of submerged vegetative habitats and the influence of an apex predator

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ABSTRACT

Objective: Apex-predator-initiated trophic cascades occur in many nearshore marine habitats that simultaneously serve as critical habitat and food sources for commercially and ecologically important species, including juvenile Pacific salmon *Oncorhynchus* spp. Yet the potential relationships among apex predators (e.g., sea otters *Enhydra lutris*), submerged aquatic vegetation, and juvenile salmonids are not well understood. In Southeast Alaska, we investigated (1) juvenile salmonid abundance in eelgrass *Zostera marina* meadows and understory kelp beds and (2) potential drivers of juvenile Chum Salmon *Oncorhynchus keta* and Pink Salmon *O. gorbuscha* abundance in eelgrass meadows.

Methods: We analyzed historic (1998–2007) beach seine surveys to compare juvenile salmonid abundance in nearshore habitats. We then employed the same survey (2017, 2019) in eelgrass to quantify juvenile salmonid abundance alongside the influence of sea otter density (number/km²), distance from anadromous stream (km), seasonality, sediment categorization, and aboveground eelgrass biomass (g/m²).

Results: We found greater abundance of Chum Salmon in understory kelp compared with eelgrass, whereas Pink Salmon abundance was similar between habitats. In eelgrass, Chum Salmon abundance peaked in June and was positively associated with sea otter density. Pink Salmon abundance varied seasonally, peaking in May. We found increased Pink Salmon abundance with increasing sea otter density and distance from anadromous stream and decreased abundance with increased eelgrass biomass.

Conclusion: Growth and survival while juvenile salmonids are out-migrating from streams and relying on nearshore vegetated habitats can determine if they recruit to fisheries as adults. Here, we highlight the use of multiple habitats, eelgrass and understory kelp, indicating that both should be explored as critical nursery habitat. We present evidence of indirect effects of sea otters influencing the abundance of juvenile salmonids, with potential further implications as sea otter populations expand. Apex predators, quality of vegetated habitats, and their structuring roles in the nearshore are critical for informing adaptive coastal fisheries management.

KEYWORDS: juvenile salmon, nearshore structured habitats, nursery, sea otters, submerged aquatic vegetation

LAY SUMMARY

Eelgrass is often highlighted as a nursery habitat for juvenile salmon that provides foraging grounds and refuge from predation, but this research suggests that understory kelp should also be assessed as critical habitat. Additionally, the presence of juvenile salmon in the nearshore is modulated by sea otter density (number/km²), distance from anadromous stream (km), seasonality, and aboveground eelgrass biomass (g/m²). We identified indirect effects of an apex predator influencing the abundance of juvenile Pink Salmon and to a lesser extent juvenile Chum Salmon and highlight implications for habitat quality as sea otters continue to expand spatially in Southeast Alaska.

INTRODUCTION

Many nearshore marine ecosystems have high primary productivity and support a diverse community of organisms. Of these, submerged aquatic vegetation, including seagrasses and

algae, are considered critical nursery habitats for various species (Beck et al., 2006; Lefcheck et al., 2019). As such, coastal regions are a vital location to examine the role of biotic and abiotic forces on fishes, in particular, commercially important

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species. Juvenile salmonids are one such group of species that migrate through the nearshore marine environment during their transition from freshwater to marine life stages (Beck et al., 2006; Kennedy et al., 2018; Murphy et al., 2000). This early marine juvenile phase is a critical time period for growth and can influence their survival to adulthood (Beamish et al., 2004) and recruitment to fisheries. The relationship between juvenile salmonids and nearshore habitats varies by species (Johnson et al., 2012; Sharpe et al., 2019) and can be altered through external forces, including apex predators, that exert strong driving forces in ecosystems (Estes & Duggins, 1995; Raymond et al., 2021), and their presence should be evaluated as a potential factor in fisheries management (Davis et al., 2019).

Trophic cascades, resulting from changes in the abundance of top predators, can cause structural changes in food webs due to strong relationship among species (Paine, 1980). Sea otters *Enhydra lutris* are an example of an apex predator that induces trophic cascades with resulting increases in kelp and eelgrass *Zostera marina* through reduction of grazers, control of mesopredators, and reduction in competitors (Estes & Duggins, 1995; Foster et al., 2021; Hughes et al., 2013; Raymond et al., 2021; Saavedra, 2021). Specifically within eelgrass meadows, sea otter recolonization is associated with increased eelgrass biomass (Raymond et al., 2021), greater genetic diversity through physical disturbance of eelgrass when foraging (Foster et al., 2021), and enhanced eelgrass growth rates by removing belowground competitors (clams) (Saavedra, 2021). The reintroduction of sea otters indirectly impacts trophic feeding levels of rockfishes *Sebastes* spp. in canopy kelp forests (Markel & Shurin, 2015), changes species abundance in canopy kelp forests (Reisewitz et al., 2006; Silberg, 2015), increases fish community species richness in eelgrass meadows, and shifts fish community composition in understory kelp beds (Domke, 2023). However, these studies focused primarily on greenlings (family Hexagrammidae) and rockfishes in canopy kelp forests, leaving gaps in our understanding of indirect effects of sea otters on fish communities.

Considering the importance of nearshore habitats for juvenile salmonids and the strong role of apex predators in the nearshore, we aim to compare juvenile salmonid use of two common types of nearshore habitats and the influence of environmental variables, including sea otters, on juvenile salmonids in eelgrass meadows. Our first objective compared juvenile salmonid use of eelgrass meadows and understory kelp beds in Southeast Alaska using historical (1998–2007) National Oceanic and Atmospheric Administration (NOAA) beach seine surveys (Johnson et al., 2012) and identified coastline extent of each habitat. Our second objective explored a range of environmental and biological drivers of abundance of juvenile Chum Salmon *Oncorhynchus keta* and Pink Salmon *O. gorbuscha*, including sea otter density, distance from anadromous stream, date, sediment classification, and eelgrass biomass using contemporary seines (2017, 2019) only in eelgrass meadows. The focus on eelgrass meadows in the second objective is founded on observed trophic interactions between sea otters in eelgrass meadows in the same region (Raymond et al., 2021). Given the dependence of juvenile salmonids on nearshore habitats during a critical time frame for growth and survival, their recruitment to commercial harvest is likely linked to the availability of habitats like eelgrass

and understory kelp. Therefore, understanding how juvenile salmonids use nearshore habitats and the role of apex predators in explaining patterns in their abundance will contribute to managing the fisheries and coastal resources.

METHODS

Study area

Our study was located in Southeast Alaska, which is composed of a mosaic of nearshore vegetated habitats, including understory kelps and eelgrass, and varied sea otter abundance. Following sea otter reintroduction in the 1960s, the combination of sea otter expansion and legal hunting by coastal Alaska Native peoples created a gradient of sea otters, with a current total population size around 22,000 (Burris & McKnight, 1973; Raymond et al., 2019; Schuette et al., 2023). Our sampling areas for both the historical NOAA data and contemporary data encompassed southern Southeast Alaska (57°N, 131°W to 54°N, 134°W) along the western coast of Prince of Wales Island, in the vicinity of Revillagigedo Island, and surrounding smaller islands (Figure 1). These two regions, western Prince of Wales Island and Revillagigedo Island, have similar oceanographic conditions and species distribution to one another as described in Johnson et al. (2012). Prince of Wales Island, the largest island in the Alexander Archipelago, is exposed to the Gulf of Alaska along its west coast and to Dixon Entrance at the south. Revillagigedo Island, located east of Prince of Wales Island and closer to the mainland, is exposed in the south to the Nichols and Revillagigedo channels, which connect to Dixon Entrance. The sampling region includes a diversity of habitats, ranging from highly exposed rocky habitats to low-energy, soft-sediment estuaries and protected bays. In high-energy areas, understory kelps (*Laminaria* spp. and *Saacharina* spp., among others) and canopy kelps (bull kelp *Nereocystis luetkeana* and giant kelp *Macrocystis pyrifera*) occupy rocky shores (Harper & Morris, 2014). Protected shorelines have both expansive and narrow, fringing sea grass meadows (eelgrass and surfgrass *Phyllospadix* spp.) in the low intertidal to subtidal zones.

Comparison of habitat use by juvenile salmonids using historical NOAA surveys

We analyzed historical (1998–2007) NOAA beach seine data from eelgrass and understory kelp habitats (Johnson et al., 2012) to evaluate juvenile salmonid use of these habitats. We subset the data to include sites ($n = 42$) in the southern Southeast Alaska outside region, which included the western and southeastern coasts of Prince of Wales Island, southern Revillagigedo Island, Gravina Island, Annette Island, Duke Island, and the southern tip of the mainland of the southeast panhandle (Figure 1A; Table S1 [see online Supplementary Material]). Most sites were seined once; however, at a subset of sites ($n = 12$), the fish community was resampled across multiple months for a total number of 72 seine events across all 42 sites sampled during the 10-year NOAA effort. Juvenile salmonid abundance was quantified as number per seine set (number/seine) standardized using the same methods and net, a 37-m beach seine with variable mesh that tapered in width from 10 m in the center to 5 m in the sides, with a mesh size of 32 mm along the sides, decreasing to 6 mm towards the center,

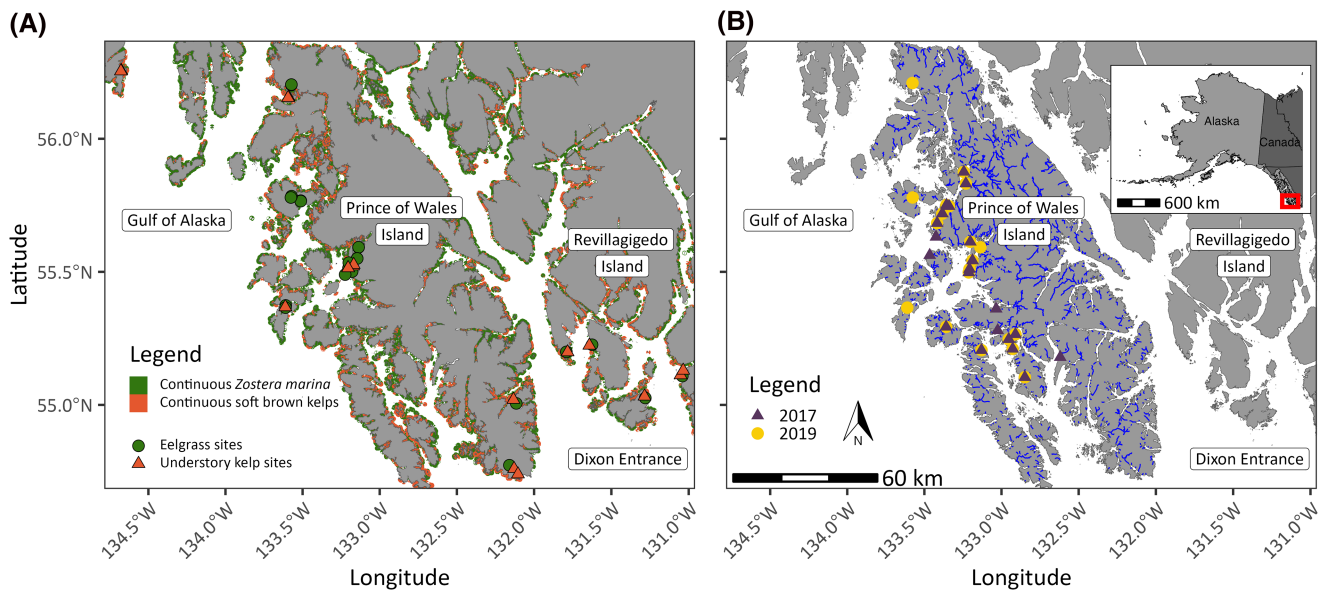


Figure 1. Maps showing (A) eelgrass *Zostera marina* (green) and understory kelp (orange) shoreline extent (data from ShoreZone, Harper & Morris, 2014) and historical NOAA eelgrass (green circles) and understory kelp (orange circles) sites sampled in southern Southeast Alaska (Johnson et al., 2012) and (B) eelgrass sites sampled in 2017 (purple triangle) and 2019 (yellow circle) with known anadromous streams (blue) (data from Anadromous Waters Catalog, Alaska Department of Fish and Game [ADFG], 2019).

with a 3.2-mm square mesh set in a round haul (described in Johnson et al., 2012). To contextualize juvenile salmonid use of eelgrass and understory kelp beds, we calculated the percentage of coastline extent that each coastal habitat occupied in outer southern Southeast Alaska. We used ShoreZone habitat classifications from approximately the same time frame as the historical beach seines (Harper & Morris, 2014) and subset the spatial extent to the same area where historically fish sampling took place to calculate linear coastline (km) and resulting percentage of continuous eelgrass and soft brown kelp (representing the understory kelp bed habitat) in outer southern Southeast Alaska. ShoreZone data were generated from aerial imagery from daylight low tides with GIS classification of coastal habitats between 2004 and 2010 (Harper & Morris, 2014).

We analyzed the historical abundance of Chum Salmon and Pink Salmon per seine using a generalized additive mixed-model framework implemented with the R package mgcv to allow inclusion of smoothed spatial terms and random effect, using a negative binomial error distribution to account for the overdispersion in these count data (Wood et al., 2016). Each species was analyzed separately using the same suite of candidate models and testing the inclusion of random effect of site, as some sites were resampled across months (April–July), month, and spatial terms. We compared random effect structure, including a random intercept of month and site or a random intercept of site fit, with restricted maximum likelihood. After determining the best random effect structure, we fit the model using maximum likelihood and included categorical fixed effects of habitat type and month, if month was not included as a random effect. We incorporated sampling date as categorical months since sampling time was clustered during negative low-tide cycles which occur bimonthly. Due to the repeat sampling of sites, a random effect of site was retained in each model. Spatial terms were included as a smoothed thin plate regression spline of latitude, smoothed

thin plate regression spline of latitude by longitude, or tensor product smooth of latitude by longitude. We evaluated goodness of fit for both the random effect structure and fixed effects using second-order Akaike information criterion (Burnham & Anderson, 2002) suited for small sample size (AIC_c) and Bayesian information criterion (BIC). The best model was refit using restricted maximum likelihood to better estimate model parameters for models with random effects.

Drivers of juvenile salmonids in eelgrass meadows in contemporary surveys

In addition to the historical data, we conducted contemporary beach seines (2017, 2019) in eelgrass meadows to quantify juvenile salmonids. We sampled eelgrass fish communities using the identical methods to the historical NOAA surveys along the western coast of Prince of Wales Island in 2017 (sites = 21) and 2019 (sites = 20) (Figure 1B; Table S1). We identified all fish to the lowest possible taxonomic level and counted and measured individual fish (fork length or total length depending on the species) to the nearest millimeter. All seines occurred around the negative low tides of the month (−0.03 to −0.91 m below mean lower low water) as the tide dropped. We selected sites based on presence of eelgrass across a gradient of sea otter density (Raymond et al., 2021).

At each beach seine location in 2017 and 2019, we focused on understanding potential drivers of salmonid abundance in the nearshore. This approach investigated the influence of sea otters using a gradient of sea otter density (number/km²), distance from anadromous stream (km), day of year, qualitative sediment categorization, and aboveground eelgrass biomass (g/m²). At each site, we calculated eelgrass biomass by first counting eelgrass density (including flowering shoots) in five to eight 0.5 × 0.5-m quadrats adjacent to where the beach seine occurred and at the same tidal height (approximately −0.5 m

below mean lower low water). We then collected 8 to 15 shoots from each quadrat ($n = 75$ per site) and measured their maximum length to the nearest millimeter. We calculated eelgrass biomass for each site based on the ratio of total length to dry biomass (g/m^2) calculated from data (biomass and lengths by shoot) collected from Raymond et al. (2021) and extrapolated to grams per square meter based on eelgrass quadrat density (Equation 1; adjusted $r^2 = 0.84$; Figure S1 [see online Supplementary Material]):

$$\log(\text{dry biomass}) = -7.78 + 1.57 \times \log(\text{maximum length}). \quad (1)$$

In addition to eelgrass biomass, we accounted for the substrate present at each site, as sediment was previously correlated with other environmental metrics in this region (sea otters and eelgrass biomass) (Raymond et al., 2019) and perhaps plays a role in determining habitat for juvenile salmonids. We classified primary and secondary sediment type categorically using a 10-point scale adapted from Folk (1954) where 1 represents mud and 10 represents bedrock or reef. To account for the location of salmon-bearing streams, we calculated distance via water from seine location to the mouth of known anadromous streams using qGIS and Alaska known anadromous streams in the Anadromous Waters Catalog (Figure S2). The Anadromous Waters Catalog is a geospatial layer maintained and updated by the ADFG and identifies over 20,000 streams, rivers, or lakes that are important for spawning and rearing of anadromous fishes (<https://www.adfg.alaska.gov/sf/sarr/awc/>; ADFG, 2019). To quantify sea otter density (number/ km^2), we completed two boat-based sea otter surveys around each seine location. We surveyed the water area within 3.8 km of a site by boat, traveling at 14 km/h around each beach seine site in 2017 and 2019, enumerating and geolocating sea otters. Surveys occurred a minimum of 2 weeks apart. Based on the varied coastline, we converted sea otter numbers to density by dividing by total water area surveyed and averaging the two surveys and then log-transformed values plus a small constant (0.1) sea otter density to better visualize patterns in abundance along sea otter density.

We analyzed the total number of juvenile Chum Salmon and Pink Salmon caught per seine, using a species-specific generalized additive model framework for Chum Salmon to fit a tweedie error distribution and a generalized linear model framework for Pink Salmon. Full models included all explanatory parameters with interactions between fixed-effect parameters (day of year, day of year squared, year, log-transformed sea otter density, qualitative sediment classification, distance from anadromous stream, and eelgrass biomass). Squared day of year was included to incorporate the increase, peak, and then decline of juvenile salmonids across months when sampling occurred. We used a tweedie error distribution model for Chum Salmon with the “gam” function in the mgcv package to estimate the power parameter (Wood et al., 2016) and a log-link function to account for overdispersion in the catch data. For Pink Salmon we used a negative binomial error distribution and a log-link function to account for overdispersion in the catch data. Starting with the full model, we used backward selection and evaluated model fit using second-order AIC_c and BIC and, for Pink Salmon models, model probability based on

the weight of evidence using both AIC and BIC (AIC and BIC weights). For top models with $\Delta\text{AIC}_c < 2$, we averaged model coefficients using only the top models and the explanatory parameters included therein with the “model.avg” function in the MuMIn package (Bartoń, 2022; Burnham & Anderson, 2002). Additionally, we summed each parameter weight to interpret as a measure of the relative importance of the parameter. Model-predicted figures presented are back-transformed into the response space as predicted juvenile salmonid catch for each species per beach seine set. All analyses were performed in RStudio R version 4.1.2 (R Core Team, 2021).

RESULTS

Comparison of habitat use by juvenile salmonids using historical NOAA surveys

After holding month constant in the historical NOAA surveys, the role of habitat varied by species. The best-fit model for juvenile Chum Salmon included habitat, month, and smoothed latitude as fixed effects and a random site effect for the intercept term (Table S2). The best-fit model for juvenile Pink Salmon included habitat and month as fixed effects and a random site effect for the intercept term (Table S3). For both species, a negative binomial distribution (Chum Salmon overdispersion parameter = 0.32, Pink Salmon overdispersion parameter = 0.14) minimized the AIC_c and BIC compared to using a tweedie distribution. We found strong evidence of a positive effect of understory kelp on Chum Salmon abundance relative to eelgrass meadows (P -value = 0.016) (Figure 2A; Table 1), whereas we observed a negligible difference of juvenile Pink Salmon abundance (P -value = 0.58) between understory kelp and eelgrass habitats (Figure 3A; Table 1). Latitude strongly influenced juvenile Chum Salmon catch, with more fish caught at mid-latitudes (between 55.3°N and 55.5°N, P -value = 0.013; Figure 2C; Table 1). As expected, salmonid abundance varied over time. Month had a strong effect on juvenile Chum Salmon abundance (Figure 2B; Table 1). Compared to juvenile Chum Salmon abundance in April, fewer individuals were observed in June and July (P -value < 0.001 and P -value = 0.001). Similarly, the month in which juvenile Pink Salmon were sampled strongly effected abundance of juvenile Pink Salmon (Figure 3B; Table 1), with declines in abundance in June and July compared with April (P -value = 0.001 and P -value < 0.001). The greatest number of Pink Salmon caught in a single seine occurred in eelgrass meadows in the months of April and May, and in those five cases, abundance was greater than 1,000 each time, stretching the box plot while the mean value remained low for eelgrass in April (Figure S3). Most of the juvenile Pink Salmon (82.7%) were caught in a small fraction of the total seines (6.9%) (e.g., only at a few sites during April and May).

Across the sampling region of southern Southeast Alaska, understory kelp and eelgrass meadows constitute different proportions of coastal habitat available for juvenile salmonids. Of the approximately 16,000 km of coastline in southern Southeast Alaska at the time of aerial survey (2004–2010), we calculated that continuous soft brown kelps constitute 6,080 km (37.8%) of the coastline and eelgrass occupies 1,300 km (8%) of the coastline (represented in Figure 1A). Together, these two structured habitats represent nearly half of the coastal habitat for juvenile salmonids.

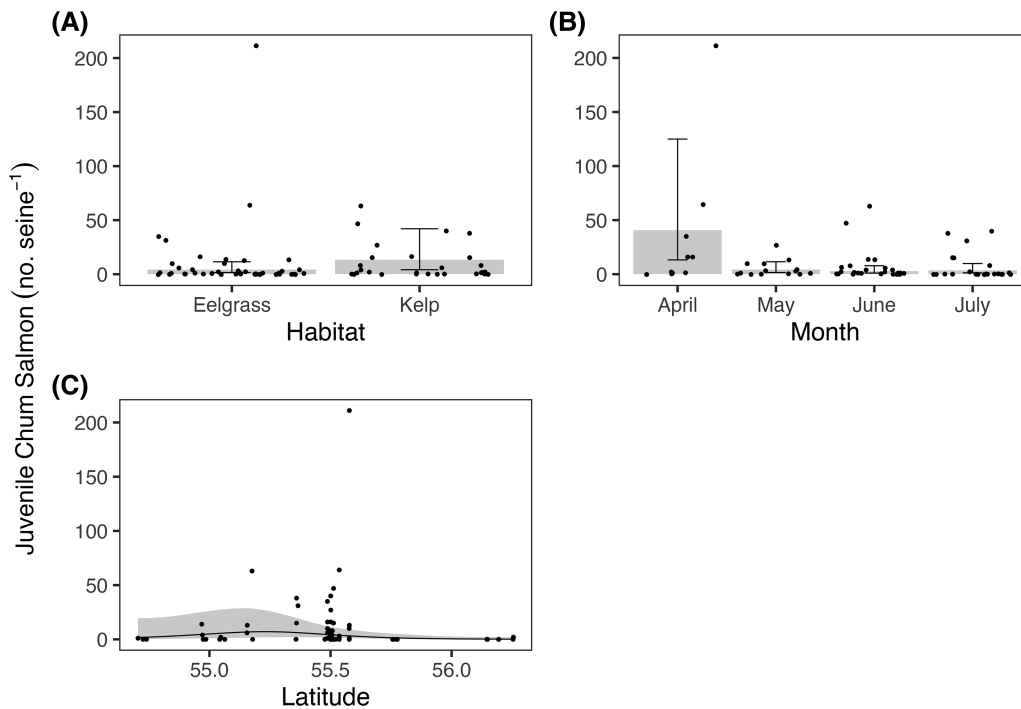


Figure 2. Panel (A) shows the model-predicted number of juvenile Chum Salmon (error bars show 95% confidence interval) between habitat type (eelgrass meadows and understory kelp) from the historical NOAA surveys while holding month constant on May, latitude at the median value, and incorporating the average effect of site. Panel (B) shows the model-predicted number of juvenile Chum Salmon across month (April–July) while holding habitat constant on eelgrass, latitude at the median value, and incorporating the average effect of site. Panel (C) shows the model-predicted number of juvenile Chum Salmon across latitude while holding habitat constant on eelgrass, month constant on May, and incorporating the average effect of site. Points are the number of Chum Salmon per seine.

Table 1. Results of the best-fit model and the associated predictors for juvenile Chum Salmon and juvenile Pink Salmon from the historical NOAA surveys. The best-fit models included predictors that significantly ($\alpha = 0.1$) contributed to explaining variability in juvenile salmonid numbers per seine based on their estimate, standard error (SE), statistic (stat), and *P*-value. Coefficients presented are in log space.

Predictors	Juvenile Chum Salmon				Juvenile Pink Salmon			
	Estimate	SE	Stat	<i>P</i> -value	Estimate	SE	Stat	<i>P</i> -value
(Intercept)	3.39	0.60	5.86	<0.001	3.09	1.58	2.03	0.043
Habitat [Kelp]	1.14	0.47	2.41	0.016	0.44	0.80	0.55	0.580
Mon [Jul]	−2.45	0.74	−3.29	0.001	−848	1.15	−7.40	<0.001
Mon [Jun]	−2.66	0.75	−3.53	<0.001	−14.91	4.45	−3.35	0.001
Mon [May]	−2.26	0.75	−3.03	0.002	−0.82	1.13	−0.73	0.465
Smooth latitude			9.48	0.013				
Site (r. effects)			0.00	0.502			7.33	0.006
Observations				72				72

Chum and Pink Salmon abundance in eelgrass meadows in contemporary surveys

Within eelgrass meadows sampled in contemporary (2017 and 2019) seines at 41 sites, juvenile Chum Salmon and Pink Salmon were caught between April and July along the western coast of Prince of Wales Island. The average number of fish caught varied by the two species (Chum Salmon = 15.0 ± 28.2 [mean $\pm$ SD] and Pink Salmon = 12.9 ± 49.8), and catch numbers per site ranged between 0 and 128 individuals for Chum Salmon and 0 and 287 for Pink Salmon. However, at a large percentage of sites, no fish were caught for either juvenile Chum Salmon (39% of sites) or juvenile Pink Salmon (58.5% of sites).

Environmental drivers of juvenile salmonid abundance were species-specific. The singular best-fit model for juvenile Chum Salmon included date, squared date, sea otter density, and secondary sediment grain size with a tweedie error distribution model (Table 2; Table S5; power parameter = 1.56). Chum Salmon catch increased with increasing sea otter density and was positively related to juvenile Chum Salmon abundance ($P = 0.011$; Table 2; Figure 4B). Chum Salmon abundance and day of year were related, with a peak abundance at the end of May to beginning of June (Figure 4A), and the day of year parameter estimate did not overlap with zero (Table 2). Secondary sediment grain size contributed to explaining juvenile Chum Salmon abundance ($P = 0.05$ Table 2; Figure 4C).

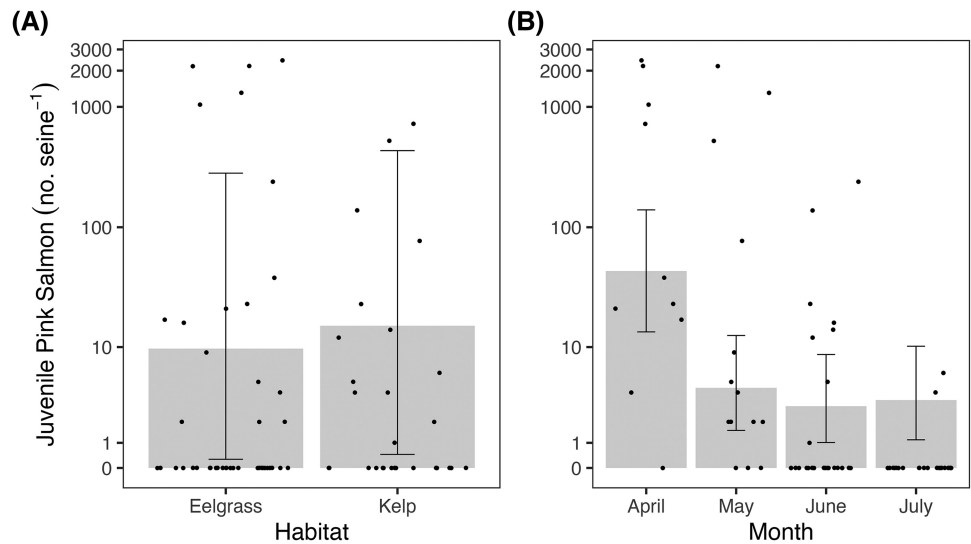


Figure 3. Panel (A) shows the model-predicted number of juvenile Pink Salmon (error bars show 95% confidence interval) between habitat type (eelgrass meadows and understory kelp) from the historical NOAA surveys while holding month constant on May and incorporating the average effect of site. Panel (B) shows the model-predicted number of juvenile Pink Salmon across month (April–July) while holding habitat constant on eelgrass and incorporating the average effect of site. Points are the number of Pink Salmon per seine. The y-axis scale is a pseudo log scale to smoothly transition to linear scale at zero to better visualize the patterns across large and small catch numbers.

Table 2. Best-fit model and associated predictors for juvenile Chum Salmon and model-averaged and associated predictors for juvenile Pink Salmon catch in contemporary seines in eelgrass meadows. The best-fit and model-averaged models included predictors that significantly ($\alpha = 0.05$) explained variability in juvenile salmonid catch based on their estimate, standard error (SE), statistic (stat), and *P*-value. The model-averaged top juvenile Pink Salmon model predictors are reported with the sum of weights or relative importance (AIC_w) across top models for each factor and the number of models containing each given factor. Coefficients are presented in log space.

Predictors	Juvenile Chum Salmon				Juvenile Pink Salmon					
	Estimate	SE	Stat	<i>P</i> -value	Relative importance (AIC_w)	N.models	Estimate	SE	Stat	<i>P</i> -value
Intercept	−20.91	7.57	−2.76	0.009			−172.7	53.99	3.09	0.001
Day of year	0.31	0.10	3.20	0.003	1	3	2.404	0.746	3.119	0.002
Quadratic day of year	0.0	0.0	−3.46	0.001	1	3	−0.008	0.003	3.134	0.002
Average sea otter density	0.41	0.15	2.67	0.011	1	3	0.93	0.22	4.085	0
Average eelgrass biomass					1	3	−0.034	0.016	2.066	0.039
Distance from anadromous stream					1	3	0.778	0.294	2.561	0.01
Average secondary sediment score	0.46	0.16	2.98	0.005	0.30	1	0.131	0.239	0.541	0.589
Average primary sediment score					0.18	1	0.071	0.212	0.33	0.742
Observations				40						40

with a positive relationship, although at higher grain size values with large uncertainty. Secondary grain size parameter estimates did not overlap with zero (Table 2).

The top two models for Pink Salmon had $\Delta AIC_c < 2$, with a third model within $\Delta AIC_c 2.2$; therefore, the average model included day of year, squared day of year, eelgrass biomass, log-transformed sea otter density, distance from anadromous stream, and primary and secondary sediment grain size (Table 2; Table S5). Similar to Chum Salmon, juvenile Pink Salmon abundance and day of year were related, with a peak slightly earlier than Chum Salmon (Figure 5A). Pink Salmon

abundance and log-transformed sea otter density and distance from anadromous stream were positively related, while abundance was negatively related with increased eelgrass biomass (Figure 5B–D; Table 2), although all three had large uncertainty. In addition to day of year, sea otter density, distance from anadromous stream, and eelgrass biomass were included in all three top models and was the most important predictor variable ($AIC_w = 1$; Table 2). Parameter estimates associated with day of year and squared day of year did not overlap with zero (Table 2), indicating a nonlinear relationship between catch rate and day of year. Log-transformed sea otter density, eelgrass

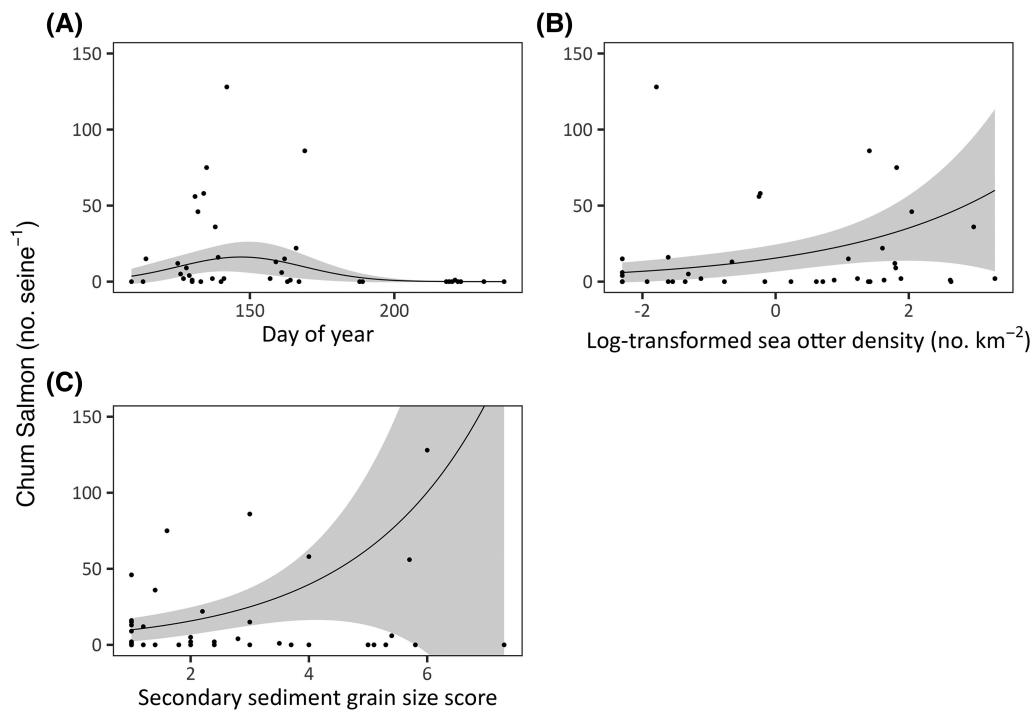


Figure 4. The average model relationship between juvenile Chum Salmon abundance from the contemporary studies and (A) day of year, (B) sea otter density, and (C) secondary sediment grain size. The black line indicates the relationship based on the best-fit model while holding the other explanatory variables at the median values, with gray 95% confidence bands and number of Chum Salmon per seine (points).

biomass, and distance from anadromous stream parameter estimates did not overlap with zero (Table 2; P -value < 0.001 , P -value = 0.039, P -value = 0.01, respectively). Conversely, sediment grain size (primary and secondary) did not significantly contribute to explaining juvenile Pink Salmon catch, with each only included in a single top model and low summed AIC weights ($AIC_w = 0.18$ and $AIC_w = 0.30$, respectively; Table 2; Figure SE, F). Both parameter estimates overlapped with zero (Table 2).

DISCUSSION

In this study, we found juvenile Chum Salmon and Pink Salmon present in both eelgrass meadows and understory kelp beds, with Chum Salmon in greater abundance in understory kelp compared with in eelgrass. Environmental drivers of juvenile salmonid abundance in eelgrass meadows were species-specific. Juvenile Chum Salmon abundance was informed by seasonality and increased with sea otter density and sediment grain size, albeit with large variability in particular in the relationship with sediment. Juvenile Pink Salmon abundance was informed by seasonality, sea otter density, distance from anadromous stream, eelgrass biomass, and both metrics of sediment grain size, although the relationship with grain size was not strong. Sea otter density and distance from anadromous stream were positively related to juvenile Pink Salmon catch, although the magnitude of effect had high uncertainty. Interestingly, we found that eelgrass biomass negatively influenced juvenile Pink Salmon abundance, with fewer fish encountered at greater biomass values. Across both data sets, historical and

contemporary, we found that juvenile salmonids use these habitats episodically, with patchy and at times incredibly abundant groups of juvenile salmonids encountered.

We hypothesized that juvenile salmonid abundance may be tied to the availability of suitable nearshore nursery habitats that provide refuge and prey supply and that the habitat may be altered or modulated by the presence of an apex predator, therefore impacting the associated fish community (Raymond et al., 2021; Saavedra, 2021). We observed different responses of salmon species to sea otter presence, with a positive relationship for juvenile Chum Salmon but a weak, variability relationship with Pink Salmon. In nearshore habitats sea otters can induce trophic cascades, which has led to clear indirect impacts of sea otters on fish communities. Sea otters are connected to increased genetic diversity, growth, and biomass of eelgrass beds (Foster et al., 2021; Raymond et al., 2021; Saavedra, 2021); therefore, indirect effects on fish communities are likely more apparent with fish species that reside longer than juvenile salmonids in these nearshore habitats. This research took advantage of a low to high sea otter density gradient, but we did not see the same gradient in the aboveground biomass of eelgrass meadows across our study sites as seen in other studies in the region (Raymond et al., 2021). This makes it difficult to observe and test indirect effects of sea otters on juvenile salmonids through changes in eelgrass biomass. Interestingly, sediment grain size, sea otters, and eelgrass biomass were correlated in a previous study corroborating the inclusion of sediment scores in the model for juvenile Pink Salmon and Chum Salmon despite their variable relationship with catch in this current study (Raymond et al., 2021). In our study, we found

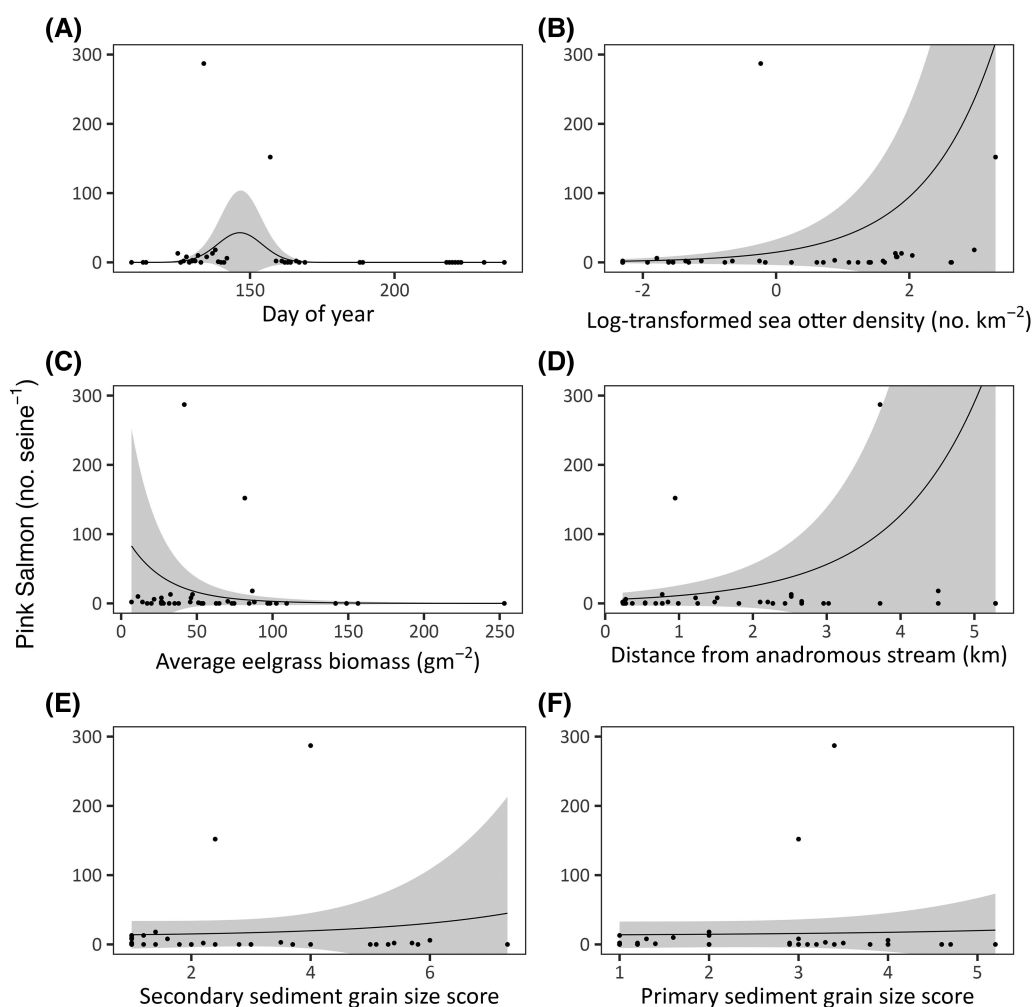


Figure 5. The relationship between juvenile Pink Salmon abundance from the contemporary studies and (A) day of year, (B) average sea otter density, (C) average eelgrass biomass, (D) distance from anadromous stream, (E) secondary sediment grain size, and (F) primary sediment grain size. The black line indicates the relationship based on the averaged model while holding the other explanatory variables at the median value, with gray 95% confidence bands and number of Pink Salmon per seine (points).

a moderate correlation with log-transformed sea otter density and sediment grain size scores likely contributing to the high uncertainty seen with these parameters in the averaged Pink Salmon model. Therefore, disentangling the myriad of forces or mechanisms that impact nearshore habitats, the indirect impact of sea otters, and the difference in response of Chum Salmon and Pink Salmon hinders our ability to suggest if one species over the other will be more impacted by increased sea otter density. Additionally, the indirect signal of sea otters may not be clear because of the migratory nature of juvenile salmonids, so if conditions are not adequate, that is, if the habitat does not provide enough refuge, they get eaten, and/or if prey are not available, they continue to migrate in search of prey.

The wide distribution of abundance observations of juvenile salmonids made it difficult to disentangle clear patterns in habitat preference and environmental drivers of juvenile salmonids in eelgrass. In the historical NOAA surveys, nearly 79% of the total catch of juvenile Pink Salmon occurred at five eelgrass sites. In our contemporary work, we see a similar patchy occurrence of juvenile salmonids. While certain environmental variables are important for predicting juvenile numbers,

only a few sites with extremely abundant catches appear to drive this pattern, leading us to interpret the models presented here with caution, in particular for juvenile Pink Salmon. Intuitively we would have expected to see a positive relationship between juvenile salmonid abundance and eelgrass biomass, if juvenile salmonids are prioritizing refuge from predation and solely relying on eelgrass for refuge (Semmens, 2008), and a negative relationship between juvenile salmonids and distance from anadromous stream. Instead, we see a weak but opposite relationship between eelgrass biomass and distance from anadromous streams from what we expected for juvenile Pink Salmon and no relationship with Chum Salmon. These weak patterns could be attributed to interannual variation in salmonid populations although for Pink Salmon, which has a 2-year life cycle, we mitigated by sampling only the odd-year population. However for Chum Salmon, evidence from northern Southeast Alaska correlated increased abundance with regional scale environmental variability, which we were unable to account for in this short time series (Kohan et al., 2019). The weak pattern with eelgrass biomass could be related to not sampling a large enough gradient in our explanatory

variables, and we could be missing the effect of extremely low or high eelgrass biomass on salmonids through lack of informative contrast. In our study, average dry weight of leaf biomass ranged from 7.4 to 240.2 g/m². Our maximum biomass is just below the median summertime dry weight of leaf biomass (245 g/m²) found in a meta-analysis of eelgrass across its temperate ranges excluding Alaska (northern Europe; western USA; eastern USA; and Canada, Mexico, and Japan) (Olesen & Sand-Jensen, 1994). This perhaps indicates that eelgrass meadows in southern Southeast Alaska may support greater leaf biomass than what we observed, with greater potential to influence juvenile salmon abundance.

Juvenile salmonids may not be tied to the anadromous streams listed, as the Anadromous Waters Catalog (ADFG, 2019) contains a small fraction of the total watersheds that salmon species use and/or juvenile salmonids may originate from hatcheries rather than streams (Southern Southeast Regional Aquaculture Association, 2023). Of note, however, is that Pink Salmon are not released by hatcheries near our study area in southern Southeast Alaska, and we observed patterns between anadromous streams only with juvenile Pink Salmon. The lack of association for Chum Salmon and anadromous streams may be influenced by hatchery releases.

Another factor driving our results could be catch efficiency. Beach seine sampling efficiency may be reduced with macrophytes present and can have large unpredictable variability in species catch, causing difficulty and uncertainty when identifying patterns in nearshore fish communities (Pierce et al., 1990; Rozas & Minello, 1997). While these are possible explanations for the weak relationships, with a few sites having much larger juvenile salmonid abundances than others, this indicates that surveys across hundreds of kilometers on juvenile salmonids in eelgrass meadows is too vast to disentangle the complex relationship between quickly migrating species (moving from streams to open ocean in 2 to 3 months) and their reliance on the nearshore as stop-over habitats.

In southern Southeast Alaska, eelgrass and understory kelps compose just under half of coastlines available for juvenile salmonids. We observed Pink Salmon not distinguishing between habitats, while Chum Salmon are more present in understory kelps. For juvenile Pink Salmon, this indicates that the presence alone of structured habitats, regardless of the type, may be beneficial during migration to the open ocean compared with Chum Salmon that may be more reliant on understory kelps. Despite the smaller percentage of eelgrass habitat available (8%) compared with understory kelps (37.8%), we still see periodically high abundance of juvenile salmonids within eelgrass, demonstrating that less prevalent structured habitats can serve as crucial habitat. We may not have seen these patterns if the nearshore habitats were impacted by high anthropogenic disturbance, declining eelgrass meadows, or diminished food web stability. Additionally, identifying suitable nearshore habitat for juvenile salmonids is more nuanced than the study presented here and would require more research on small- to large-scale variation within and among habitats across seascapes (Chalifour et al., 2019). Likely, the presence of these nearshore habitats and the complex and resilient ecosystem they support collectively supplies migratory habitat for juvenile salmonids.

Juvenile salmonids utilize nearshore submerged vegetation for reasons unrelated to the environmental drivers explored in this study, in particular predator avoidance and prey availability (Kennedy et al., 2018; Semmens, 2008; Sharpe et al., 2019). The morphological structure in the water column differs between the habitat types studied here, with most understory kelp beds in Southeast Alaska composed of large flat-lying *Saccharina* spp. and smaller bushy red and brown algae underneath the mats of bladed kelps, while eelgrass blades can extend up to 2 m in the water column. Since juvenile salmonids are generally surface-oriented, the potential refuge benefit of understory kelps could be reduced compared with canopy kelps and eelgrass meadows. However, other studies found increased numbers of juvenile salmonids with increasing macroalgae cover and near sea grass meadows compared with more open-water, rocky, and sandy habitats (Sharpe et al., 2019). This corroborates our findings of juvenile salmonid use of both macroalgae/understory and eelgrass meadows, as abundant groups of juvenile Chum Salmon and Pink Salmon were observed in both habitats. In addition, juvenile salmonids are extremely reliant on prey sources, and their out-migration timing is connected with prey availability (Orsi et al., 2000). Therefore, their use of nearshore habitats could be connected to the diverse invertebrate and vertebrate community that the submerged aquatic vegetation hosts. Certain sites having more productive sources of prey may explain some of the patchy distributions of juvenile salmonids at some sites over others. Perhaps juveniles convene among these structured habitats (eelgrass and kelps) due to the ability of the habitats to host high prey abundances similar to what is seen in eelgrass meadows in British Columbia (Kennedy et al., 2018). Future work may benefit from investigating diet composition and prey availability in addition to predator abundance rather than just the number of fish present across habitat types throughout their early marine phase.

The relationships among juvenile salmonids and environmental metrics described in this study likely differ across regions within Southeast Alaska and at broader spatial scales. Regional (freshwater input, fjords, wave exposure, salmonid productivity) and site-specific (habitat structure, prey availability) metrics may all be impacting juvenile salmonid use and presence in nearshore areas. Furthermore, other structured habitats like canopy kelp forests could provide similar refuge for salmonids, or host important prey species in the nearshore, indicating that all these structured habitats should be equally considered when identifying important coastal nurseries for juvenile salmonids.

Regardless of available habitat type or structure of that habitat, simply due to the geology of the southeastern Alaska archipelago, juvenile salmonids must navigate complex channels and coastlines before reaching the open ocean. These marine corridors likely influence distance, duration, and migratory paths for juvenile salmonids. As such, juvenile salmonids occur in patchy distributions, where they are nearly absent or present in extreme numbers. While emphasis on the nearshore as a critical habitat is warranted, perhaps more important is the availability of prey within the nearshore. Further studies could expand on juvenile salmonid habitat associations by including prey sampling and stable isotope and/or diet analysis to disentangle the role of prey availability versus predation avoidance

in the nearshore. This current work reinforces the generalized use of nearshore submerged vegetated habitats, both eelgrass and understory kelp beds, by juvenile salmonids during their transition and growth to the open ocean. Further, we highlight the need to consider various aspects of the early marine phase of juvenile salmonids, the role of apex predators, the differential use of nearshore habitats, the impacts of environmental variability, and the costs of coastal development on the productivity of salmonids.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Marine and Coastal Fisheries* online.

DATA AVAILABILITY

Data and analysis code are available through Knowledge Network for Biocomplexity (Domke et al., 2024) or by contacting the corresponding author directly.

ETHICS STATEMENT

We conducted fish sampling with permits from the Alaska Department of Fish and Game (CF-17-50 and CF-19-067) and with approval from the Institutional Animal Use and Care Committee at the University of Alaska Fairbanks (project 892147).

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CONFLICTS OF INTEREST

The authors declare no conflict of interest in this article.

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visualization, and wrote the original draft. Rebecca J. Cates collected data and reviewed and edited the manuscript. Wendel W. Raymond collected data and reviewed and edited the manuscript. Ginny L. Eckert acquired funding, administered and supervised the project, collected data, and reviewed and edited the manuscript.

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