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Spatiotemporal Variation and Size-Selective Predation on Hatchery- and Wild-Born Juvenile Chum Salmon at Marine Entry by Nearshore Fishes in Southeast Alaska

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Abstract

Juvenile Pacific salmon *Oncorhynchus* spp. experience high mortality at marine entry, yet our quantitative understanding of predation during this critical period is limited. We evaluated spatial, temporal, and size-based patterns of predation on hatchery- and wild-born juvenile Chum Salmon *O. keta* by two abundant predators in Southeast Alaska estuaries: the Pacific Staghorn Sculpin *Leptocottus armatus* and Dolly Varden *Salvelinus malma*. For the predators we sampled, Chum Salmon comprised 4.5% of the diet by weight for Pacific Staghorn Sculpin ($n = 937$) and 19.6% of the diet by weight for Dolly Varden ($n = 448$), with 88% of the individual Chum Salmon consumed originating from hatcheries. Variation in occurrence of Chum Salmon in diets was driven by date, site, and local Chum Salmon density. The quantity of Chum Salmon consumed by Pacific Staghorn Sculpin varied with predator length, Chum Salmon density, and the proportion of hatchery fish present; however, date was the only important predictor for Dolly Varden. The mean length of Chum Salmon in the diets of both predators was significantly shorter than that of concurrent hatchery releases or seine catches, suggesting size-selective predation on smaller individuals. This pattern indicates that hatchery strategies of releasing larger individuals may reduce the initial vulnerability of hatchery salmon to estuarine predators.

Pacific salmon *Oncorhynchus* spp. experience variability in year-class strength that can be linked to a range of environmental and ecological factors in their early life history. A critical period occurs as salmon enter marine waters and are subject to intensive predation (Parker 1968; Beamish and Mahnken 2001). During this time, a salmon cohort can experience up to 85% mortality, which often represents the single largest component of marine mortality in the salmon life cycle (Ricker 1976; Quinn 2005). The importance of early marine predation is widely acknowledged and has motivated previous studies examining the predators of juvenile salmon, including harbor seals (Yurk and Trites 2000), sea birds (Simenstad et al. 1979; Scheel and Hough 1997), and a variety of fishes (Mace 1983; Beamish et al. 1992;

Orsi et al. 2000). However, there is limited information on predation by nearshore fishes that may contribute substantially to the mortality of juvenile salmon during estuarine rearing (Healey 1982; Bax 1983).

Assessing the vulnerability of juvenile salmon to nearshore consumers first requires knowledge of the spatial and temporal overlap between predators and potential prey. From April to June, juvenile salmon are abundant in estuaries and adjacent habitats as they leave freshwater (Groot and Margolis 1991; Quinn 2005). During nearshore marine residency, juvenile salmon are small (25–200 mm FL; Quinn 2005), which makes them susceptible to consumers of many species and sizes (Parker 1971; Hargraves and Lebrasseur 1985; Sogard 1997; Furey et al.

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2014). Given their high energy content (Anthony et al. 2000) and potentially high densities during the period of marine entry (Weitkamp et al. 2014), juvenile salmon may serve as a particularly beneficial source of post-winter nutrition to nearshore consumers. Quantifying size-based relationships between nearshore consumers and their juvenile salmon prey is important because size-selective predation at the juvenile stage can influence the number of returning adults (Parker 1968; Ricker 1976; Beamish and Mahnken 2001; LaCroix et al. 2009).

Hatcheries in Alaska produce more than 1.5×10^9 salmon each year (Stopha 2016, 2017), which are released into the nearshore marine environment as juveniles and may increase local densities of both salmon and their predators beyond naturally occurring levels. In some instances, hatchery releases have been shown to attract more predators or to increase predation rates relative to areas of natural salmon production (Beamish et al. 1992; Brannon et al. 2004; Chenoweth et al. 2017). However, the net impact on salmon mortality is uncertain, as other studies have indicated that large releases of hatchery salmon could reduce overall predation on co-occurring wild-born salmon through predator buffering or swamping (Willette et al. 2001; Briscoe et al. 2005). The size structure, spatial distribution, and behavior of juvenile hatchery salmon differ substantially from those of their wild-born counterparts, which can result in differential predation on hatchery- and wild-born salmon (Hargreaves and Lebrasseur 1985; Wertheimer and Thrower 2007; Duffy and Beauchamp 2008). For example, hatchery fish are fed in captivity and thus are released at larger sizes than wild-born individuals at marine entry (Olla et al. 1998; Sturdevant et al. 2012). This is thought to confer a survival advantage because fish predators frequently consume smaller individuals due to limitations in gape width and ease of capture (Parker 1971; Healey 1982; Sogard 1997; Olla et al. 1998). Additionally, the larger hatchery fish may migrate offshore more rapidly, which could limit their duration of overlap with nearshore predators (Healey 1982; Orsi et al. 2004; Sturdevant et al. 2012).

An understanding of the responses of nearshore predators to hatchery releases and their contribution to juvenile salmon mortality requires quantitative information about spatial, temporal, and size-based patterns of predation on hatchery- and wild-born salmon. Here, we examined patterns of predation on juvenile salmon by two abundant nearshore consumers: Pacific Staghorn Sculpin *Leptocottus armatus* and Dolly Varden *Salvelinus malma*. Both species are commonly found in estuaries along the north Pacific Ocean and have been observed to prey upon juvenile salmon (Lagler and Wright 1962; Robert 1965; Armstrong 1970; Whitney et al. 2017, 2018). Previous studies suggest that the impacts of these consumers on juvenile salmon can be substantial but variable. Mace (1983) estimated that Pacific Staghorn Sculpin had the potential to consume 5% of

juvenile Chum Salmon *O. keta* and more than 42% of juvenile Coho Salmon *O. kisutch* out-migrating from the Big Qualicum River on Vancouver Island, British Columbia. In Southeast Alaska, Whitney et al. (2017) found that juvenile salmon constituted 9.1% of the Pacific Staghorn Sculpin diet by weight during spring and summer months. Dolly Varden are well-documented salmon egg consumers in freshwater spawning habitats (e.g., Denton et al. 2010; Armstrong and Bond 2013) and consume juvenile salmon in nearshore marine ecosystems (Robert 1965; Whitney et al. 2018). A study in Hanus Bay, Southeast Alaska, showed that 28% of the Dolly Varden diet by volume was composed of juvenile salmon and that 22% of the Dolly Varden sampled had consumed juvenile Pink Salmon *O. gorbuscha* or Chum Salmon (Armstrong 1965). However, Roos (1959) found that juvenile Sockeye Salmon *O. nerka* made up 9% of the diet by weight and only occurred in 4% of sampled Dolly Varden near Chignik, Alaska. This documented variability in the use of juvenile salmon prey by both Pacific Staghorn Sculpin and Dolly Varden suggests that anticipating their responses to changes in prey resources requires an understanding of how patterns in their diets vary with environmental and ecological factors.

The objectives of our study were to (1) quantify the contribution of juvenile Chum Salmon prey to the diets of Pacific Staghorn Sculpin and Dolly Varden in Southeast Alaska estuaries, including the sizes and origin of the salmon prey consumed; (2) characterize spatial and temporal patterns in predation on hatchery- and wild-born Chum Salmon; and (3) evaluate the relative importance of time, location, predator size, and prey characteristics in explaining variation in predation on juvenile salmon. We hypothesized that the quantity and sizes of salmon consumed would increase with predator size and that predators would be size-selective for smaller individuals, as is common among piscivores (Juanes 1994). Additionally, we expected that the contribution of juvenile salmon to predator diets would increase with local salmon density. We focused on predation of Chum Salmon *O. keta*, the primary species produced by hatcheries in Southeast Alaska. More than 500 million juvenile Chum Salmon are released from Southeast Alaska hatcheries annually, and in 2017 hatchery production constituted 83% of Chum Salmon harvests in the region (Stopha 2017). A better understanding of predators' ecological responses to hatchery releases is important for hatchery operators who want to optimize enhancement strategies and for resource managers who must work to conserve co-occurring wild-born stocks.

STUDY AREA

The study was conducted in 2016 and 2017 at four estuaries (i.e., intertidal sites adjacent to river deltas) along Lynn Canal near Juneau, Alaska: Sheep Creek estuary

(58.26°N, -134.33°W), Eagle River estuary (58.53°N, -134.85°W), Mendenhall River estuary (58.33°N, -134.61°W), and Cowee Creek estuary (58.68°N, -134.95°W; Figure 1). The Douglas Island Pink and Chum, Inc. (DIPAC), Macaulay Salmon Hatchery releases around 130 million juvenile salmon each year, with over 98% consisting of Chum Salmon (Stopha 2016, 2017). Hatchery salmon were released from net-pens located at multiple sites near Juneau (Figure 1) and on multiple dates between late April and early June, with most releases occurring in May 2016 and June 2017 (A. Zaleski, DIPAC, personal communication; Figure 2); this coincides with the period of out-migration for wild-born salmon (Sturdevant et al. 2012). Our study sites were positioned along a gradient of distances from the hatchery Chum Salmon release sites. The shortest water-connected distances from each study site to the nearest hatchery release site are as follows: 0.2 km for Sheep Creek estuary; 6.5 km for Eagle River estuary; 10.5 km for Mendenhall River estuary; and 15.5 km for Cowee Creek estuary (Figure 1).

METHODS

Sample collection.—Our intent was to initiate sampling prior to releases of all hatchery fish; however, in 2016 the hatchery released some net-pens early due to heat-related stress in the fish. Because this was an unanticipated event, we began sampling as soon as possible thereafter. In 2016, sample collection began in May after the unexpected emergency releases but before the vast majority of fish were released (Figure 2). In 2017, sampling began in April, prior to all hatchery releases (Figure 2). All sites were sampled twice per month through July (Appendix Table A.1). Juvenile salmon and focal predators were primarily collected with beach seines. Beach seining was conducted within 2 h of negative low tides during morning daylight hours following the methods of Whitney et al. (2017). Habitat was consistent across sites, made up of shallow sloping sand or mud with occasional patches of exposed cobble (Whitney et al. 2017). We used three seine nets of varying sizes, with the goal of capturing as wide a range of fish species and sizes as feasible. On each sampling day, we conducted four to eight sets that were each 6–8 min in duration, alternating between two 15.2-m-long \times 2.4-m-deep seine nets with different mesh sizes (0.95- and 1.27-cm stretched knotless mesh). Small, narrow-bodied fish, including some juvenile salmon, were able to escape through the mesh; therefore, we conducted one additional set with a smaller-mesh seine (10-m-long \times 2.4-m-wide net with 0.64-cm stretched knotless mesh) to increase our sample size of juvenile salmon for determining length distributions and proportions of hatchery- and wild-born salmon. Given the capability for large Dolly Varden to avoid beach seines, we opportunistically used hook-and-line sampling with 10.631-g (0.375-oz) silver

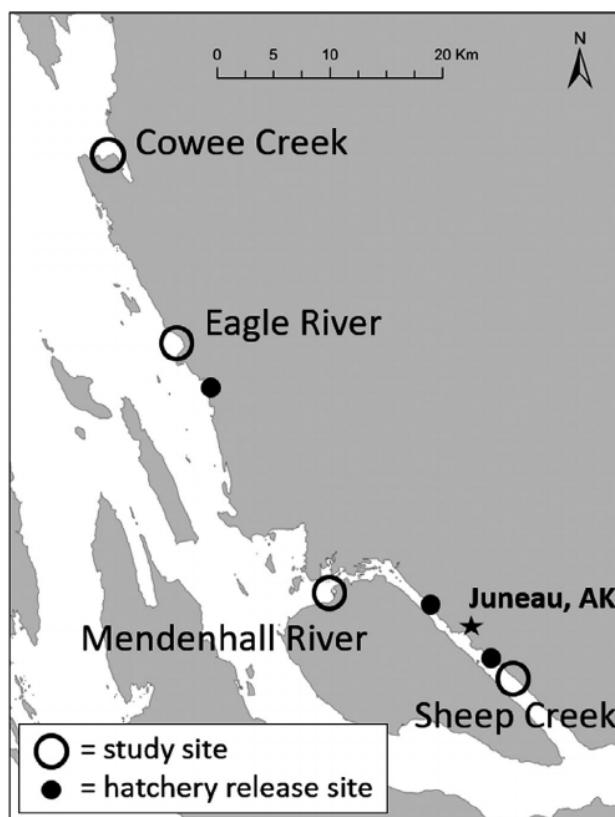


FIGURE 1. Map of the study area in Southeast Alaska, indicating study sites (filled circles) and hatchery release sites (open circles).

spoons (Kastmaster) at the study sites between seine sampling days to supplement the catch of larger-bodied Dolly Varden (Table A.1).

Immediately after each beach seine set, large and small fish were sorted into separate buckets for holding prior to processing (i.e., to avoid predation). We did not find any evidence of net feeding by predators (i.e., some digestion of prey had occurred). Predators and Chum Salmon from each set were identified, counted, and measured. Up to 30 Pacific Staghorn Sculpin and 30 Dolly Varden that were large enough for piscivory were randomly subsampled (e.g., Scharf et al. 2000) from multiple seine sets during each sampling event (day \times site), euthanized, and retained for stomach content analysis. The minimum lengths for retained predators were determined from prior research, which indicated that Pacific Staghorn Sculpin and Dolly Varden do not begin incorporating fish into their diets until they reach approximately 150 mm TL and 170 mm FL, respectively (E. J. Whitney and A. H. Beaudreau, unpublished data). The sample sizes retained for stomach content analysis were adequate to characterize diversity in diets based on previous research on these species in Juneau-area estuaries (Whitney et al. 2017, 2018). Up to

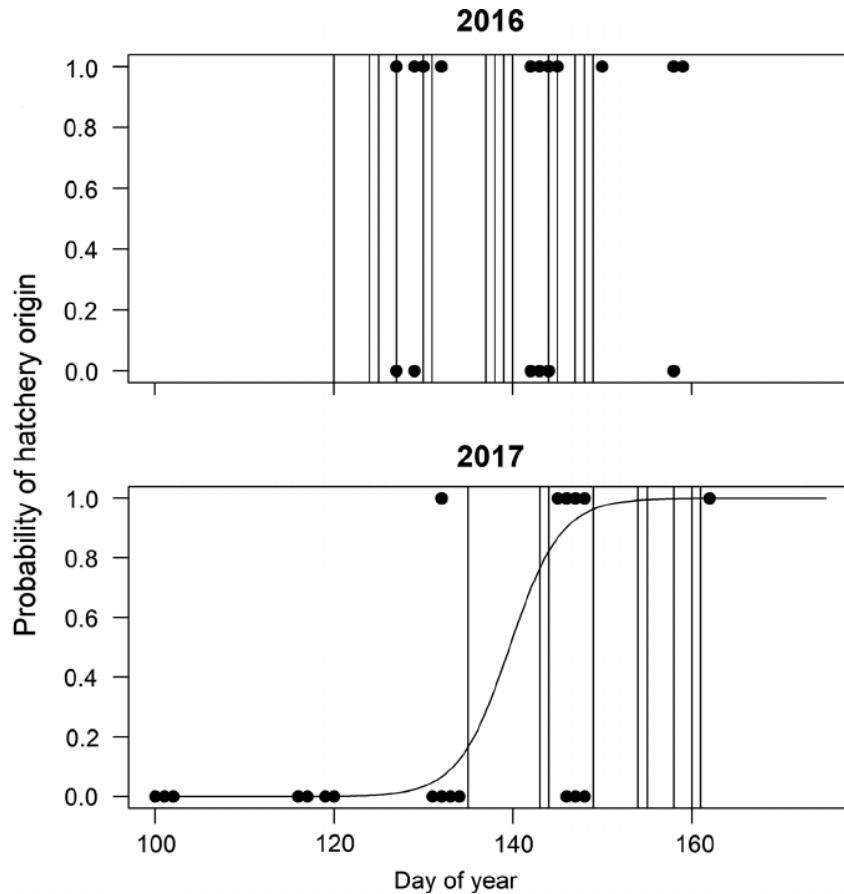


FIGURE 2. Occurrence of hatchery Chum Salmon caught in seines and observed in predator diets over time. Vertical lines indicate days when hatchery releases occurred. Day of year was not significant in 2016 ($n=195$), when the proportion of hatchery Chum Salmon in diets and seine catches averaged over 85% during the entire sampling season. For 2017, the curve is a fitted logistic regression estimating the probability of hatchery Chum Salmon occurrence over time ($n=281$).

30 juvenile Chum Salmon captured in beach seines were retained from multiple seine sets during each sampling event to determine their origin (i.e., hatchery or wild born). Additionally, 30 juvenile Chum Salmon provided by DIPAC were randomly subsampled from each net-pen and measured to assess size frequency at release. This research was reviewed and approved by the Institutional Animal Care and Use Committee at the University of Alaska Fairbanks (Protocol 880562).

Laboratory analysis.—Retained predators were measured and weighed, and their stomach contents were extracted and preserved in 80% ethanol (Pacific Staghorn Sculpin: 92–329 mm TL, $n=937$; Dolly Varden: 121–516 mm FL, $n=448$). Once all contents were removed from a stomach, they were weighed together to obtain a total blotted wet weight. Next, individual prey items were identified to the lowest possible taxonomic level by using fish and invertebrate identification keys (i.e., McCafferty 1983; Kozloff and Price 1987; O'Clair

and O'Clair 1998; Harvey et al. 2000; Mecklenburg et al. 2002). Prey items were counted, measured, weighed, and assigned a qualitative condition code based on the extent of digestion observed (Beaudreau and Essington 2009; Alaska Fisheries Science Center 2015).

We used the presence or absence of otolith thermal marks to distinguish between hatchery and wild salmon (Volk et al. 1999) that were captured in beach seines or found in predator stomachs. The Macaulay Salmon Hatchery marks 100% of the released Chum Salmon by exposing incubating eggs to fluctuations in water temperature, thus creating recognizable banding on the otoliths (Stopka 2017). Marks were evaluated using a compound microscope with the assistance and expertise of the Alaska Department of Fish and Game (ADFG) Mark, Tag, and Age Laboratory, Juneau. Sagittal otoliths of retained salmon were cleaned before being mounted to a glass slide with clear resin and then ground on abrasive discs to expose the

primordia and any thermal marks that were diagnostic of hatchery origin (Courtney et al. 2000). Fish without thermal marks were interpreted as wild born. Although reader error is possible, previous research at the ADFG Mark, Tag, and Age Laboratory suggested that misclassification error of Chum Salmon otolith origin (i.e., classifying a hatchery fish as wild or vice versa) is very low, and agreement among readers typically exceeded 90% (Blick and Hagen 2002). Among Chum Salmon that were identified in predator diets, origin was determined for all individuals with recoverable otoliths ($n = 158$); the remaining 32 Chum Salmon found in stomachs had otoliths that were degraded due to digestion or that were damaged while being prepared for reading. In beach seine catches, origin was determined for retained subsamples from May and early June 2016 and from May 2017 ($n = 282$; Table 1), the time periods when the largest quantities of Chum Salmon were found in predator stomachs (Figure 3). In April 2017, no hatchery releases had occurred and all Chum Salmon in predator stomachs during the month were identified as wild born, so beach seine catches were assumed to be of wild origin.

Diet composition of predators.—To assess the contribution of Chum Salmon to predator diets, we used two standard indices: proportion by weight (W_i) and frequency of occurrence (O_i ; Chipp and Garvey 2007). The W_i was calculated by dividing the weight of each prey taxon by the weight of all prey; W_i provides information about the energetic contribution of prey groups to a predator's diet. The O_i was calculated as the number of predator stomachs containing a particular prey taxon divided by the total number of sampled stomachs; O_i indicates the proportion of predators that

incorporated a specified prey group into their diet. Nonbiological material (e.g., gravel), gut parasites, and vegetation found in stomachs were excluded from analyses.

Size- and origin-based patterns of predation.—We quantified prey size spectra to assess size-based relationships (Scharf et al. 2000) between the focal predators and salmon prey. These diagrams relate predator body length to prey body length and indicate the range of prey lengths consumed by individuals across the sampled size range (Pearre 1986). Quantile regression (R package "quantreg"; R Core Team 2018) was used to quantify the upper (95th quantile) and lower (5th quantile) boundaries of prey length consumed as a function of predator length (Scharf et al. 1998). Box plots were used to compare length frequency distributions of Chum Salmon released from hatchery net-pens, caught in beach seines, and found in predator stomachs over each sampling year. As only a subsample of Chum Salmon was analyzed for origin, these plots do not distinguish hatchery- and wild-born fish. When origin was known, one-way ANOVA and Tukey's honestly significant difference (HSD) post hoc tests were used to evaluate differences in mean length among Chum Salmon released from hatchery net-pens, those caught in beach seines, and those observed in stomachs. Size distributions were also compared among Chum Salmon groups by using Kolmogorov-Smirnov (K-S) tests. These comparisons allowed us to infer potential size selectivity by comparing the lengths of Chum Salmon consumed to the lengths of Chum Salmon present at the sites.

Spatial and temporal patterns of predation.—To visualize spatial and temporal patterns of predation on salmon,

TABLE 1. Sample sizes and mean (\pm SD) SLs of juvenile Chum Salmon subsampled from beach seine catches to determine the proportion of hatchery-origin fish (ER = Eagle River; CC = Cowee Creek; MR = Mendenhall River; SC = Sheep Creek). A subsample of 20 individuals from each sampling event was assessed for origin; however, in the event that fewer than 20 individuals were caught, all were assessed for origin.

Year	Variable	Early May sampling				Late May sampling				Early June sampling	
		ER	CC	MR	SC	ER	CC	MR	SC	MR	
2016	Proportion marked	0	N/A	1	1	0.85	0.9	0.85	1	0.95	
	Count	3	0	20	20	20	20	20	20	20	
	Mean SL (mm), hatchery-born fish	N/A	N/A	55.1 (5.0)	61.7 (3.3)	54.6 (10.6)	69.2 (7.8)	55.8 (5.2)	56.4 (7.5)	62.7 (9.1)	
	Mean SL (mm), wild-born fish	57.4 (6.3)	N/A	N/A	N/A	49.0 (13.2)	57.0 (5.7)	51.2 (2.9)	N/A	61.0 (0.0)	
2017	Proportion marked	0	0	0	0.15	1	0.8	0.95	0.85	N/A	
	Count	20	1	20	20	18	20	20	20	N/A	
	Mean SL (mm), hatchery-born fish	N/A	N/A	N/A	50.0 (2.0)	64.2 (8.0)	63.7 (6.5)	65.4 (4.9)	54.1 (3.8)	N/A	
	Mean SL (mm), wild-born fish	38.1 (4.0)	46 (0.0)	38.0 (5.0)	35.6 (2.6)	N/A	50.0 (7.7)	44.0 (0.0)	46.3 (4.7)	N/A	

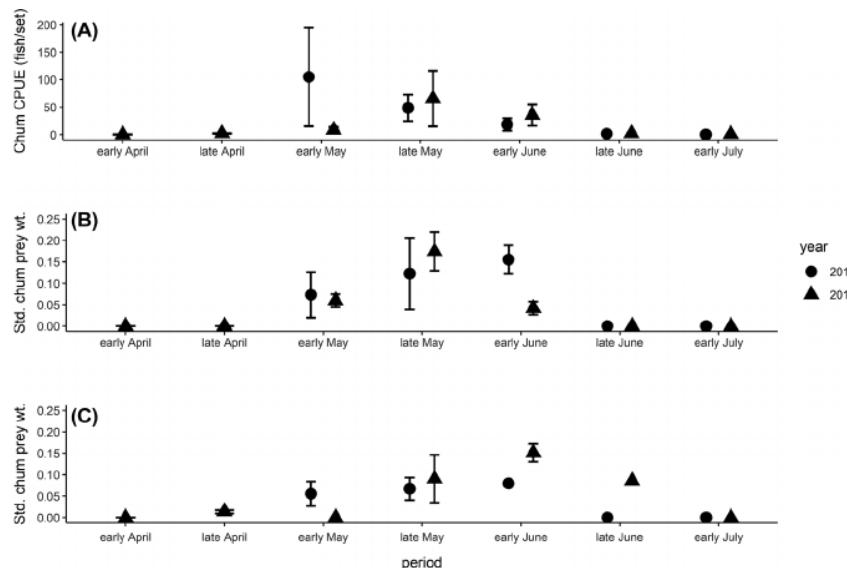


FIGURE 3. (A) Average Chum Salmon beach seine CPUE (number of fish per set), (B) average standardized mass of Chum Salmon in Pacific Staghorn Sculpin stomachs, and (C) average standardized mass of Chum Salmon in Dolly Varden stomachs across sites and sampling periods. Whiskers show ± 1 SE. Standardized mass of Chum Salmon was calculated as $[(\text{Chum Salmon prey weight})/(\text{predator weight} - \text{stomach contents})]^{0.75}$. Sampling was not conducted in April 2016.

we plotted the mean standardized mass of Chum Salmon consumed per predator and the mean (\pm SE) Chum Salmon CPUE from beach seines across sites for each sampling period. The CPUE was calculated as the number of juvenile Chum Salmon caught per set, averaged for each seine sampling day; we calculated CPUE using only data from the 15.2-m seines because they provided a more robust quantitative measure of catch rates compared to the smaller seine, which was towed at more variable speeds due to its greater tendency to retain algae. To characterize the temporal shift in potential availability of hatchery salmon to predators, we used logistic regression to determine the probability that Chum Salmon captured in beach seines or found in predator stomachs were of hatchery origin as a function of sampling date, with the binary response variable coded as 1 if the fish was of hatchery origin and as 0 if it was not (i.e., wild born). Due to low sample sizes, we were unable to fit separate regressions for Chum Salmon captured by beach seines and Chum Salmon found in predator stomachs. Therefore, origin data for Chum Salmon from seine catches and predator stomachs were analyzed together. Analyses were performed separately for each year because (1) sampling was only conducted after hatchery releases had already begun in 2016 and (2) the timing of subsequent releases differed between years.

Factors explaining variation in predation on Chum Salmon.—We used a multiple regression approach to identify the extent to which predation on juvenile Chum

Salmon could be explained by the date, location of sampling, predator size, and the relative densities and origins of juvenile salmon. As most sampled predators did not incorporate salmon into their diets, the response variable—Chum Salmon in diets—was zero-inflated. To address this, we first used the full data set to model the occurrence of salmon consumed (i.e., binary response of presence or absence in a predator stomach) by using a generalized linear model with a logit link function. Using data for only those predators that had consumed Chum Salmon, we then modeled the quantity of Chum Salmon in predator stomachs by using a generalized linear model with a Gaussian distribution. This is akin to a delta (or hurdle) modeling framework (e.g., Maunder and Punt 2004) and follows the approach used by Beaudreau and Essington (2007) to evaluate variation in the probability of prey occurrence and prey mass in predator diets. Regression analyses were performed separately for Pacific Staghorn Sculpin and Dolly Varden. Predators with empty stomachs (~1% of individuals from each species) were excluded from analyses.

First, we estimated the probability of juvenile Chum Salmon occurrence in predator stomachs by using multiple logistic regression, with the binary response variable being the presence or absence of Chum Salmon in a predator's stomach. The full model included the following predictors: year, day of year, site, predator length, and juvenile Chum Salmon CPUE. Day of year is the month and day on which the predator stomach sample was collected; this predictor was included to evaluate seasonal variation in

prey occurrence. Site, rather than distance from the nearest hatchery net-pen, was selected as a predictor because Chum Salmon from multiple hatchery release sites are known to mix at individual study sites (Zaleski, personal communication). Additionally, there were likely differences among sites that affected the feeding environment for predators—differences that were unrelated to local hatchery production, such as circulation or physical features of the river delta. Therefore, inclusion of site as a potential predictor variable in the models also accounted for spatial variation resulting from environmental variables that were not directly measured.

We then used multiple linear regression to model the quantity of salmon consumed when present. The response variable was the standardized mass of Chum Salmon, calculated as $[(\text{Chum Salmon prey weight})/(\text{predator weight} - \text{stomach contents})]^{0.75}$, where 0.75 is the assumed allometric slope of consumption for teleosts (Essington et al. 2001)—to control for the effects of predator size on consumption rate (i.e., consumption rates increase with body size). The full model included the same potential predictors as the logistic regression model plus one additional parameter for Pacific Staghorn Sculpin: the proportion of hatchery-born Chum Salmon present during a given seine sampling event. The proportion of hatchery salmon was not included as a factor in Dolly Varden models because relative densities of hatchery salmon were unavailable for the days when Dolly Varden were sampled via hook and line. Predator length was included to determine whether quantity consumed was higher or lower than could be explained by expected increases in consumption due to size alone. Diagnostic probability plots generated from the full model showed nonlinearity, so a square-root transformation of the response was selected for Dolly Varden and a log transformation was selected for Pacific Staghorn Sculpin by using the Box–Cox procedure (Weisberg 1985). All analyses were performed using R software (R Core Team 2018).

We used Akaike's information criterion (AIC) to identify the best explanatory model or set of models. For linear regression models, we calculated AIC_c (Burnham and Anderson 2002), which is bias-corrected for small sample size (function “AICc” in the “MuMIn” package; R Core Team 2018). The AIC_c assumes normally distributed errors, so logistic regression models were compared by using the uncorrected AIC (function “AIC” in the “stats” package; R Core Team 2018). Following convention, models with AIC (or AIC_c) values within 2 units of each other ($\Delta\text{AIC} \leq 2$) were considered to perform equivalently (Burnham and Anderson 2002). To identify predictors with the highest relative importance in explaining variation in occurrence or quantity of salmon in diets, we calculated Akaike parameter weights ($w_{+}[j]$), which scale from 0 to 1 and are interpreted as the weight of evidence in support of a given parameter's inclusion in the best model

(Burnham and Anderson 2002). The Akaike parameter weight of parameter j is calculated as the sum of model weights (relative likelihoods) across all models that included parameter j (Burnham and Anderson 2002).

RESULTS

Contribution of Chum Salmon Prey to Predator Diets

Across sites and years, juvenile salmon made up 6.5% of Pacific Staghorn Sculpin diets by weight; specifically, 4.5% of the diet consisted of Chum Salmon, 2.0% consisted of Coho Salmon, and less than 0.1% was not identifiable to the species level. Chum Salmon occurred in 2.8% of the Pacific Staghorn Sculpin stomachs sampled; each Pacific Staghorn Sculpin containing Chum Salmon had consumed two individual Chum Salmon on average. Of the 54 Chum Salmon identified in Pacific Staghorn Sculpin stomachs across sampling periods, otoliths were recovered and evaluated for thermal marks in 47 individuals; 87.2% were found to be of hatchery origin. By weight, the remainder of the Pacific Staghorn Sculpin diet was composed of other teleosts (52.3%), invertebrates (38.1%), and eggs or unidentifiable tissue (3.1%; Table A.2). The teleost contribution was dominated by Pacific Sand Lance (14.5%) and Pacific Herring (13.2%). Approximately 9.3% of fish prey were not identifiable to a taxonomic level below Teleostei. The invertebrate category was primarily composed of isopods (13.1%), annelid worms (8.3%), crabs (Pleocyemata; 6.5%), amphipods (3.0%), and unidentified crustaceans (3.7%). All other individual invertebrate prey groups made up 2% or less of the diet by weight.

For Dolly Varden, juvenile salmon made up 34.9% of the diet by weight; specifically, 19.6% of the diet consisted of Chum Salmon, 15.0% consisted of Coho Salmon, and 0.3% consisted of unidentifiable salmon. Chum Salmon occurred in 10.0% of Dolly Varden stomachs, with an average of 3.4 individual Chum Salmon per predator with Chum Salmon prey present. Of the 136 Chum Salmon identified in Dolly Varden stomachs, 111 were evaluated for thermal marks and 91.9% were found to be of hatchery origin. The remainder of the diet consisted of 39.5% teleost prey and 22.0% invertebrate prey by weight (Table A.2). Prey fish were predominantly Pacific Herring (22.3%) and Pacific Sand Lance (8.0%). Other relatively important fish prey groups included Stichaeidae (pricklebacks; 4.2%), Agonidae (poachers; 1.8%), and unknown teleosts (1.8%). The most prevalent invertebrate prey groups were amphipods (12.3%) and cumaceans (4.1%), which occurred frequently in Dolly Varden diets (present in 63.6% and 57.6% of stomachs, respectively) and composed a high percentage of the diet by number (Table A.2). Although many other invertebrate prey groups were consumed, including terrestrial insects, none made up more than 2% of the total diet by weight.

Size- and Origin-Based Patterns of Predation

The prey size spectra for Pacific Staghorn Sculpin and Dolly Varden were wedge-shaped, illustrating that as predator length increased both longer fish prey and a wider size range of fish prey were consumed (Figure 4). For Pacific Staghorn Sculpin, the estimated slopes of upper and lower bounds from the quantile regression were significant (95th quantile: $\beta = 0.546$, $P < 0.001$; 5th quantile: $\beta = 0.047$, $P < 0.001$); however, the relatively flat slope of the lower bound indicated that the minimum size of fish prey consumed did not change substantially over the sampled size-classes. Focusing on salmon prey, Pacific Staghorn Sculpin across the sampled size range incorporated Chum Salmon into their diets and the lengths consumed were largely consistent across predator lengths, with an average (\pm SD) size of 51.9 ± 6.9 mm SL. For Dolly Varden, the estimated slopes of upper and lower bounds from the quantile regression were significant (95th quantile: $\beta = 0.209$, $P < 0.001$; 5th quantile: $\beta = 0.024$, $P < 0.001$). When only salmon prey were considered, Dolly Varden consumed a wider range of Chum Salmon lengths compared to Pacific Staghorn Sculpin (Figure 4). Dolly Varden across the sampled size range consumed Chum Salmon, and the average (\pm SD) length of Chum Salmon prey was 48.5 ± 12.1 mm SL.

For Chum Salmon of known origin (i.e., those sampled in early May to early June 2016 and in early April to late May 2017), length varied significantly by origin and sampling group (ANOVA: $F = 187.2$, $df = 4$, $P < 0.001$; Figure 5). Chum Salmon from hatchery net-pens at release (60.7 ± 9.5 mm SL) and hatchery Chum Salmon captured in beach seines (60.1 ± 8.3 mm SL) did not differ significantly in mean length (Tukey's HSD test: $P = 0.931$) or length distributions (K-S test: $D = 0.092$, $P = 0.126$). Hatchery Chum Salmon in beach seine catches were significantly longer than measurable hatchery Chum Salmon found in predators' stomachs (50.7 ± 10.1 mm SL; Tukey's HSD test: $P < 0.001$), and their length distributions differed significantly (K-S test: $D = 0.418$, $P < 0.001$). Hatchery Chum Salmon in beach seine catches were significantly longer than wild-born Chum Salmon in beach seine catches (39.9 ± 7.8 mm SL; Tukey's HSD test: $P < 0.001$), and their length distributions differed significantly (K-S test: $D = 0.828$, $P < 0.001$). The mean lengths of wild-born Chum Salmon in beach seine catches and predator stomachs (38.7 ± 9.4 mm SL) did not differ (Tukey's HSD test: $P = 0.994$), but their length distributions differed significantly (K-S test: $D = 0.407$, $P = 0.029$). Across all sampling periods, Chum Salmon of all origins (including unknown) found in Pacific Staghorn Sculpin stomachs (51.9 ± 6.9 mm SL) and Dolly Varden stomachs (48.5 ± 12.1 mm SL) were shorter on average than Chum Salmon released from the hatchery (60.7 ± 9.5 mm SL) or captured in beach seines (57.3 ± 10.6 mm SL). Box plots showing the length frequency distributions of

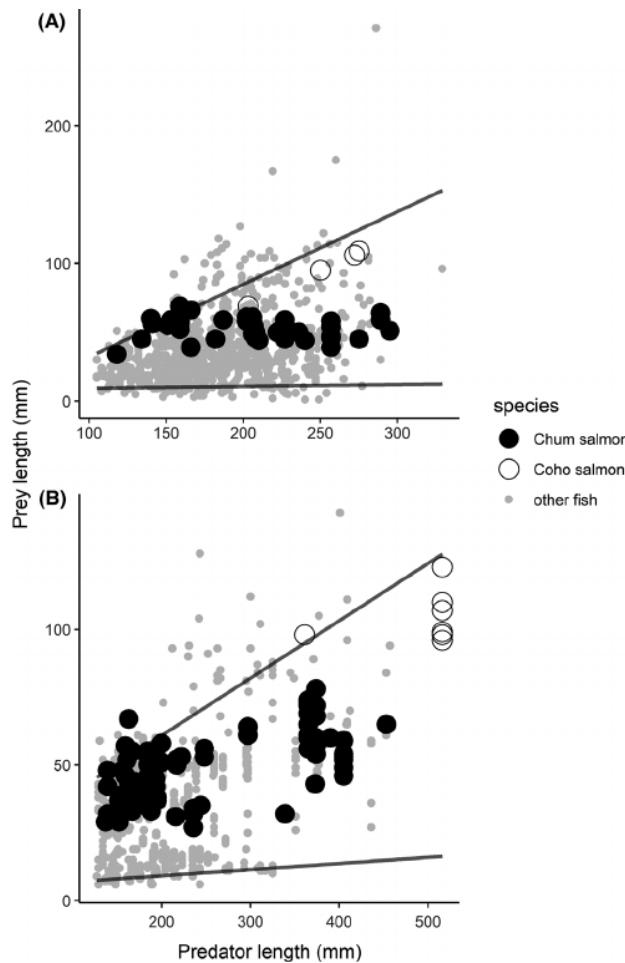


FIGURE 4. Prey size spectra for (A) Pacific Staghorn Sculpin and (B) Dolly Varden. Axis scales are different for each species. Lines indicate the upper (95th quantile) and lower (5th quantile) bounds of prey length consumed across predator lengths.

Chum Salmon released from hatchery net-pens, caught in beach seines, and found in predator stomach contents at each sampling period (Figures 6, 7) showed similar patterns to the size distribution data aggregated across sampling periods. In general, predators consumed smaller Chum Salmon individuals compared to those in beach seine catches and hatchery net-pens.

Spatial and Temporal Patterns of Predation

Qualitatively, temporal trends in the mean mass of Chum Salmon consumed mirrored trends in beach seine Chum Salmon CPUE, with a peak in late May, and were similar across sites (Figure 3). The contribution of Chum Salmon by weight to predator diets varied across sites; the W_i ranged from 0.0% to 46.7% (average = 4.8%) for Cowee Creek, from 0.0% to 2.5% (average = 0.2%) for the Eagle River,

from 0.0% to 30.7% (average = 8.5%) for the Mendenhall River, and from 0.0% to 95.2% (average = 13.8%) for Sheep Creek, depending on the sampling period. In 2016, all sampling was conducted after hatchery releases and day of year was not a significant predictor of origin based on logistic regression ($z = -0.049$, $df = 1$, $P = 0.961$), as the probability of being a hatchery fish was estimated to be uniformly high (~85%) from early May to early June. In 2017, sampling was conducted before and after hatchery Chum Salmon releases, which occurred in May, and day of year was a significant predictor of the probability that a Chum Salmon was of hatchery origin ($z = 8.247$, $df = 1$, $P < 0.001$; $\beta = 0.349$). The probability that Chum Salmon in seine catches and stomachs were hatchery born increased dramatically after hatchery releases in 2017 (Figure 2). At the Mendenhall River and Sheep Creek estuaries, the two sites with the highest numbers of salmon in predator stomachs, the proportions of hatchery Chum Salmon in diets after hatchery release (86–95%) were similar to the proportions of hatchery Chum Salmon found concurrently in beach seine catches (85–100%).

Factors Explaining Variation in Predation on Chum Salmon

For Pacific Staghorn Sculpin, the top logistic regression model (lowest AIC) predicting the occurrence of

Chum Salmon included the parameters site, day of year, Chum Salmon CPUE, and predator length; however, three other candidate models received equivalent support (Table 2). The best linear regression model for the quantity of salmon prey included the predictors predator length and proportion of hatchery fish present at the site (Table 3). Two other models received equivalent support based on AIC and included the predictors Chum Salmon CPUE, predator length, and proportion of hatchery fish. Parameter weights $w_{+}(j)$ calculated from all fitted models indicated that site, Chum Salmon CPUE, and day of year were the most important factors ($w_{+}[j] > 0.8$) explaining the occurrence of Chum Salmon in Pacific Staghorn Sculpin stomachs, while predator length was moderately important ($w_{+}[j] = 0.546$) and year was relatively unimportant ($w_{+}[j] = 0.349$; Table 4). The proportion of hatchery Chum Salmon and predator length were relatively important ($w_{+}[j] > 0.7$); Chum Salmon CPUE was moderately important ($w_{+}[j] = 0.548$); and day of year, year, and site were relatively unimportant ($w_{+}[j] < 0.2$) for explaining variation in the quantity of Chum Salmon in the diets (Table 4). Based on the signs of the estimated regression coefficients, the frequency of Chum Salmon occurrence in Pacific Staghorn Sculpin stomachs was higher at the Mendenhall River and Cowee Creek sites than at the Eagle River and Sheep Creek sites; the occurrence of

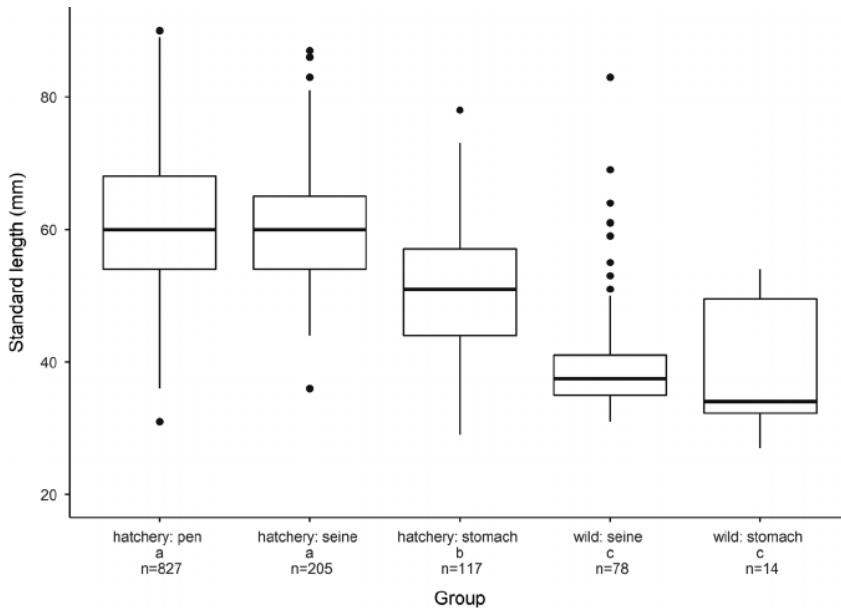


FIGURE 5. Length distributions of hatchery Chum Salmon from net-pens and hatchery- and wild-born Chum Salmon observed in predator stomachs and beach seine catches. Different letters indicate significant differences in mean length between groups, as determined by Tukey's honestly significant difference tests. The line within each box is the median and the bottom and top edges of the box are the 1st quartile (25th percentile) and 3rd quartile (75th percentile), respectively. The lower whisker shows the first quartile minus the interquartile range multiplied by 1.5, and the points are outliers.

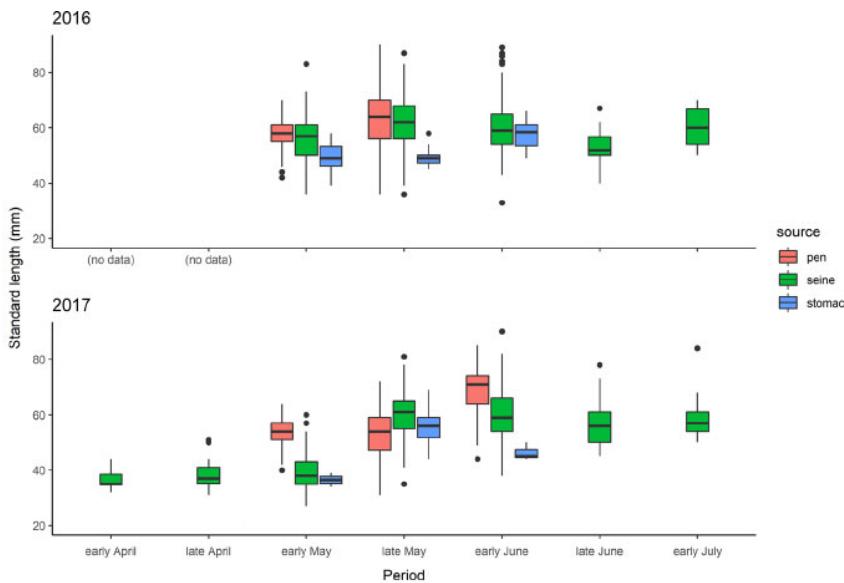


FIGURE 6. Length distributions of Chum Salmon released from hatchery net-pens, captured in beach seines, and observed in Pacific Staghorn Sculpin stomachs for each sampling period. Chum Salmon from seine catches and predator stomachs included both hatchery- and wild-born individuals, whereas net-pen fish were exclusively hatchery origin. The line within each box is the median and the bottom and top edges of the box are the 1st quartile (25th percentile) and 3rd quartile (75th percentile), respectively. The lower whisker shows the first quartile minus the interquartile range multiplied by 1.5, the upper whisker shows the third quartile plus the interquartile range multiplied by 1.5, and the points are outliers.

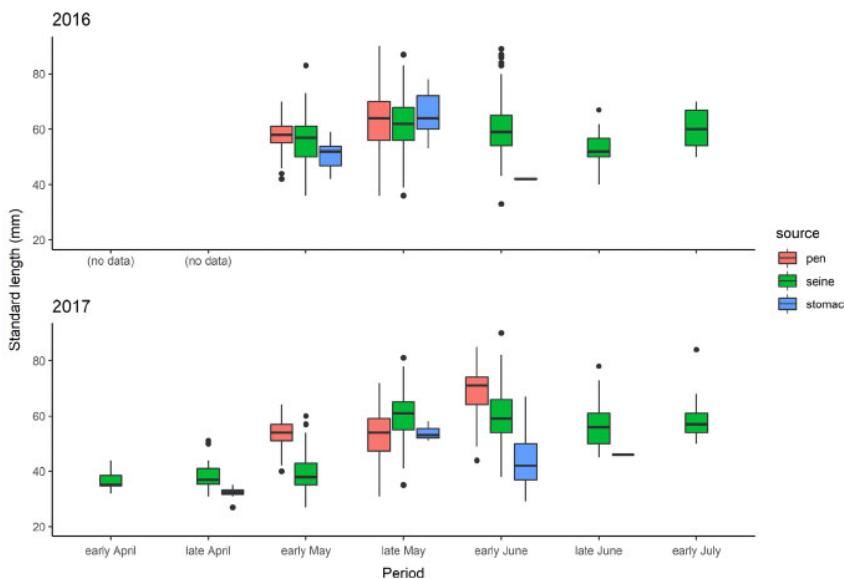


FIGURE 7. Length distributions of Chum Salmon released from hatchery net-pens, captured in beach seines, and observed in Dolly Varden stomachs for each sampling period. Chum Salmon from seine catches and predator stomachs included both hatchery- and wild-born individuals, whereas net-pen fish were exclusively hatchery origin. The line within each box is the median and the bottom and top edges of the box are the 1st quartile (25th percentile) and 3rd quartile (75th percentile), respectively. The lower whisker shows the first quartile minus the interquartile range multiplied by 1.5, the upper whisker shows the third quartile plus the interquartile range multiplied by 1.5, and the points are outliers.

Chum Salmon also decreased with sampling date and increased with salmon CPUE (Table A.3). The estimated quantity of Chum Salmon consumed decreased with predator length and increased with the proportion of hatchery Chum Salmon present and Chum Salmon CPUE (Table A.4).

TABLE 2. Model summaries for logistic regression of Chum Salmon occurrence (presence/absence) in Pacific Staghorn Sculpin stomachs ($n = 928$) and Dolly Varden stomachs ($n = 442$). In total, 32 regression models for Pacific Staghorn Sculpin and 32 models for Dolly Varden were evaluated that represented all combinations of predictors for each species. Predictors included site (factor), day of year, Chum Salmon CPUE (Chum CPUE), year (factor), and predator length (K = total number of parameters estimated; AIC = Akaike's information criterion; Δ AIC = difference in AIC between the given model and the best-performing model [lowest AIC]; w_i = model Akaike weight).

Model number	Model parameters	K	AIC	Δ AIC	w_i	Evidence ratio
Pacific Staghorn Sculpin						
1	Site + day of year + Chum CPUE + predator length	8	190.3	0.0	0.293	1
2	Site + day of year + Chum CPUE	7	191.1	0.8	0.196	1
3	Site + year + day of year + Chum CPUE + predator length	9	191.7	1.4	0.145	2
4	Site + year + day of year + Chum CPUE	8	192.1	1.8	0.119	2
5	Day of year + Chum CPUE	4	193.6	3.3	0.056	5
6	Day of year + Chum CPUE + predator length	5	194.2	3.9	0.042	7
7	Null	2	239.2	48.9	<0.001	>100
Dolly Varden						
1	Site + year + day of year + Chum CPUE	8	128.0	0.0	0.630	1
2	Site + year + day of year + Chum CPUE + predator length	9	129.9	1.9	0.243	3
3	Site + day of year + Chum CPUE	7	132.0	4.0	0.085	7
4	Site + day of year + Chum CPUE + predator length	8	133.9	5.9	0.033	19
5	Site + year + Chum CPUE + predator length	8	138.4	10.4	0.003	181
6	Year + day of year + Chum CPUE	5	139.5	11.5	0.002	314
7	Null	2	270.5	142.5	<0.001	>100

TABLE 3. Model summaries for linear regression of the standardized mass of Chum Salmon prey in Pacific Staghorn Sculpin stomachs ($n = 26$) and Dolly Varden stomachs ($n = 40$). In total, 64 models were evaluated for Pacific Staghorn Sculpin, with all combinations of the following predictors: site (factor), day of year, Chum Salmon CPUE (Chum CPUE), year (factor), predator length, and proportion of hatchery Chum Salmon present in seine catches (hatchery prop). Overall, 32 models were evaluated for Dolly Varden, with all combinations of the following predictors: site (factor), day of year, Chum CPUE, year (factor), and predator length (K = total number of parameters estimated; AIC_c = Akaike's information criterion, bias-corrected for small sample size; Δ AIC = difference in AIC_c between the given model and the best-performing model [lowest AIC_c]; w_i = model Akaike weight).

Model number	Model parameters	K	AIC_c	Δ AIC _c	w_i	Evidence ratio
Pacific Staghorn Sculpin						
1	Predator length + hatchery prop	4	54.2	0.0	0.316	1
2	Chum CPUE + predator length + hatchery prop	5	54.8	0.6	0.234	1
3	Chum CPUE + hatchery prop	4	55.2	1.0	0.191	2
4	Year + predator length + hatchery prop	5	57.9	3.7	0.050	6
5	Day of year + predator length + hatchery prop	5	58.1	3.9	0.045	7
6	Day of year + Chum CPUE + predator length + hatchery prop	6	58.5	4.3	0.037	9
7	Null	2	78.1	23.9	<0.001	>100
Dolly Varden						
1	Day of year	3	-55.5	0.0	0.486	1
2	Year + day of year	4	-53.9	1.6	0.222	2
3	Day of year + predator length	4	-53.5	2.0	0.181	3
4	Year + day of year + predator length	5	-51.3	4.2	0.060	8
5	Site + day of year	6	-47.7	7.7	0.010	48
6	Site + predator length	6	-47.7	7.7	0.010	48
7	Null	2	-40.3	15.2	<0.001	>100

TABLE 4. Akaike parameter weights ($w_{+}[j]$) for logistic regression of Chum Salmon occurrence (presence/absence) in predator stomachs (see Table 2) and linear regression of the standardized mass of Chum Salmon prey in predator stomachs (see Table 3).

Parameter	$w_{+}(j)$
Logistic regression: Pacific Staghorn Sculpin	
Day of year	0.998
Chum Salmon CPUE	0.913
Site	0.841
Predator length	0.546
Year	0.349
Linear regression: Pacific Staghorn Sculpin	
Hatchery proportion	1.000
Predator length	0.717
Chum Salmon CPUE	0.548
Day of year	0.127
Year	0.125
Site	0.007
Logistic regression: Dolly Varden	
Chum Salmon CPUE	1.000
Site	0.996
Day of year	0.994
Year	0.881
Predator length	0.282
Linear regression: Dolly Varden	
Day of year	0.974
Year	0.301
Predator length	0.262
Site	0.044
Chum Salmon CPUE	0.005

For Dolly Varden, the best logistic regression model included site, year, day of year, and Chum Salmon CPUE as predictors of Chum Salmon occurrence in diets; one other model, which also included predator length, received equivalent support (Table 2). The best linear regression included only the predictor day of year, but there was equivalent support for the model including year and day of year as well as for the model including day of year and predator length (Table 3). Parameter weights $w_{+}(j)$ indicated that Chum Salmon CPUE, site, day of year, and year were the most important factors ($w_{+}[j] > 0.8$) explaining variation in Chum Salmon occurrence in Dolly Varden stomachs, while predator length was unimportant ($w_{+}[j] = 0.282$; Table 4). Day of year was important ($w_{+}[j] = 0.974$) and all other predictors were relatively unimportant ($w_{+}[j] < 0.4$) in explaining variation in the quantity of Chum Salmon in the diets (Table 4). The frequency of Chum Salmon occurrence in Dolly Varden stomachs was relatively higher at the Sheep Creek and Mendenhall River sites, was higher in 2017 than in 2016, and decreased with sampling date (Table A.3). The estimated quantity of Chum Salmon consumed increased with sampling date (Table A.4).

DISCUSSION

This study provides insight into the ecological processes underpinning juvenile salmon mortality and vulnerability to predation during the critical early marine phase. Across 2 years, we found that juvenile Chum Salmon were consistent components of the diets of two abundant nearshore predators during the spring period of hatchery releases and out-migration of wild-born salmon. The majority of Chum Salmon consumed were hatchery born, reflecting their high abundance at our study sites. Chum Salmon consumed by predators were smaller on average than those caught in seines and released by the hatchery. This result is consistent with research showing a preference for smaller prey by piscivorous fishes (Juanes 1994; Sogard 1997; Scharf et al. 2000) and with studies on size-selective mortality of juvenile salmon, which found higher mortality rates among smaller individuals (Parker 1971; Healey 1982; Duffy and Beauchamp 2008). However, the mean lengths and length distributions of wild-born Chum Salmon in diets were not significantly different from those of wild-born Chum Salmon in beach seine catches. This suggests different patterns of selectivity for hatchery and wild fish, perhaps due to behavioral differences, but could also be an artifact of few observations of wild-born fish in diets and beach seine catches. Overall, our results indicate that predators were selective for smaller-than-average fish, with the caveat that the assessment of Chum Salmon sizes potentially available to consumers was influenced by beach seine selectivity. We periodically observed the smallest Chum Salmon escaping through the mesh, which may have resulted in the underrepresentation of smaller size-classes. Furthermore, the beach seines were not able to capture fish that had migrated further offshore but were still within the foraging range of the mobile consumers.

The largest size-classes of Chum Salmon caught in beach seines or released from the hatchery were rarely found in predator diets, particularly during 2017. This is noteworthy because as a strategy to minimize early marine predation, the Macaulay Salmon Hatchery holds and feeds some Chum Salmon in net-pens for an extra 2–3 weeks to grow them to a larger size before release. Over the period of this study, 44% of hatchery Chum Salmon were released at or above a 4-g average weight threshold, which corresponds to a length of approximately 66 mm SL based on a length-weight regression that we developed from Chum Salmon sampled in hatchery net-pens immediately before release (our unpublished data). In contrast, the average size of a wild-born Chum Salmon in our seine catches was just 0.93 g or 39.9 mm SL. The intent of enhanced growth in hatchery fish is to improve survival by increasing escape ability and minimizing the amount of time fish spend in nearshore habitats. Increased size at marine entry has been shown to improve salmon smolt survival in both hatchery and natural settings (Healey 1982; Hargreaves and Lebrasseur 1985; Willette et al. 2001). Our results appear to support the effectiveness of

this strategy for reducing predation by Pacific Staghorn Sculpin and Dolly Varden, as 93% of measurable Chum Salmon prey were below the 66-mm average release size target.

Although increased size at release may help hatchery Chum Salmon to avoid predation at marine entry, it is important to note the potential drawbacks of this strategy, including match/mismatch dynamics with predators or food resources later in their life history and earlier maturation leading to smaller returning adults (McConnell et al. 2018), which are less desirable in fisheries (Morita et al. 2005). Vulnerability to predators may also depend on body condition, which can vary independently of size (Tucker et al. 2016). In addition, survival bottlenecks occurring later in Chum Salmon life history could render predation mortality at the juvenile stage less important. Ultimately, determining whether nearshore predation by Dolly Varden and Pacific Staghorn Sculpin could have a significant impact on hatchery Chum Salmon population dynamics requires more information about predator population sizes and their consumption rates as well as other sources of mortality. Estimated rates of salmon consumption by local predator populations could be used in population models for hatchery Chum Salmon that explicitly include predation as a source of natural mortality (e.g., Hollowed et al. 2000).

The prevalence of Chum Salmon in predator diets was not consistently higher at sites closest to hatchery net-pens, suggesting that proximity to hatchery release areas alone does not explain spatial variation in the contribution of juvenile Chum Salmon to diets. For example, the proportion of Chum Salmon in predator diets was relatively low at the Eagle River site, despite its proximity to a hatchery release area. Chum Salmon are released near the south side of the Eagle River delta and may move offshore or southward rather than northward along the delta where we sampled; however, fine-scale migration routes of juvenile salmon out of the nearshore waters are unknown and likely variable among years. Additionally, it is plausible that the direction of tidal currents at the time of release could influence the direction in which fish move when released from hatchery net-pens. All sites showed similarly high proportions of hatchery Chum Salmon in the beach seines after multiple hatchery releases had occurred in May. This suggests that hatchery fish are widely distributed after release but aggregate more heavily in certain areas, which is supported by the Macaulay Salmon Hatchery's unpublished data on juvenile Chum Salmon movement (Zaleski, personal communication). Factors such as bathymetry, currents, temperature, habitat, salmon density, and food availability have been shown to play a role in where salmon aggregate during early marine residency (Orsi et al. 2000; Sturdevant et al. 2012).

Although seasonal patterns of Chum Salmon CPUE and proportion of hatchery Chum Salmon in seines were similar

across sites, the absolute CPUE differences among sites could be large. The Cowee Creek and Eagle River sites, where the proportions of Chum Salmon in predator diets were relatively low, averaged 6.6 Chum Salmon per beach seine set. The Mendenhall River and Sheep Creek sites, where proportions of Chum Salmon in the diets of both predators were higher, averaged 36.5 Chum Salmon per set. This is consistent with a positive functional response in which prey encounter rates impact the probabilities of capture for piscivores (Juanes et al. 2008), suggesting that differences in Chum Salmon density likely contributed to the differences in predation observed among sites. In addition, predators may exhibit an aggregative numerical response to spatial or temporal prey pulses: for example, humpback whales *Megaptera novaeangliae* and common mergansers *Mergus merganser* are attracted to hatchery salmon release sites (Wood 1985; Chenoweth et al. 2017). Determining the mechanisms underlying the predatory responses of nearshore fishes to hatchery salmon would require in-depth investigation of predator foraging behavior and more robust measures of predator densities in the presence and absence of hatchery salmon releases.

Chum Salmon CPUE was positively related to both the occurrence and quantity of Chum Salmon in predator diets. Although Chum Salmon CPUE was among the most important predictors of Chum Salmon occurrence in Pacific Staghorn Sculpin and Dolly Varden stomachs, it was less important as a predictor of Chum Salmon quantity in the diets for both predators. The low importance of CPUE for explaining the quantity of Chum Salmon in Dolly Varden stomachs in particular may also reflect the mobile nature of the predator species. Dolly Varden move daily and seasonally to optimize foraging (Armstrong 1970; Schutz and Northcote 1972). In contrast, Pacific Staghorn Sculpin exhibit more sedentary ambush tactics to capture prey (Mace 1983). Our CPUE measurements only reflect juvenile salmon densities in a small intertidal area and may not be representative of densities further offshore or in adjacent habitats that active predators could access more easily.

Predator length was of moderate to high importance in predicting the occurrence and quantity of Chum Salmon in Pacific Staghorn Sculpin stomachs but was of low importance for Dolly Varden. For Pacific Staghorn Sculpin, the relationship between predator length and the occurrence of Chum Salmon in stomachs was positive, suggesting that larger predators had a higher probability of capturing Chum Salmon. However, the relationship between Pacific Staghorn Sculpin length and the quantity of Chum Salmon consumed was negative, indicating that small to intermediate size-classes of sculpin consumed a larger mass of Chum Salmon relative to their body size. Pacific Staghorn Sculpin generally transition from an invertebrate-dominated diet at smaller sizes to incorporating more fish at larger sizes

(Whitney et al. 2017), which is common among fishes, particularly those with large gapes relative to body size (Mittelbach and Persson 1998). The larger size-classes of both predators tended to consume fish prey that were larger than juvenile Chum Salmon, including Pacific Sand Lance, Pacific Herring, and juvenile Coho Salmon.

Differences in predator preference for hatchery- and wild-born Chum Salmon are of interest to hatchery operators and salmon managers. Overall, more than 88% of Chum Salmon prey were of hatchery origin. This is similar to the estimated proportion of hatchery-origin Chum Salmon in beach seines at times of peak Chum Salmon consumption (80–100%), which suggests that predators consumed Chum Salmon relative to their abundance in the environment (i.e., no preference based on origin alone). Hatchery- and wild-born salmon can occupy different habitats during nearshore residency (Reese et al. 2009; Sturdevant et al. 2012) and migrate into offshore habitats at different times (Orsi et al. 2004). Therefore, given the limited geographic scope of our sampling, we were not able to assess preference quantitatively. All of the sites evaluated for this study reached hatchery proportions of 85% or higher, so a site with exclusively wild-born Chum Salmon was not available for us to evaluate baseline predation in the absence of hatchery inputs.

The potential for competition between wild-born and hatchery Chum Salmon exists at multiple stages of their life history. At the early smolt stage examined here, apparent competition (sensu Holt 1977) between wild-born and hatchery smolts could potentially arise if predation rates on wild-born Chum Salmon are elevated compared to estuaries without hatchery salmon input. Alternatively, large hatchery releases could swamp predators to reduce predation risk (e.g., Furey et al. 2016) on less abundant, smaller wild fish. Wild-born and hatchery smolts could also interact directly, competing for space and prey resources (e.g., Cooney and Brodeur 1998). Spatial or temporal mismatches between wild-born and hatchery Chum Salmon could serve to limit their interactions (e.g., Levings et al. 1986); for example, in April 2017 (this study) and in April 2019 (unpublished data), we caught Chum Salmon whose origin was known to be exclusively wild born because the hatchery had not yet released any fish. Furthermore, although hatchery Chum Salmon have a size advantage over smaller wild fish, they could display reduced predator avoidance capabilities due to domestication, as has been observed for other salmonids (Berejikian 1995; Einum and Fleming 2001).

Most of the salmon consumption by Pacific Staghorn Sculpin and Dolly Varden coincided with periods of relatively high hatchery Chum Salmon densities in the nearshore. This suggests that hatchery releases provide an accessible food source to nearshore consumers; however, hatchery subsidies to the nearshore food web are not a new phenomenon. The DIPAC Macaulay Salmon

Hatchery has been producing and releasing juvenile salmon in the Juneau area since 1977. Ecological baselines from a system of exclusive natural production have likely shifted in ways that are unknown. Our understanding of the broader ecological effects of hatcheries would be greatly informed by research focused on times and places where hatchery production is just beginning or where significant changes to hatchery release strategies are occurring.

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Appendix: Sample Sizes, Diet Composition, and Model Summaries

TABLE A.1. Sampling periods in 2016 and 2017, with the number of beach seine (BS) sets conducted at each site and whether or not hook-and-line (HL) sampling occurred (yes [Y] or no [N]). Only Dolly Varden were captured during HL sampling. Sampling was not conducted in April 2016.

Sampling period	Cowee Creek		Eagle River		Mendenhall River		Sheep Creek	
	BS	HL	BS	HL	BS	HL	BS	HL
2016								
Early April	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Late April	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Early May	6	Y	6	N	6	Y	4	Y
Late May	6	Y	6	Y	5	Y	6	Y
Early June	6	N	6	N	6	Y	7	N
Late June	6	N	6	Y	5	N	7	Y
Early July	5	N	6	N	6	N	6	N
2017								
Early April	7	N	7	N	7	N	6	N
Late April	7	N	7	N	7	N	6	N
Early May	7	N	7	N	7	N	7	Y
Late May	7	N	7	N	7	Y	7	N
Early June	7	N	7	Y	7	N	7	Y
Late June	7	N	6	N	7	N	7	Y
Early July	7	N	7	N	7	N	8	Y

TABLE A.2. Percent weight (W_i) and percent frequency of occurrence (O_i) of prey groups for Pacific Staghorn Sculpin and Dolly Varden across seven sampling periods in 2016–2017.

Prey group	May 2016		Jun 2016		Jul 2016		Apr 2017		May 2017		Jun 2017		Jul 2017		Overall		
	W_i	O_i	W_i	O_i													
Pacific Staghorn Sculpin																	
Juvenile salmon																	
Chum Salmon	9.6	8.0	4.5	2.2	0.0	0.0	0.0	0.0	10.2	8.1	0.9	1.3	0.0	0.0	4.5	2.8	
Coho Salmon	8.7	3.4	0.0	0.0	0.0	0.0	0.0	0.0	3.3	0.7	0.0	0.0	0.0	0.0	2.0	0.4	
Salmon, unidentified	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.4	0.0	0.0	0.0	0.0	0.1	
Other fishes																	
Pacific Herring <i>Clupea pallasii</i>	9.0	2.3	2.5	2.2	14.0	4.9	0.0	0.0	21.0	11.8	17.3	6.9	18.6	6.5	13.2	5.6	
Pacific Sand Lance <i>Ammodytes hexapterus</i>	13.4	5.7	10.0	9.5	20.9	27.0	33.4	28.6	22.9	11.0	14.1	9.1	1.2	4.1	14.5	11.0	
Cottidae	5.7	9.2	6.8	16.5	2.1	3.3	0.0	0.0	0.0	0.7	0.0	0.0	0.1	0.8	2.6	5.5	
Osmeridae	0.3	1.1	0.0	0.0	7.0	4.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.6	
Pleuronectiformes	8.8	9.2	11.7	13.0	2.1	9.0	0.0	0.0	0.2	1.5	4.2	3.0	3.6	7.3	5.4	7.1	
Stichaeidae	1.5	9.2	5.0	14.3	1.9	1.6	0.0	0.0	9.6	0.7	0.3	1.7	0.6	2.4	3.5	5.4	
Other teleost	0.0	0.0	1.8	6.9	0.2	2.5	0.0	0.0	0.7	2.2	0.0	0.4	0.0	0.0	0.5	2.4	
Teleost adult scavenge	2.1	1.1	4.9	0.9	0.0	0.0	0.0	0.0	1.9	0.7	0.0	0.0	5.6	1.6	2.3	0.6	
Teleost, unidentified	5.2	33.3	11.2	53.2	15.4	50.8	1.6	28.6	8.8	34.6	9.5	35.9	4.6	21.1	9.3	39.6	

TABLE A.2. Continued.

Prey group	May 2016		Jun 2016		Jul 2016		Apr 2017		May 2017		Jun 2017		Jul 2017		Overall	
	<i>W_i</i>	<i>O_i</i>														
Invertebrates																
Amphipod	1.6	42.5	5.4	72.7	3.2	76.2	0.8	28.6	1.8	48.5	2.4	42.4	3.7	62.6	3.0	57.6
Annelida	9.9	54.0	9.3	50.6	6.2	47.5	40.6	42.9	4.5	45.6	11.8	37.7	5.1	35.8	8.3	44.5
Bivalve	0.1	8.0	1.9	15.2	0.2	16.4	5.5	28.6	0.0	8.1	0.4	20.8	0.9	37.4	0.7	18.0
Pleocyemata	8.5	29.9	6.8	26.4	2.3	14.8	15.7	28.6	3.5	10.3	10.0	27.3	6.3	26.8	6.5	23.1
Malacostraca	2.8	26.4	3.2	40.3	1.8	47.5	1.2	14.3	0.7	16.2	1.4	12.6	0.8	20.3	1.9	26.7
Isopod	4.6	39.1	9.2	57.6	14.4	63.1	0.0	0.0	3.7	51.5	19.3	64.1	37.7	74.0	13.1	58.8
Crustacean	1.6	25.3	4.3	41.6	6.4	49.2	1.2	42.9	2.1	39.7	3.7	38.5	4.8	44.7	3.7	40.3
Other invertebrates	2.6	23.0	0.5	34.2	0.2	31.1	0.0	0.0	0.7	29.4	0.7	35.1	1.2	41.5	0.9	32.7
Eggs																
Salmon eggs	0.0	0.0	0.0	0.0	1.4	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.2	3.3	0.2	0.6
Eggs, unidentified	3.9	1.1	0.0	0.0	0.0	0.0	0.0	0.0	3.2	2.2	0.0	0.0	0.0	0.0	1.2	0.4
Other																
Tissue, unidentified	0.2	9.2	0.7	13.9	0.4	3.3	0.0	0.0	0.9	8.1	3.8	6.9	4.9	11.4	1.7	9.0
Empty	0.0	2.3	0.0	0.9	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.9	0.0	0.8	0.0	1.0
Dolly Varden																
Juvenile salmon																
Chum Salmon	28.4	15.1	0.4	0.8	0.0	0.0	4.3	15.6	16.1	4.5	45.0	18.1	0.0	0.0	19.6	8.9
Coho Salmon	39.7	1.4	0.0	0.0	0.0	0.0	0.0	0.0	31.2	2.3	0.0	0.0	0.0	0.0	0.0	15.0
Salmon, unidentified	0.7	4.1	0.1	0.8	1.9	7.7	0.0	0.0	0.0	0.2	0.9	0.0	0.0	0.3	0.3	1.3
Other fishes																
Pacific Herring	7.2	6.8	13.7	1.5	0.0	0.0	0.0	0.0	6.7	2.3	7.8	3.4	0.0	2.5	8.0	2.9
Pacific Sand Lance	1.7	5.5	34.3	43.8	13.7	15.4	72.8	37.5	1.7	2.3	29.8	24.1	15.9	15.0	22.3	24.6
Pleuronectiformes	0.0	1.4	0.0	1.5	3.3	23.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	1.3
Stichaeidae	0.0	0.0	14.1	13.1	0.0	0.0	0.3	3.1	0.6	2.3	0.5	1.7	3.0	5.0	4.2	5.1
Agonidae	4.5	19.2	0.5	7.7	0.0	0.0	0.0	0.0	3.8	4.5	0.0	1.7	0.0	0.0	1.8	6.3
Pholidae	0.0	0.0	1.9	16.9	0.0	0.0	0.6	3.1	0.0	0.0	0.1	1.7	0.0	0.0	0.6	5.6
Cottidae	0.2	12.3	0.4	11.5	0.0	0.0	6.5	34.4	0.0	0.0	0.0	0.9	0.0	0.0	0.7	8.0
Other teleost	0.0	0.0	0.0	0.0	0.2	7.7	0.0	0.0	0.0	0.0	0.7	0.9	0.0	0.0	0.1	0.4
Teleost, unidentified	2.8	26.0	1.0	26.9	5.5	46.2	0.5	18.8	0.2	9.1	2.0	15.5	0.1	10.0	1.8	20.5
Invertebrates																
Polychaeta	0.8	9.6	0.1	9.2	0.0	0.0	2.1	21.9	0.2	2.3	0.2	4.3	0.1	5.0	0.5	7.6
Amphipod	8.1	64.4	23.9	78.5	42.7	76.9	8.7	65.6	19.2	70.5	3.5	41.4	4.7	65.0	12.3	63.6
Pleocyemata	0.2	6.8	0.0	4.6	0.7	15.4	0.0	0.0	0.1	6.8	0.0	0.9	0.0	0.0	0.1	3.8
Malacostraca	0.1	4.1	2.6	45.4	7.9	61.5	2.4	37.5	1.6	9.1	0.4	10.3	0.5	27.5	1.2	24.3
Crustacean	0.6	11.0	0.3	6.9	2.6	23.1	0.2	18.8	8.9	45.5	0.4	7.8	1.4	27.5	0.9	14.7
Insect	0.1	17.8	0.7	44.6	0.3	15.4	0.2	21.9	2.4	50.0	4.9	44.0	3.2	70.0	1.5	40.4
Copepod	0.6	17.8	0.1	15.4	0.0	0.0	0.0	0.0	1.7	36.4	1.1	24.1	0.1	12.5	0.5	18.3
Cumacean	4.0	46.6	4.8	69.2	6.3	61.5	0.5	28.1	4.8	72.7	2.8	49.1	8.5	70.0	4.1	57.6
Isopod	0.3	5.5	0.9	21.5	3.0	38.5	0.1	9.4	0.4	15.9	0.4	15.5	5.8	27.5	0.8	17.0
Other invertebrates	0.0	5.5	0.1	10.8	0.0	0.0	0.1	9.4	0.1	6.8	0.2	14.7	2.1	42.5	0.2	12.9
Eggs																
Salmon eggs	0.0	0.0	0.0	0.0	11.8	7.7	0.0	0.0	0.0	0.0	0.0	0.0	54.1	22.5	3.4	2.2
Eggs, unidentified	0.0	0.0	0.0	0.0	0.0	0.0	0.3	6.3	0.0	0.0	0.0	1.7	0.0	0.0	0.0	0.9
Other																
Unknown tissue	0.1	16.4	0.0	2.3	0.0	0.0	0.2	12.5	0.0	2.3	0.0	3.4	0.5	5.0	0.1	5.8
Empty	0.0	5.5	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.0	1.3

TABLE A.3. Model coefficient estimates for logistic regression of Chum Salmon occurrence (presence/absence) in Pacific Staghorn Sculpin stomachs ($n=928$) and Dolly Varden stomachs ($n=442$). In total, 32 models were evaluated for Pacific Staghorn Sculpin and Dolly Varden individually, including all combinations of the following predictors: site (factor; ER = Eagle River; MR = Mendenhall River; SC = Sheep Creek), day of year, Chum Salmon CPUE, year (factor), and predator length (K = total number of parameters estimated; AIC = Akaike's information criterion).

Model	Model coefficient									
	Intercept	Site: ER	Site: MR	Site: SC	Year: 2017	Day of year	Chum Salmon CPUE	Predator length	K	AIC
Pacific Staghorn Sculpin										
1	3.916	-2.607	0.052	-0.205	NA	-0.059	0.009	0.009	8	190.3
2	5.749	-2.190	0.400	-0.118	NA	-0.061	0.008	NA	7	191.1
3	4.330	-2.685	-0.172	-0.161	-0.397	-0.060	0.010	0.008	9	191.7
4	6.225	-2.311	0.137	-0.063	-0.495	-0.062	0.010	NA	8	192.1
5	4.021	NA	NA	NA	NA	-0.052	0.012	NA	4	193.6
6	2.319	NA	NA	NA	NA	-0.049	0.013	0.006	5	194.2
Dolly Varden										
1	3.448	-0.147	1.473	3.125	1.645	-0.062	0.029	NA	8	128.0
2	2.845	-0.164	1.491	3.095	1.640	-0.060	0.029	0.001	9	129.9
3	6.380	-0.145	0.518	3.311	NA	-0.076	0.035	NA	7	132.0
4	5.410	-0.124	0.566	3.282	NA	-0.071	0.035	0.002	8	133.9
5	-7.459	0.457	1.679	2.190	1.650	NA	0.032	0.009	8	138.4
6	0.309	NA	NA	NA	1.639	-0.035	0.048	NA	5	139.5

TABLE A.4. Model summaries for linear regression of the standardized mass of Chum Salmon prey in Pacific Staghorn Sculpin stomachs ($n=26$) and Dolly Varden stomachs ($n=40$). In total, 64 models were evaluated for Pacific Staghorn Sculpin, with all combinations of the following predictors: site (factor; ER = Eagle River; MR = Mendenhall River; SC = Sheep Creek), day of year, Chum Salmon CPUE, year (factor), predator length, and proportion of hatchery Chum Salmon present in seine catches (hatchery prop). Overall, 32 models were evaluated for Dolly Varden, with all combinations of the following predictors: site (factor), day of year, Chum Salmon CPUE, year (factor), and predator length (K = total number of parameters estimated; AIC_c = Akaike's information criterion, bias-corrected for small sample size).

Model	Model coefficient										
	Intercept	Site: ER	Site: MR	Site: SC	Year: 2017	Day of year	Chum Salmon CPUE	Predator length	Hatchery prop	K	AIC_c
Pacific Staghorn Sculpin											
1	-1.291	NA	NA	NA	NA	NA	NA	-0.014	1.939	4	54.2
2	-1.782	NA	NA	NA	NA	NA	0.005	-0.009	0.700	5	54.8
3	-2.980	NA	NA	NA	NA	NA	0.009	NA	-0.632	4	55.2
4	-1.638	NA	NA	NA	0.218	NA	NA	-0.013	1.961	5	57.9
5	0.262	NA	NA	NA	NA	-0.011	NA	-0.014	2.119	5	58.1
6	2.732	NA	NA	NA	NA	-0.033	0.006	-0.010	1.053	6	58.5
Dolly Varden											
1	-0.467	NA	NA	NA	NA	0.005	NA	NA		3	-55.5
2	-0.448	NA	NA	NA	0.038	0.005	NA	NA		4	-53.9
3	-0.373	NA	NA	NA	NA	0.005	NA	-0.000		4	-53.5
4	-0.429	NA	NA	NA	0.034	0.005	NA	-0.000		5	-51.3
5	-0.404	-0.033	-0.005	0.004	NA	0.005	NA	NA		6	-47.7
6	0.328	-0.094	-0.029	0.109	NA	NA	NA	-0.001		6	-47.7