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ORIGINAL ARTICLE

Piscine predation on juvenile salmon in sub-arctic Alaskan rivers: Associations with season, habitat, predator size and streamflow

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Abstract

Predation on anadromous salmon can have important consequences for both predators and prey. Salmon provide large seasonal pulses of energy and nutrients via carcasses, eggs and juveniles to many freshwater consumers, and conversely, predation can represent a significant source of mortality for juvenile salmon. Recent declines of Chinook salmon (*Oncorhynchus tshawytscha*) populations in Alaska have raised concern that predation might inhibit their recovery. Here, we quantify patterns of predation by freshwater fishes on juvenile salmon across seasons, habitats, predator sizes and streamflow levels in the Arctic-Yukon-Kuskokwim region of Alaska. We analysed piscivore stomach contents and identified prey using DNA sequence "barcoding." In coastal rivers, juvenile pink (*O. gorbuscha*) and chum (*O. keta*) salmon contributed heavily to Arctic grayling (*Thymallus arcticus*) and Dolly Varden char (*Salvelinus malma*) diets, coho salmon (*O. kisutch*) prey were rare, and Chinook salmon were not detected. In interior rivers, Arctic grayling, burbot (*Lota lota*) and northern pike (*Esox lucius*) consumed small numbers of Chinook salmon. Predation on Chinook salmon was documented disproportionately in sloughs during a summer of exceptionally high streamflow. Dietary and distributional patterns suggested northern pike and burbot may exclude salmon from sloughs in low-gradient river reaches that would otherwise provide suitable rearing habitat. The data also provided tentative support for the hypothesis that high streamflow induces juvenile Chinook salmon to move from mainstem habitats into sloughs, where they face an increased risk of mortality. Incorporating predation risk into climate adaptation, fisheries management and habitat restoration decisions may help to facilitate Chinook salmon recovery.

KEYWORDS

Chinook salmon, diet composition, Pacific salmon, piscivory, predation risk, stomach contents

1 | INTRODUCTION

A wide array of freshwater species feed on anadromous Pacific salmon (*Oncorhynchus* spp.), and these interactions can be consequential for predators as well as prey. From the predator's perspective, salmon eggs and juveniles provide large seasonal resource pulses that can greatly increase their annual energy budgets and growth rates (Armstrong & Bond, 2013; Denton et al., 2009; Furey et al., 2016). Conversely, from the salmon's perspective, predation in fresh water can represent an important source of mortality. For example, avian and piscine predators can consume over half of juvenile coho (*O. kisutch*) and sockeye salmon (*O. nerka*) during their freshwater rearing and initial smolt outmigration phases (Furey, Hinch, Bass, et al., 2016; Wood, 1987b), and overall mortality rates during the entire smolt outmigration can exceed two-thirds (Rechisky et al., 2018). Predation risk also influences behavioural trade-offs and habitat selection during the freshwater life stage (Abrahams & Healey, 1993; Dill & Fraser, 1984), a period of high growth and mortality that can have important consequences for salmon population dynamics (Bradford, 1995; Quinn, 2018). Finally, predator swamping can cause depensatory dynamics, whereby salmon experience greater mortality rates when their abundance is lower (Furey, Hinch, Bass, et al., 2016; Liermann & Hilborn, 2001). Under these conditions, stable populations of freshwater predators could inhibit the recovery of salmon populations from declines initially caused by other factors (Wood, 1987a).

Recent declines of Chinook salmon (*O. tshawytscha*) populations have led to fisheries restrictions and closures throughout Alaska (ADFG, 2013; Schindler et al., 2013). Salmon declines have caused especially severe impacts to subsistence fishing communities in the Arctic-Yukon-Kuskokwim (AYK) region of Western and Interior Alaska (Brown & Godduhn, 2015; NRC, 2004; Raymond-Yakoubian & Raymond-Yakoubian, 2015). The productivities of Alaskan Chinook salmon populations are associated with climatic and human-driven processes in both freshwater and marine environments, although a substantial amount of the variability in salmon returns remains unexplained (Cunningham et al., 2018; Jones et al., 2020; Neuswanger et al., 2015; Ohlberger et al., 2016). The roles of biological processes, such as predation and disease, in influencing salmon populations—and potential interactions between biological and climatic drivers—remain largely unquantified and require further study (Falke et al., 2019; Jones et al., 2020; Ohlberger et al., 2016).

Salmon co-occur with many native predators in the AYK region, including piscivorous fishes such as Arctic grayling (*Thymallus arcticus*), burbot (*Lota lota*), Dolly Varden char (*Salvelinus malma*), inconnu (*Stenodus leucichthys*) and northern pike (*Esox lucius*), as well as birds such as common merganser (*Mergus merganser*). Traditional ecological knowledge indicates predators have important effects on salmon in the region and may have contributed to the recent declines (Raymond-Yakoubian & Raymond-Yakoubian, 2015; Raymond-Yakoubian, 2009). Further, introductions of northern pike into a nearby region provide compelling evidence that predation can have large effects on Alaskan salmon populations. In southcentral Alaska, several Chinook, coho and sockeye salmon populations declined precipitously following the establishment of introduced northern pike (Dunker et al., 2018; Sepulveda et al., 2015), and some salmon populations have begun to recover following northern pike eradication or suppression (Courtney et al., 2018; Dunker et al., 2020). These findings suggest that native northern pike—and other predators—may also have important effects on salmon in the AYK region. However, little is documented in the scientific literature about factors influencing predation on juvenile salmon in the AYK region.

Predator impacts on prey populations can be strongly influenced by habitat characteristics and environmental conditions (Carey et al., 2012; Hein et al., 2014; Schoen et al., 2015). Of particular interest in the AYK region is whether habitat type and streamflow affect predation risk of juvenile Chinook salmon. Spawner-recruit analysis of two Chinook salmon populations indicates cohorts that experience above-average streamflow during the summer juvenile rearing stage return at lower than expected numbers as adults (Neuswanger et al., 2015). Subsequent research on the same populations also concluded high streamflow had a potentially large negative effect on population productivity, although the effect size was highly uncertain (Cunningham et al., 2018), potentially because streamflow is confounded with stream temperature (Falke, Huntsman, et al., 2019). One proposed mechanism for the high-flow / low-productivity pattern is that periods of high streamflow displace juvenile Chinook salmon from mainstem rearing habitats into off-channel habitats that provide a refuge from high water velocities but increased vulnerability to predators (Neuswanger et al., 2015). Off-channel habitats such as sloughs can provide juvenile salmon with greater growth opportunities than mainstem rearing habitats under certain conditions (e.g. Baldock et al., 2016; Huntsman & Falke, 2019), but it remains unclear whether these benefits are indeed associated with greater predation risk.

To better understand predation on salmon in the AYK region from both the predators' and prey's perspectives, it is necessary to determine the diet composition of piscivorous fishes, when and where they consume the most salmon, and whether high flows are associated with increased predation risk. In this study, we quantified seasonal, spatial, size-structured and streamflow-related patterns of predation by freshwater fishes on juvenile salmon. Our analysis examined both the dietary contribution of prey to predators and the predatory impacts on Chinook salmon in particular. We addressed four specific objectives: (a) quantify the diet composition of piscivorous fishes in known rearing habitats of juvenile Chinook salmon, (b) determine how the overall contribution of juvenile salmon to predator diets varies with predator size, season, and habitat type, (c) determine how the number of Chinook salmon in predator diets varies with respect to these factors and streamflow and (d) quantify patterns of predator-prey habitat overlap to determine whether predatory exclusion may limit the distribution of Chinook salmon during juvenile rearing. In particular, we tested the predictions that predator diets would contain more Chinook salmon (a) in sloughs than in mainstem habitats and (b) following high-flow conditions than following low-flow conditions.

1.1 | Study area

The Arctic-Yukon-Kuskokwim (AYK) region encompasses the rivers draining into Norton Sound, an inlet of the Bering Sea, and the Yukon and Kuskokwim Rivers draining Interior and Western Alaska (Figure 1a). These watersheds cover an area of over 1 million km^2. We focussed our sampling on three representative study areas: the Unalakleet, Chena and upper Yukon watersheds. These rivers contain a broad variety of habitat types and many of the piscivorous species found in Chinook salmon rearing areas throughout the AYK region. Importantly, the distribution and migration timing of juvenile Chinook salmon is documented in these watersheds (e.g. Daum & Flannery, 2011; Huntsman & Falke, 2019; Joy et al., 2020; Matter et al., 2018), allowing us to focus our predator sampling at times and places where Chinook salmon were likely to be present.

For purposes of the analysis, we grouped the study sites into two ecologically similar study regions: coastal (Unalakleet and North rivers) and interior (Chena and upper Yukon rivers). The Unalakleet River

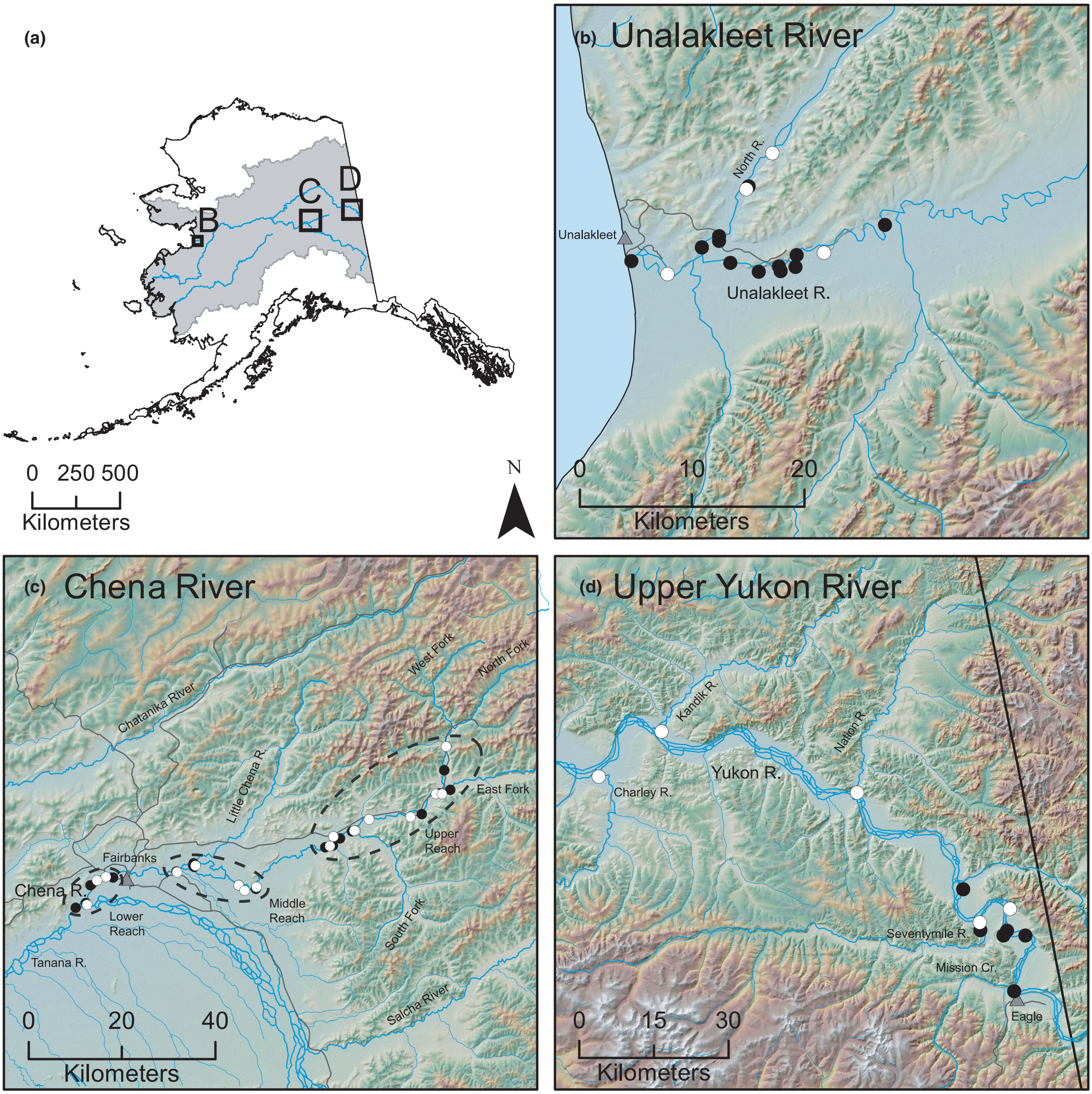

FIGURE 1 Study areas within the Arctic-Yukon-Kuskokwim region of Alaska (a) where piscivorous fishes were sampled for diet analysis: Unalakleet River (b), Chena River (c) and upper Yukon River (d). Circles indicate sampling sites in main channel (black) and off-channel (white) habitats. Additional sites used by subsistence and recreational fishers are not shown. Dashed ovals in panel C show lower, middle and upper study reaches in the Chena River basin

flows through a broad alluvial valley into Norton Sound, draining an area of about 5300 km^2 and supporting populations of Chinook, chum, coho and pink salmon. We sampled 17 sites in the Unalakleet River watershed, including its largest tributary, the North River (Figure 1b). The Chena River is a clear runoff tributary that drains an area of about 5500 km^2, flowing through the city of Fairbanks to its confluence with the glacially turbid Tanana River. The Chena River is one of the most productive Chinook salmon spawning tributaries within the Yukon River Basin (Brown et al., 2017; Eiler et al., 2014) and also supports a population of summer chum salmon. We sampled 44 sites in the Chena River watershed and adjacent Tanana River (Figure 1c). The U.S. portion of the upper Yukon River watershed between the towns of Eagle and Circle includes many rearing habitats for Canadian-origin juvenile Chinook salmon (Daum & Flannery, 2011, 2012). We sampled 11 sites in the upper Yukon River watershed (Figure 1d). We sampled predators in main channel rivers and tributaries as well as in sloughs within each region.

In the Chena River, we further stratified sampling across three contrasting reaches, where we expected Chinook salmon to have different levels of habitat overlap with predators (Figure 1c). A lower reach included the Chena River from its mouth to downtown Fairbanks (rkm 0–15) as well as the larger Tanana River within 5 km of its confluence with the Chena River. This low-gradient reach is heavily urbanised relative to other rivers in the AYK region, with armoured banks and little riparian vegetation or large woody debris (Falke et al., 2019). A small portion of the lower reach contained the invasive waterweed *Elodea* (Carey et al., 2016); however, most of our sampling sites were unaffected. A middle reach was located in another relatively low-gradient section (rkm 35–80) with more natural habitat. An upper reach was characterised by natural streambanks and a higher gradient main channel with abundant riffles and large woody debris (rkm 110–155). Densities of rearing Chinook salmon were expected to be greatest in the upper reach, moderate in the middle reach and lowest in the lower reach, based on previous minnow trap and snorkel surveys (M. Wipfli and J. Neuswanger, unpublished data, see Supporting Information). In contrast, we expected burbot and northern pike densities to be greatest in the lower-gradient lower and middle reaches based on their habitat preferences and prior research (Evenson, 1993; Pearse, 1994).

2 | METHODS

2.1 | Fish sampling

We collected the stomach contents of piscivorous fishes during 2013–2015 to quantify predator diet composition and predation on juvenile salmon. We sampled Arctic grayling and Dolly Varden in the coastal region and Arctic grayling, burbot, inconnu and northern pike in the interior region. We supplemented our sample sizes by collecting fish stomachs donated by recreational and subsistence fishers. We also sampled juvenile Chinook salmon directly in the Chena River to quantify their distribution and habitat overlap with predators.

We conducted sampling from March to September and stratified our analysis seasonally according to the life history of juvenile salmon in the study region. During spring (March–May), age-0 salmon fry emerge from the gravel. We subdivided the spring season into the periods before and after ice breakup, using data from the National Weather Service Breakup Database (https://www.weather.gov/aprfc/breakupDB) for the Chena and Upper Yukon rivers and by direct observation for the Unalakleet River. Breakup occurred between late April and mid-May at all sites in all sampling years. Salmon smolts (age-0 pink and chum salmon, age-1 Chinook salmon and age-1–2 coho salmon) migrate out to the ocean from breakup through July. During summer (June–September), age-0 Chinook and age-0–1 coho salmon parr rear in freshwater and then move into overwintering habitats.

We captured piscivorous fish using baited hoop nets, fyke nets, set lines and angling. Mesh sizes for both hoop and fyke nets (25.4-mm bar mesh) were selected to recruit the smallest possible size classes of piscivores, while allowing juvenile salmon and other small-bodied fishes to escape, in order to avoid biased diet samples due to predators feeding within nets. Nets were deployed for roughly 24-h sets. Set lines were also fished through the ice before river breakup, and hook-and-line angling was used opportunistically during the open-water season to collect additional predators. We also captured juvenile Chinook salmon using baited minnow traps in the Chena River during 2014.

Piscivorous fish were measured (total length [TL] for burbot and fork length [FL] for all other species, mm) and weighed (g). All piscivores captured in the coastal region were sacrificed, and their stomachs were collected. Gastric lavage was used to obtain stomach contents nonlethally for most fish captured in the interior region. The gastric lavage technique was ineffective on burbot, because they did not regurgitate the pumped water or their stomach contents. Therefore, we sacrificed a subset of captured burbot and collected their stomachs. Stomachs and stomach contents were preserved in 95% ethanol solution for transport and frozen upon arrival at the laboratory. Juvenile Chinook salmon were measured (FL, mm) and released at the site of capture.

Subsistence and recreational fishers provided additional predator stomach samples. Subsistence fishers on the Unalakleet and Upper Yukon rivers contributed stomachs of fish harvested using gill nets, seine nets, hoop nets, fyke nets and angling. Recreational anglers on the Chena and Tanana Rivers donated stomachs from fish harvested mostly using set lines through the ice. Subsistence and recreational fishers recorded the date, general location, species and length of each predator and preserved the stomachs either on ice or in 95% ethanol until they could be frozen and transferred to the laboratory.

2.2 | Stream flow

We assigned a standardised stream discharge value to each diet sample from the interior region using U.S. Geological Survey gage data (U.S. Geological Survey, 2020). No discharge data were available from the coastal region during the years of our study. For samples collected in the Chena River, we used station ID 15514000

(Chena River at Fairbanks) for the lower reach, 15493700 (Chena River below Moose Creek Dam) for the middle reach and 15493000 (Chena River near Two Rivers) for the upper reach. For samples collected in the Upper Yukon River basin, we used station 15356000 (Yukon River at Eagle). We accessed daily mean discharge data for a twenty-year period ending in the final study year (1996–2015), which was the longest period available at all four gages, using R package waterData (Ryberg & Vecchia, 2017). River ice prevented winter operation of some gages, so we trimmed the data set to include only the typical open-water period (26 April – 30 September, following Neuswanger et al., 2015). We $\log_e$ transformed and *z*-standardised the values from each gage separately to allow comparisons across sampling sites. To allow for time lags between actual predation events and diet sample collection, we assigned a seven-day rolling average standardised discharge value to each sample to represent streamflow during the week before the sample was collected. We also examined potential relationships between streamflow and predation at longer and shorter timescales by comparing the numbers of juvenile Chinook salmon identified per predator stomach between sampling years and by plotting the timing of documented predation events with respect to daily discharge patterns.

2.3 | Diet analysis

Stomach contents were identified in the laboratory to the species level for fish prey and to order for invertebrates. The blotted wet mass of each prey category was recorded to the nearest 0.01 g. Partially digested fish prey specimens that were unidentifiable based on gross morphology were prepared for identification by DNA sequencing. Genomic DNA was extracted from isolated prey tissues. DNA isolates were used as templates for targeted amplification and direct sequencing of the DNA barcode, a partial segment of the cytochrome oxidase I coding region on the metazoan mitochondrial genome. Amplification and sequencing relied on the FishF1/FishR1 primer pair developed by Ward et al. (2005). The DNA sequences produced were then matched to "barcode" sequences in the Barcode of Life Data System (http://boldsystems.org). By weighing and genetically identifying individual prey specimens within diet samples, we were able to calculate diet proportions by mass, rather than simply the presence or absence of prey species.

We analysed the diet data for each study region separately based on broad patterns identified in an exploratory data analysis. In the coastal region, juvenile salmon made up a large proportion of predator diets overall, but no juvenile Chinook salmon prey were detected. Thus, we tested which factors were associated with the overall contribution of juvenile salmon to predator diets. For each individual predator, we calculated the total mass of all prey items and the diet proportion by mass of juvenile salmon (all salmon species combined). For each predator species, we fit a set of hierarchical generalised linear models (GLMs) predicting the proportion of juvenile salmon in the diet of each predator, using a binomial distribution and log link (Bolker, 2008). We fit a full model with effects of season, habitat and predator length, as well as all possible reduced models including an intercept-only model. We standardised the continuous predictor predator length in all models.

In the interior region, each predator species consumed Chinook salmon, but juvenile salmon made up only a small fraction of predator diets overall. Thus, we tested which factors affected predation on Chinook salmon in particular. We were most interested in quantifying predatory impacts on a species of conservation concern (sensu Beaudreau & Essington, 2007), rather than the dietary contribution of prey to predators, so we specified the numbers of Chinook salmon per predator diet as the response variable. The data were right-skewed and overdispersed (variance $\gg$ mean), so we fit GLMs using a negative binomial distribution and a log link (Bolker, 2008). Due to the rarity of Chinook salmon in diets, we pooled data from all predator species into a single analysis to boost sample sizes. We fit a full model with effects of predator species, season, habitat, predator length, weekly stream discharge and all possible reduced models including an intercept-only model. We standardised the continuous predictors (predator length and discharge [seven-day rolling average, $\log_e$-transformed]) in all models.

We used model selection to identify the primary factors influencing predation of juvenile salmon and examined the magnitude and direction of these associations graphically. We evaluated models for both regions using Akaike's information criterion corrected for small sample size (AIC_c) (Burnham & Anderson, 2002) using the R package MuMIn (Bartoń, 2018). We identified the model with the most support from the data based on the lowest AIC_c score and interpreted alternative models within 2 AIC_c units of the best model ($\Delta AIC_c < 2$) as also receiving some support (Burnham & Anderson, 2002). We examined major dietary patterns graphically with univariate plots of predator diet composition against the predictors included in the best-supported models. For these plots, we quantified diet composition in terms of diet proportions by mass, pooled across all predators, a preferred metric for predation impact studies (Chipps & Garvey, 2007).

2.4 | Habitat associations and predator-prey overlap

We compared the habitat overlap between juvenile Chinook salmon and piscivorous fishes in the Chena River using catch per unit effort (CPUE) as an index of relative abundance. We compared the relative abundance of juvenile Chinook salmon in sloughs among the three study reaches using CPUE from minnow trap sampling in 2014, with one unit of effort defined as an overnight minnow trap set. We compared the relative abundance of juvenile Chinook salmon in the main stem among reaches by analysing data from systematic surveys collected during 2007 (M. Wipfli and J. Neuswanger data; see Supplemental Information). These surveys counted juvenile Chinook salmon using systematic baited minnow trap sampling and snorkel surveys conducted at 5 rkm intervals along the main stem from 215 rkm upstream to the river mouth. Two surveys were conducted, during June 19–22, and August 22–23, 2007, and we estimated relative abundance at each site as the mean count across the two surveys. We calculated the mean counts for all sites within the lower, middle and upper reaches of the present study. We compared the relative abundance of piscivores among mainstem, slough and tributary habitats and among reaches using CPUE in hoop and fyke net sampling during 2014, with one unit of effort defined as one 24-hour net set. We did not include piscivores captured by angling in the CPUE analysis, because the assumption of constant catchability was unlikely to be met (Hubert & Fabrizio, 2007).

We tested for spatial patterns in the relative abundance of each species by fitting hierarchical GLMs. The CPUE data were strongly right-skewed, and the variances were similar to the means, so we fit the GLMs using a Poisson distribution and a log link, specifying catch (counts) as the response variable and the number of nets set per sampling event as a scalar offset (Bolker, 2008; Gray, 2005). For each piscivore species, we fit full models including main effects of gear type (hoop or fyke net), reach, habitat and a reach × habitat interaction, as well as all reduced models. For juvenile Chinook salmon, we tested whether CPUE varied among reaches by fitting separate GLMs to the data collected in the main stem during 2007 and in sloughs during 2014. We did not compare CPUE among habitats because habitat was confounded with sampling year, and salmon abundance varies substantially among years. In each habitat, we evaluated the support for a model with a main effect of reach against a null (intercept-only) model. We evaluated the models using AIC_c as described above. All analyses were conducted in Program R version 4.0.5 (R Core Team, 2021).

3 | RESULTS

3.1 | Diet composition

All four species of predators consumed juvenile salmon in a patchy and episodic manner in both study regions, with predation concentrated in seasonal pulses and particular habitats. We collected diets from 593 piscivorous fish in total, of which 406 had nonempty stomachs (Table S1). In the coastal region, we sampled 110 Arctic grayling (95 nonempty) and 101 Dolly Varden (49 nonempty). The diets of these species contained large fractions of salmon eggs and juvenile pink salmon and smaller fractions of chum and coho salmon (Figures 2 and 3). We identified no Chinook salmon prey in diets from the coastal region. In the interior region, we collected diets from 169 Arctic grayling (140 nonempty), 49 burbot (38 nonempty), 157 northern pike (82 nonempty) and 7 inconnu (2 nonempty). We excluded inconnu from subsequent analyses due to low sample sizes. Arctic grayling, burbot and northern pike in the interior each consumed juvenile Chinook and chum salmon as a small fraction of their overall diets (Figures 4 and 5).

3.1.1 | Coastal region

Arctic grayling in the coastal region consumed primarily fish and fish eggs during all seasons, including juvenile pink, chum and coho salmon (Figure 2). Predation on juvenile salmon was strongly associated with season and habitat type (Table S2). Arctic grayling fed primarily on nonsalmonid fishes between ice breakup and the end of

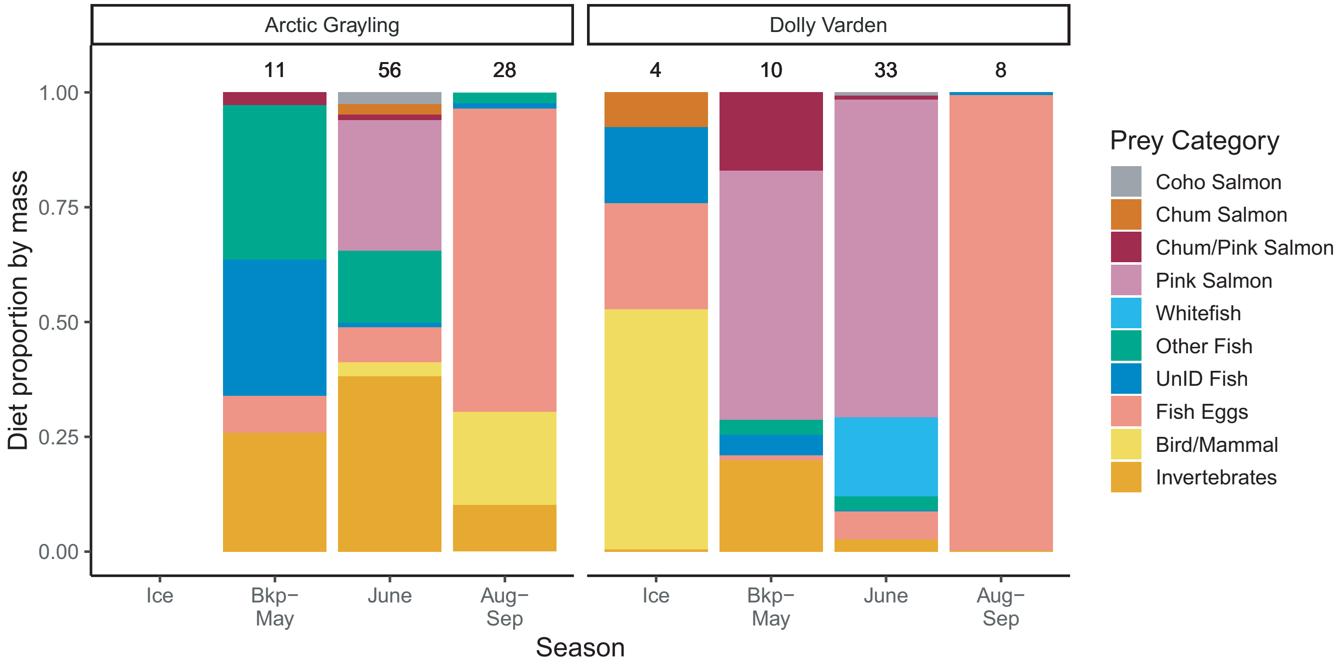

FIGURE 2 Seasonal diet composition (proportions by mass) of Arctic grayling and Dolly Varden char in the coastal region (Unalakleet and North rivers). "Ice" indicates the period from March 1 until the breakup of river ice, and "Bkp – May" indicates the period from breakup until May 31. "Chum/Pink Salmon" indicates prey specimens that were indistinguishable between those species. Numerals above bars indicate numbers of nonempty stomach content samples. No data were available for Arctic grayling before ice breakup

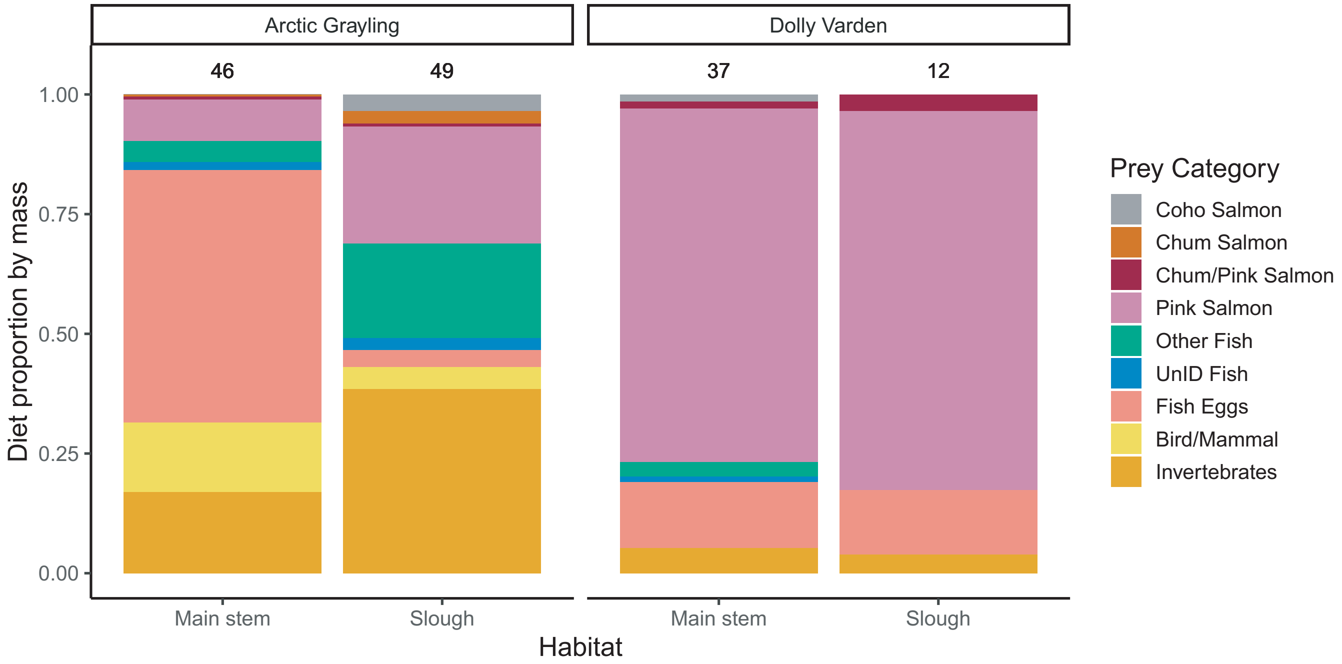

FIGURE 3 Diet composition (proportions by mass) of Arctic grayling and Dolly Varden captured in two habitat types in the coastal region (Unalakleet and North rivers). Numerals above bars indicate numbers of nonempty stomach content samples. Sample sizes are slightly less than those in Figure 2 because habitat type was not reported for some samples donated by recreational and subsistence fishers

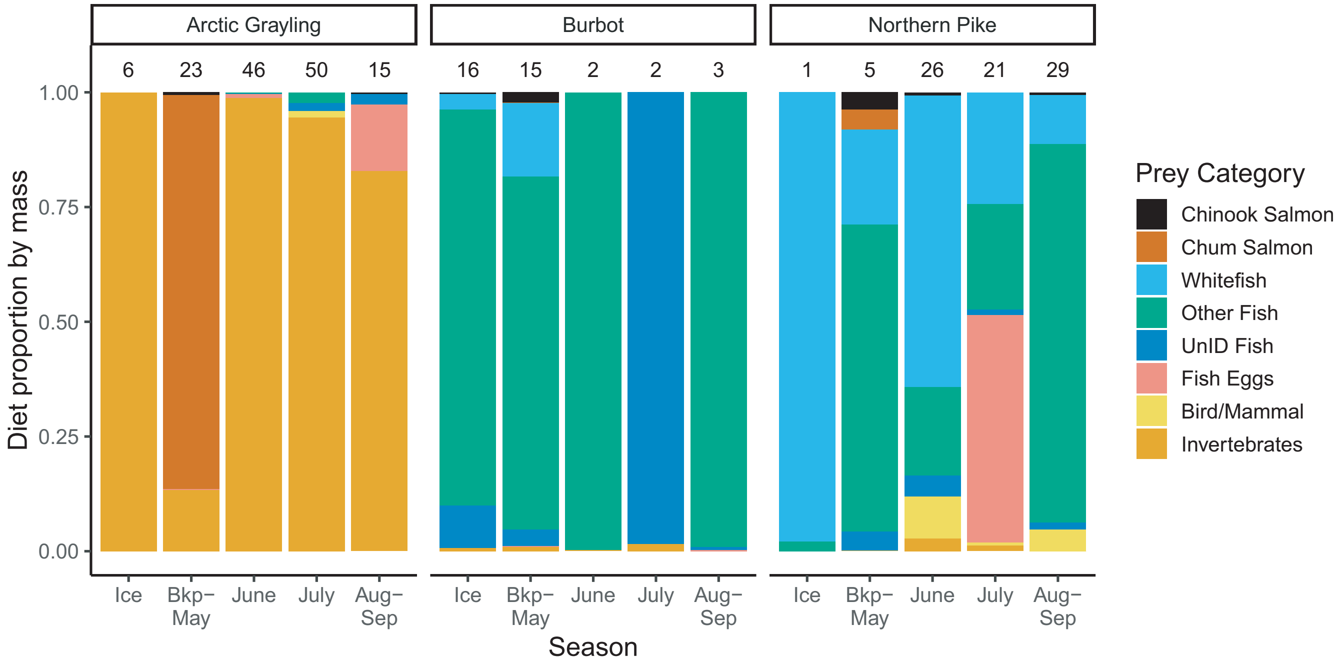

FIGURE 4 Seasonal diet composition (proportions by mass) of Arctic grayling, burbot and northern pike in the interior region (Chena and Upper Yukon rivers). "Ice" indicates the period from March 1 until the breakup of river ice, and "Bkp – May" indicates the period from breakup until May 31. Numerals above bars indicate numbers of nonempty stomach content samples

May, including large proportions of sculpins (*Cottus* spp.) and nine-spine stickleback (*Pungitius pungitius*), with pink and chum salmon representing <3% of the diet by mass. Arctic grayling fed heavily on juvenile salmon during June, especially pink salmon (29% of the diet by mass), with coho salmon, chum salmon and prey that could not be distinguished between pink or chum salmon each comprising <3% of the diet. During August and September, Arctic grayling consumed primarily salmon eggs (66% of the diet). Invertebrates contributed between 10 and 38% of the diet in each season, and mammals contributed 20% of the diet during August and September. Across

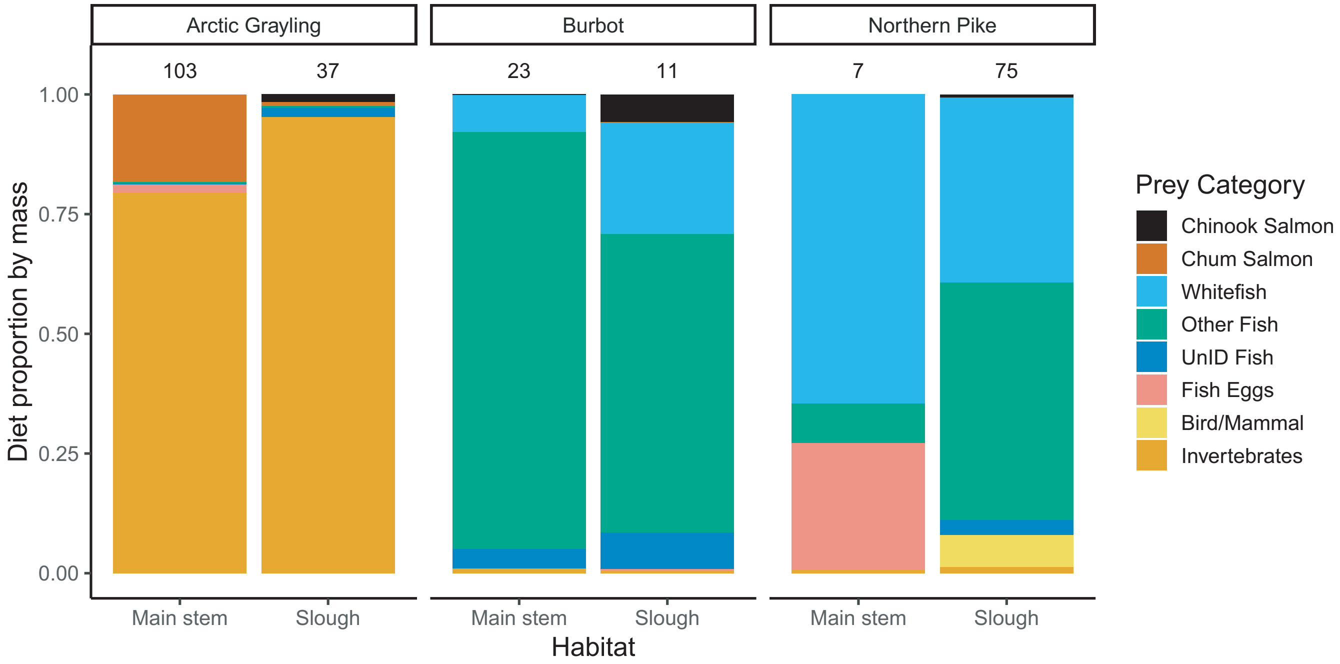

FIGURE 5 Diet composition (proportions by mass) of Arctic grayling, burbot and northern pike captured in two habitat types in the interior region (Chena and Upper Yukon rivers). Numerals above bars indicate numbers of nonempty stomach content samples. Total sample sizes are slightly less than those in Figure 4 because habitat type was not reported for some samples donated by recreational and subsistence fishers

all seasons, Arctic grayling fed more heavily on juvenile salmon in sloughs (28% of the diet) than in mainstem habitats (9%; Figure 3). However, they relied more heavily on salmon eggs in mainstem habitats (53%) than in sloughs (4%). Arctic grayling across the entire size range sampled in this study (216–435 mm FL) consumed juvenile salmon, and the data provided some support for a slight increase in the dietary contribution of juvenile salmon with increasing Arctic grayling length (Figure 6; Table S2).

Dolly Varden char in the coastal region fed heavily on juvenile pink salmon and salmon eggs and also consumed juvenile chum and coho salmon (Figure 2). Dolly Varden predation of juvenile salmon was strongly associated with season and predator length (positively; Table S2). Diets of Dolly Varden captured through the ice during March included 8% chum salmon. Dolly Varden fed primarily on pink salmon (54%) and indistinguishable pink or chum salmon (17%) from breakup through May. During June, diets contained primarily pink salmon (69%) as well as small fractions (< 1% each) of coho salmon and indistinguishable pink or chum salmon. Dolly Varden switched to feed nearly entirely on salmon eggs (99%) during August and September (Figure 2). Across all seasons, Dolly Varden fed on juvenile salmon slightly more in main stems (77%) than sloughs (83%; Figure 3; Table S2). Fish eggs (predominantly salmon eggs) represented 14% of Dolly Varden diets in both habitats. The contribution of juvenile salmon to Dolly Varden diets increased strongly with increasing predator length, from near 0% for the smallest (<300 mm FL) to 75% for the largest (>450 mm FL) predators (Figure 6; Table S2).

3.1.2 | Interior region

Arctic grayling in the interior region fed mostly on invertebrates, but also consumed juvenile Chinook and chum salmon in particular seasons and habitats. Juvenile chum salmon represented 87% of the Arctic grayling diet by mass from breakup—May (Figure 4). Juvenile Chinook salmon represented <1% of interior Arctic grayling diets from breakup—May and August to September. Salmon eggs also contributed to Arctic grayling diets from August to September (14%). Interior Arctic grayling relied more heavily on juvenile chum salmon in mainstems (18% of the diet) than in sloughs (<1%), whereas Chinook salmon were only identified in stomachs of Arctic grayling sampled in sloughs (Figure 5).

Burbot in the interior region were highly piscivorous, consuming mostly whitefish, including humpback whitefish (*Coregonus pidschian*), round whitefish (*Prosopium cylindraceum*) and least cisco (*C. sardinella*), as well as Arctic grayling and Arctic lamprey (*Lethenteron camtschaticum*). Juvenile Chinook salmon made up a small fraction of burbot diets collected through the ice (<1%) and from breakup—May (2%; Figure 4). Chum salmon also made up a small proportion (<1%) of burbot diets from breakup—May. No juvenile salmon were identified in burbot diets collected during the remaining seasons; however, sample sizes were very low ($n = 2–3$ per season) due to our inability to sample diets nonlethally and permit limitations on lethal sampling. Reliance of burbot on juvenile salmon prey was greater in sloughs (6%) than in mainstem habitats (<1%; Figure 5).

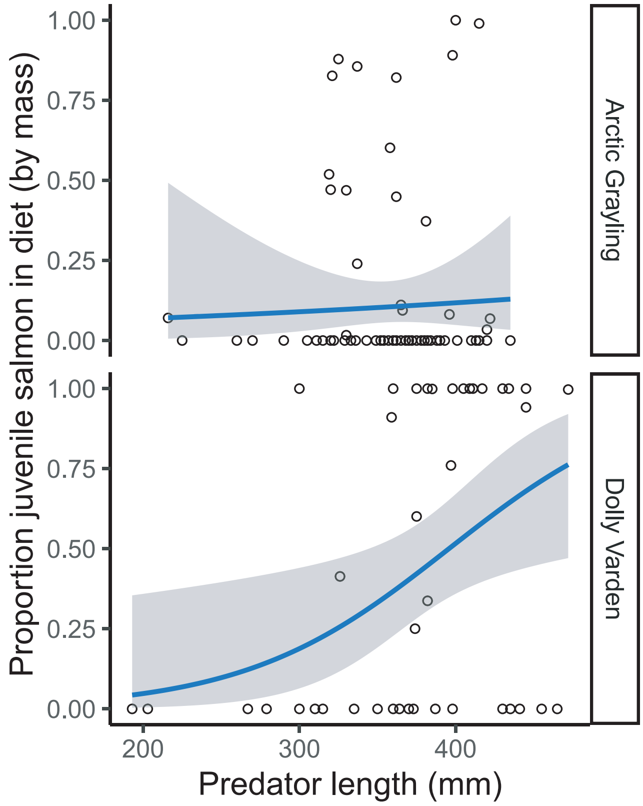

FIGURE 6 Size-based patterns of predation on juvenile salmon by Arctic grayling and Dolly Varden in the coastal region. Circles represent proportions by mass of juvenile salmon (all species combined) in the stomach contents of individual predators. Curves represent logistic regression fits, and shaded bands indicate 95% confidence intervals

Northern pike in the interior region were also highly piscivorous, consuming mostly whitefish, Arctic grayling, lamprey and other fish species, as well as small dietary contributions from juvenile Chinook and chum salmon. Birds, mammals and fish eggs also made up a large fraction of the stomach contents of some individual northern pike. Northern pike consumed both Chinook (4% of diet) and chum salmon (4%) from breakup—May, as well as Chinook salmon during June (< 1%) and August to September (<1%; Figure 4). Northern pike also relied heavily on salmon eggs (50%) during July. Juvenile salmon were identified only in diets of northern pike captured in sloughs, whereas salmon eggs were identified only in the diets of northern pike captured in mainstem habitats (Figure 5).

3.1.3 | Patterns of predation on Chinook salmon

Overall, we identified 14 individual juvenile Chinook salmon in the stomach contents of Arctic grayling, burbot and northern pike sampled in the interior region. The number of Chinook salmon prey per predator stomach was strongly associated with season and habitat (Table S3). The number of Chinook salmon per predator stomach was greatest during spring (breakup—May), with a secondary peak during August to September (Figure 4). During the open-water season, predator stomachs contained seven juvenile Chinook salmon during May (2–5 weeks after ice breakup), two during June and four during September. We also identified one Chinook salmon in the stomach of a burbot captured through the ice during March. Notably, 93% of Chinook salmon prey were identified in stomachs of predators captured in sloughs, including all of the prey consumed during the ice-free period (Figure 5).

Predator diets contained more Chinook salmon during a summer with very high streamflow than during a summer with lower streamflow, but any relationship between flow and predation was less evident at shorter time scales. During a very high-flow year (2014; median summer discharge = 2.8 SD above average) in the Chena River, we identified 12 Chinook salmon prey in 133 predator diets (0.1 Chinook salmon per diet). In contrast, during a year of slightly above-average flow (2015; median summer discharge = 0.6 SD above average), we identified no Chinook salmon prey in 167 predator diets (0 Chinook salmon per diet). Streamflow did not differ substantially between study years in the Yukon River, where two additional Chinook salmon prey were detected, so we restricted the interannual comparison to the Chena River. At the weekly time scale included in the statistical analysis, the best-supported model did not include an effect of streamflow; however, a model including streamflow also received substantial support from the data ($\Delta AIC_c = 1.82$; Table S3). In the second model, the effect of 7-day average streamflow was positive and large but highly uncertain: each one-standard-deviation increase in streamflow was associated with a 55% increase (± 80% SE) in the numbers of Chinook salmon prey per predator diet. On a daily timescale, a detailed graphical examination of predation timing with respect to streamflow indicated Chinook salmon were generally not detected in the stomachs of predators sampled at or near the peaks of high-streamflow events, but rather on the descending limb of the hydrograph, 2–23 days after the most recent peak flow (Figure 7).

3.1.4 | Habitat associations and predator-prey overlap

Juvenile Chinook salmon exhibited considerable habitat overlap with Arctic grayling, but little overlap with burbot and northern pike in the Chena River. Chinook salmon catch rates were greatest in the upper reach, 92% less on average in the middle reach and 99–100% less in the lower reach, in both mainstem and slough habitats (Figure 8). Arctic grayling were captured in all three reaches, and catch rates were greater in mainstem habitats than in sloughs (Figure 9). No Arctic grayling were captured in sloughs in the lower reach. In contrast, burbot and northern pike catch rates were greatest in sloughs in the lower reach. Burbot catch rates were 75% less on average in mainstem and tributary habitats in the lower reach, 91% less in sloughs in the middle reach and zero in all other habitat/

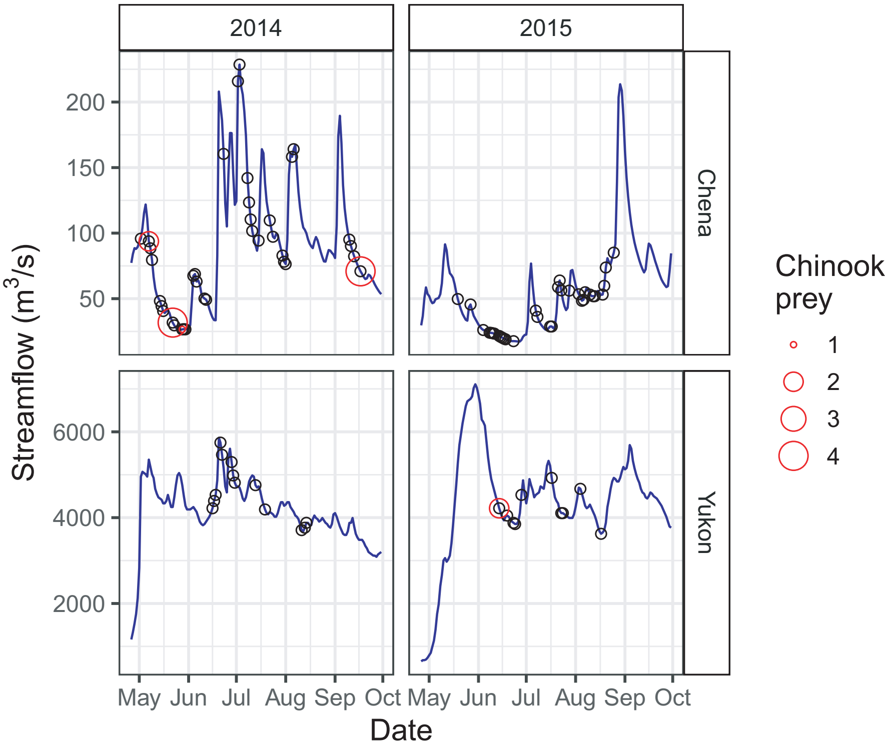

FIGURE 7 Predation on juvenile Chinook salmon with respect to streamflow in the Chena and upper Yukon rivers. Blue lines indicate daily mean discharge (U.S. Geological Survey, 2020). Chena River streamflow is shown as the mean of three gages for simplicity (station IDs 15514000, 15493700 and 15493000). Black circles represent predator diet sampling events, red circles represent Chinook salmon prey identified in diets, and circle size indicates the numbers of individual Chinook salmon in each stomach. Predators sampled through the ice before gages were operational are not shown

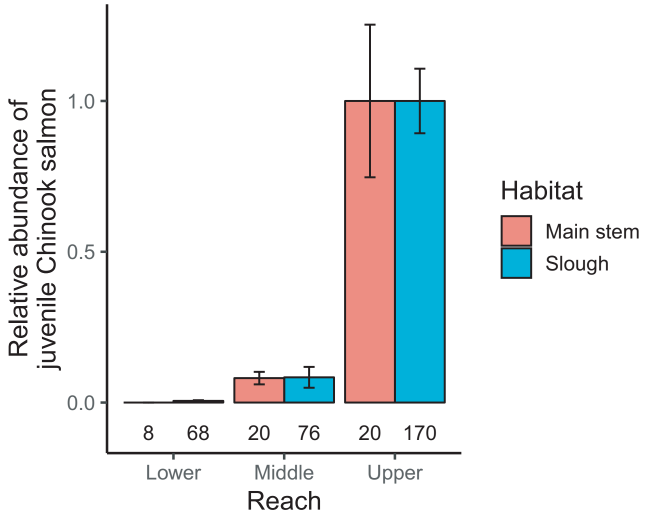

FIGURE 8 Relative abundance of juvenile Chinook salmon among reaches in the main stem and sloughs of the Chena River. Relative abundance was estimated in the main stem as mean counts in standardised minnow trap/snorkel surveys and in sloughs as catch per unit effort in minnow traps. Relative abundance in the upper reach was scaled to 1 in both habitats to facilitate comparisons among reaches within each habitat. Error bars represent +/− 1 SE. Numerals below *x*-axis indicate total effort (minnow trap/snorkelling sampling events or minnow trap sets)

reach combinations. Northern pike catch rates were 66% less in sloughs in the middle reach relative to sloughs in the lower reach and were zero in all other habitat/reach combinations. All catch rate differences reported here were strongly supported by the data (Tables S4 and S5).

4 | DISCUSSION

Here, we show that predation on juvenile salmon is patchy and episodic across a vast region that has experienced dramatic and sustained declines in salmon populations. In coastal rivers, Dolly Varden char fed heavily on juvenile pink, chum and occasional coho salmon before switching to focus on salmon eggs during late summer. In both coastal and interior rivers, Arctic grayling fed on juvenile pink and chum salmon during spring and early summer, and salmon eggs during late summer. These findings were consistent with prior studies of Dolly Varden char, which are well known to feed heavily on salmon eggs, carcasses and juveniles (Armstrong & Bond, 2013; Denton et al., 2010; Rinella et al., 2012), and to time their movements into streams to coincide with salmon spawning runs (Sergeant et al., 2015) in other regions. However, the high dietary reliance of Arctic grayling on salmon eggs and juveniles was surprising, because this species feeds predominantly on aquatic invertebrates even as large numbers of salmon spawn in Bristol Bay streams (Scheuerell et al., 2007). Arctic grayling in the AYK region may be able to capitalise on salmon resources more directly due to the absence of a competitor, rainbow trout (*O. mykiss*), which is abundant in salmon streams in more southerly regions.

Juvenile Chinook salmon were absent from the diets of piscivorous fishes in the coastal region and represented only a small fraction of the diets of Arctic grayling, burbot and northern pike in the interior region, at least at the locations and times that we sampled these predators. This may be partly due to the timing of our study during a major salmon population downturn. Chinook salmon spawning abundance was historically low throughout the AYK region during 2013 (Bell & Leon, 2018; Joint Technical Committee

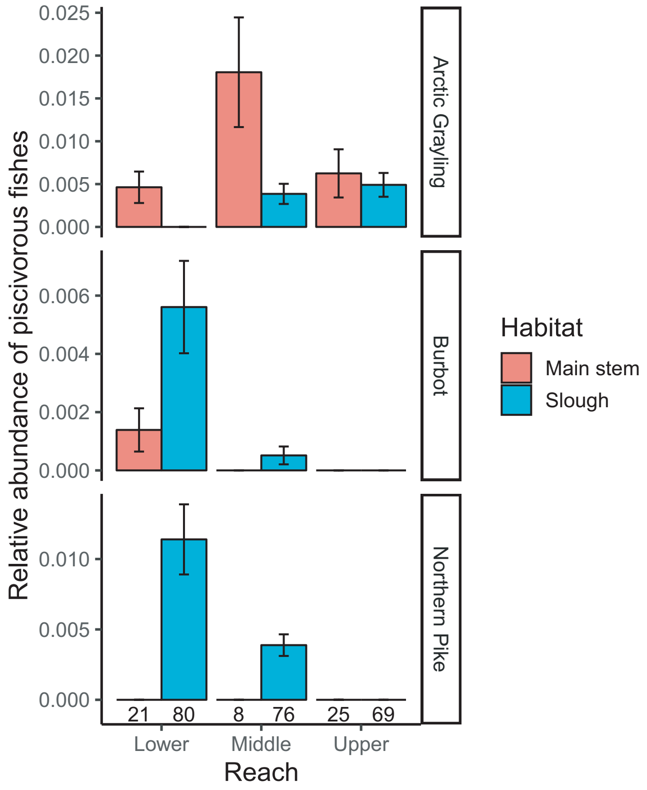

FIGURE 9 Relative abundance (catch per unit effort in hoop and fyke nets) of piscivorous fishes in the Chena River, broken down by reach and habitat type. Error bars represent +/− 1 SE. Numerals below *x*-axis indicate total effort (numbers of overnight sets). Predators captured by angling with hook-and-line are not shown

of the Yukon River U.S./Canada Panel, 2020), so juvenile Chinook salmon densities were likely unusually low during 2014, our first major field season. However, the following field season (2015) followed the relatively strong 2014 brood year, and surprisingly, we documented even less predation on juveniles in this cohort during summer 2015. Thus, the low density of juvenile Chinook salmon did not fully explain the rarity of predation. It is also possible that predators had already suppressed juvenile Chinook salmon numbers prior to our sampling bouts, giving the appearance of low predation rates. Despite the small number of Chinook salmon prey detected in this study, we observed important differences in predation among habitats and seasons.

The AYK region is vast and remote, and no study of this scale could quantify the full extent of piscine predation on salmon across the region. In particular, we sampled only a small number of inconnu, which have been documented to consume substantial quantities of juvenile Chinook salmon in other Yukon River tributaries (Alt, 1965). Inconnu are uncommon in the Chena River, but they are regularly caught by recreational fishers in the lower river during May, and their stomachs often contain Chinook salmon smolts (M. S. Wipfli, personal observation). The potential impact of avian predators such as common merganser is another important area for future study. While our study was not comprehensive, it revealed several clear patterns and provided a valuable step towards understanding how predation influences salmon in the region.

4.1 | Greater predation risk in sloughs

In the interior region, the data strongly supported the prediction that predator diets would contain more juvenile Chinook salmon in sloughs than in mainstem habitats. In fact, during the open-water season, predation was solely documented in sloughs. Interestingly, this pattern held for Arctic grayling, which were commonly captured in both habitat types, as well as for burbot and northern pike, which were primarily captured in sloughs. An important consideration with any diet study is whether predators consumed prey in the habitat in which they were captured. It is possible that predators consumed Chinook salmon in the mainstem habitats and then moved into warmer sloughs to digest before we captured them. Such behaviour has been observed among northern pike inhabiting off-channel habitats along the Upper Yukon River in Alaska (Randy Brown, U.S. Fish and Wildlife Service, personal communication) and Canada (Al von Finster, Yukon River Panel, personal communication) However, none of the predators we captured in mainstem habitats had Chinook salmon in their stomachs, so it is most likely that predation indeed occurred in sloughs. The recent establishment and spread of *Elodea* in a major slough of the lower Chena River could exacerbate predation risk by enhancing spawning and rearing habitat for northern pike and improving its efficiency at ambushing juvenile salmon (Carey et al., 2016). We did not observe *Elodea* at any sites where we documented predation on juvenile salmon; however, it is possible that the presence of *Elodea* in the general vicinity indirectly contributed to the patterns we observed by enhancing northern pike densities throughout the lower watershed.

Our findings suggest sloughs are risky habitats, but prior research shows they can also provide benefits relative to mainstem habitats, in terms of additional food resources and more optimal temperatures for growth, for Chinook salmon in the Chena River (Huntsman & Falke, 2019) as well as coho salmon in other systems (Armstrong & Schindler, 2013; Baldock et al., 2016; Rine et al., 2016). Thus, sloughs appear to offer a high-risk/high-reward habitat option, with the level of predation risk diminishing in higher gradient, cooler parts of the watershed. If this growth/predation risk trade-off is widespread, it may help to explain an apparent disparity in habitat use by juvenile Chinook salmon among Alaskan watersheds. Juvenile Chinook salmon rear in sloughs and low-gradient tributaries of other Alaskan rivers lacking northern pike, including the Taku (Murphy et al., 1989), Copper (Bidlack et al., 2014) and middle Susitna rivers (Rine et al., 2016), but they are rarely found in these habitats within the native or introduced range of northern pike, such as the upper Yukon (Daum & Flannery, 2012) or lower Susitna rivers (Sepulveda et al., 2013). The interacting effects of environmental conditions and predation risk on habitat selection and growth of juvenile salmon are an important area for future research.

Differential patterns of predation risk at the macrohabitat scale may have broader consequences for salmon distribution at the basin scale. Chinook salmon are distributed patchily throughout the vast AYK region, maintaining major spawning populations on only a small proportion of the available tributaries (Brown et al., 2017). Due to the well-established ability of Pacific salmon to colonise new habitats (Milner et al., 2000; Quinn, 2018), it seems unlikely that other tributaries remain unoccupied or sparsely occupied due to dispersal limitation. It is possible that a predatory gauntlet in the lower reaches of other potential spawning tributaries limits juvenile survival, and thus, that native predators such as northern pike limit the distribution of Chinook salmon to a fraction of the otherwise suitable habitat available in the AYK region. As the resolution and coverage of geospatial data improve in the region, this hypothesis could be examined using intrinsic potential models (Bidlack et al., 2014; Jalbert, 2021; Matter et al., 2018).

4.2 | Seasonal patterns of predation

Predation on juvenile salmon was highly seasonal in both regions. This was expected for juvenile pink and chum salmon, which only spend a brief period of days or weeks in their natal streams before migrating out to the ocean. Our findings were consistent with previous studies documenting the ephemeral, yet substantial subsidies pink and chum salmon provide to freshwater consumers through their eggs, juveniles and adult carcasses (e.g. Dunlop et al., 2021; Lowery & Beauchamp, 2015; Rinella et al., 2012). Recent work in the Unalakleet River shows that these subsidies also benefit juvenile Chinook and coho salmon at the watershed scale, through enhanced body size, growth and condition (Joy et al., 2021).

Interestingly, predation on Chinook salmon also had a strong seasonal component, even though juvenile Chinook are continuously present in natal streams in our study area, with each cohort rearing for one year before migrating out as smolts. Although the sample size was small, predation on Chinook salmon in the Chena River was detected disproportionately during May, when salmon fry move into their summer rearing habitats and smolts migrate to the ocean, as well as September, when parr move into overwintering habitats. Predation was also documented in the upper Yukon River during mid-June, when juvenile Chinook salmon migrate downriver from natal streams in Canada into Alaskan rearing habitats (Bradford et al., 2008; Daum & Flannery, 2012). No predation was documented in either river between late June and August, the core of the summer rearing season, despite substantial sampling effort. Together, these results suggest that juvenile salmon are more vulnerable to predation during periods of seasonal movement than during the rearing season.

The smolt outmigration can be a period of very high salmon mortality, in some cases comparable to or greater than the mortality experienced during the early marine period (Furey, Hinch, Bass, et al., 2016; Rechisky et al., 2018). In the AYK region, evidence from spawner-recruit studies indicates environmental conditions experienced during the smolt life stage have a strong influence on the population productivity of Chinook salmon. In particular, later river ice breakup during the year of the smolt outmigration is strongly associated with reduced population productivity of Chinook salmon (Cunningham et al., 2018; Ohlberger et al., 2016). The mechanism for this effect is unknown; it may involve a mismatch in the timing of ocean entry with respect to the spring bloom in the Bering Sea, or it could be related to mortality experienced during the smolt outmigration, which can involve distances exceeding 3000 km in the Yukon River Basin. Smolt ecology is not well understood in most of Alaska due to logistical challenges of sampling during river ice breakup. We dealt with these challenges by engaging with subsistence and recreational fishers, who donated stomachs from predators caught before, during and immediately after breakup. We found relatively little evidence of predation before breakup: only a single juvenile Chinook salmon prey was consumed by a burbot captured through the ice. The ecology and mortality rates of salmon smolts during their outmigration are important areas for future study, which could be productively addressed with a combination of tagging studies and additional predator sampling by citizen scientists.

4.3 | Streamflow and predation risk

Our data provided only weak support for the prediction that predator diets would contain more Chinook salmon during periods of higher streamflow. A simple annual comparison was entirely consistent with this prediction. Strikingly, all predation on Chinook salmon in the Chena River was documented during an extremely high-flow year (2014), despite greater predator sampling effort during the following year (2015), which had substantially lower flows. However, most of the predation during the high-flow year took place before the onset of anomalously high flows in mid-June (Figure 7). Rather than due to flow per se, the difference in observed predation between years might be an artefact of a more compressed sampling schedule during the lower-flow year (2015), when we sampled fewer predators during May and none during September due to logistical constraints. After accounting for other factors, including habitat and season, the statistical model indicated some support for increased predation risk when flows during the previous week were greater, but this effect was highly uncertain. Finally, a detailed examination of the timing of predation events did not indicate any clear relationship with recent changes in flow. Together, this evidence suggests that any relationship between streamflow and predation risk is more likely driven by longer-term than shorter-term flow patterns.

Although this study provided only limited evidence for a direct link between high flows and greater predation risk, more recent field observations do suggest that juvenile Chinook salmon move from mainstem rearing habitats into off-channels during summers with sustained high-flow conditions. During a recent period of very low flows on the Chena River (May–July 2019), Chinook salmon densities and catch rates were very high in mainstem habitats such as logjams. In contrast, during a rainier summer (2020) with higher flows, very few Chinook salmon were observed or captured in the same mainstem habitats. Instead, large numbers of Chinook salmon were observed and captured in nearby sloughs (E. R. Schoen, unpublished data). In combination with the findings from the current study that vast majority of predation was documented in sloughs, these observations support the hypothesis that extended high-flow periods induce juvenile Chinook salmon to redistribute into sloughs, where they face greater predation risk, thereby reducing their survival. This hypothesis deserves further study, potentially by tracking movements of juvenile salmon and predators in response to streamflow using PIT tags.

4.4 | Inferring interaction strengths from diet and distribution

Although juvenile Chinook salmon made up only a small fraction of predator diets in the interior region, this does not necessarily imply that predation impacts on Chinook salmon populations were weak. In fact, very strong predation interactions can result in low proportions of preferred prey in predator diets, due to prey being functionally extirpated from a given habitat (Paine, 1980). In contrast, if predation interactions are weaker, the prey can persist and make up a larger proportion of predator diets. For example, introductions of northern pike to southcentral Alaska were associated with the collapse of Chinook salmon and other salmonid populations in low-gradient Alexander Creek, whereas salmonids remained abundant in the nearby Deshka River, presumably due to its greater habitat heterogeneity (Dunker et al., 2018). Juvenile salmon made up a much smaller fraction of northern pike diets in heavily impacted Alexander Creek than in the Deshka River, where the predation interaction was presumably weaker (Sepulveda et al., 2013). Northern pike exhibit remarkable trophic plasticity, allowing them to persist on invertebrate prey while maintaining high predation impacts on rare, preferred prey such as salmonids (Cathcart et al., 2019). In sloughs adjacent to the upper Yukon and lower Chena Rivers, we never caught Chinook salmon in minnow traps, but we did find them in predator stomachs. These dietary and distributional patterns are consistent with strong predation pressure functionally extirpating juvenile Chinook salmon from sloughs along low-gradient river reaches.

In contrast, Arctic grayling were relatively abundant throughout the Chena River watershed and overlapped substantially with Chinook salmon. In this case, the small proportion of Chinook salmon in their diets is more consistent with a weak predation interaction. In particular, we did not identify any Chinook salmon in the diets of Arctic grayling captured in mainstem habitats, although we often observed these species drift feeding in close proximity to one another within the same eddies, log jams and alcoves. Neuswanger et al. (2015) proposed that Arctic grayling may be more likely to consume juvenile Chinook salmon when they enter the drift, potentially in response to increasing streamflow. Arctic grayling can be piscivorous in other circumstances, feeding heavily on pink and chum salmon fry and other fish in this study, and ninespine stickleback on Alaska's Arctic Coastal Plain (McFarland et al., 2018). As far as we are aware, our study is the first to document predation by Arctic grayling on Chinook salmon (see Neuswanger et al., 2015). However, the scarcity of Chinook salmon in diets despite considerable habitat overlap suggests Arctic grayling do not interact strongly with Chinook salmon in mainstem habitats in Interior Alaska.

4.5 | Implications for habitat restoration and fisheries management

The piscivorous fish species we sampled are harvested in subsistence and recreational fisheries in the AYK region, suggesting their predation impacts on salmon could be influenced by changes in human harvest. Traditional ecological knowledge supports an important link between human harvest of piscivorous species and their predatory impacts on salmon. Subsistence harvest of piscivores likely declined substantially in the AYK region between the 1960s and 1980s, after snowmobiles replaced dog teams as the primary mode of winter transportation, thereby reducing the need for fish as a source of dog food (Alt, 1987). Following this transition, local residents have raised concerns about whether greater densities of piscivores including Dolly Varden char (locally known as “trout”), northern pike and inconnu have increased the predation mortality rates of juvenile salmon (Raymond-Yakoubian & Raymond-Yakoubian, 2015; Raymond-Yakoubian, 2009). Our diet study represents one step towards estimating how much changing harvest patterns may have affected predation rates. The linkages between human harvest, food web interactions and salmon populations are an important area for further study.

Although the AYK region is pristine relative to many more southerly systems, human development does influence many salmon-bearing watersheds, and thus, localised habitat restoration is an important activity. An important role for scientists is to help determine what types of restoration projects in what locations are most likely to benefit salmon, now and in the future. In particular, the Chena River is the focus of active restoration programmes led by government agencies and nonprofit organisations, due to its large Chinook salmon population and its urban location, flowing through Fairbanks, the largest city in the region. Recent habitat modelling studies suggest that the lower Chena River watershed could potentially provide high-quality rearing conditions for juvenile Chinook salmon, based on its underlying geomorphology (Matter et al., 2018) and its relatively warm thermal regime (Falke, Huntsman, et al., 2019). However, juvenile Chinook salmon densities are currently very low in this reach. This might be explained by the low density of large woody debris in the main stem (Falke, Cathcart, et al., 2019), bank armouring or other effects of urban development (Tanana Valley Watershed Association, 2015).

Our findings suggest that high predation risk, especially in sloughs, may also be an important factor reducing the value of the lower watershed for salmon habitat below its potential value based solely on abiotic factors. Thus, restoration of mainstem rearing habitats and removing *Elodea* from sloughs may be more beneficial for juvenile Chinook salmon than improving connectivity of sloughs and other off-channel habitats in low-gradient reaches such as the lower Chena River. Sloughs in this reach could represent ecological traps, appearing suitable to juvenile Chinook in terms of physical habitat structure, thermal regime and food availability, but also exhibiting elevated predation risk. Alternatively, improving off-channel habitat connectivity in the upper watershed, for example through culvert upgrades, might allow salmon to access sloughs with a more beneficial balance of risk to reward.

Like high-latitude regions around the world, the AYK region is changing rapidly. The changing climate and landscape affect species directly and also influence how they interact in food webs. For example, warming water temperatures are likely to enhance the distribution, density and predation impacts of northern pike, whose consumption rate peaks at roughly 25°C (Bevelhimer et al., 1985). In contrast, juvenile salmon are likely to benefit little or suffer outright harm when warming temperatures exceed 15°C (Beauchamp, 2009; Jones et al., 2020). Due to this physiological asymmetry, even modest warming within their thermal tolerance might cause salmon to become locally extirpated from habitats where northern pike are abundant (Dunker et al., 2018), as has been projected for brown trout (*Salmo trutta*) in half of the Swedish lakes where they currently co-occur with native northern pike (Hein et al., 2014). Such climate-mediated food web interactions can cause the realised effects of climate change on aquatic communities to differ substantially from the predictions of single-species climate impact models (Gilman et al., 2010; Zillig et al., 2021). Incorporating predation risk into fisheries management and habitat restoration decisions may help to facilitate the conservation and recovery of highly valued species and the resilience of fisheries.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

ES and MW conceived and designed the investigation. KS, ES, RI, AL, BM and MW performed field and/or laboratory work. ES, KS, AL and BM analysed the data. ES, KS and MW wrote the paper.

DATA AVAILABILITY STATEMENT

Our data and code have been publicly archived on the Knowledge Network for Biocomplexity: https://doi.org/10.5063/KK996D.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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