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Trophic pathways supporting juvenile Chinook and coho salmon in the glacial Susitna River, Alaska: patterns of freshwater, marine, and terrestrial food resource use across a seasonally dynamic habitat mosaic

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Abstract

Contributions of terrestrial, freshwater, and marine-derived prey resources to stream fishes vary over time and space, altering the energy pathways that regulate production. In this study we determined large-scale use of these resources by juvenile Chinook and coho salmon (*Oncorhynchus tshawytscha* and *O. kisutch*) in the glacial Susitna River, Alaska. We resolved spatial and temporal trophic patterns among multiple macrohabitat types along a 97-km segment of the river corridor via stable isotope and stomach content analyses. Juvenile salmon were largely supported by freshwater-derived resources, and secondarily by marine and terrestrial sources. The relative contribution of marine-derived prey to rearing salmon was greatest in the fall within off-channel macrohabitats, whereas the contributions of terrestrial invertebrate prey were generally greatest during mid-summer, across all macrohabitats. No longitudinal (upstream-downstream) diet pattern was discernable. These results highlight large-scale spatial and seasonal patterns of energy flow and the dynamic interplay of pulsed marine and terrestrial prey subsidies to juvenile Chinook and coho salmon in a large, complex, and relatively pristine glacial river.

Introduction

Riverine landscapes are complex assemblages of dynamic habitats, wherein aquatic consumers receive energy and nutrients from a number of ecologically distinct sources (Polis et al. 1997). Salmon-bearing river systems are a particularly compelling example, where high quality resource pulses derived from spatially coupled riparian and marine ecosystems can supplement those produced within freshwater environments. Large-scale distribution of these food resources across space and time has the potential to affect stability, diversity, and overall productivity of river food webs (Wipfli et al. 1998; Bellmore et al. 2015; Richardson and Sato 2015), however most river food web studies have been conducted at relatively fine scales that do not account for the seasonal and spatial variability inherent in free-flowing systems.

On a broad landscape level, the availability of prey and their contributions to stream consumers may be governed by the spatial distribution of diverse habitats and by seasonal changes in abundance (Nakano and Murakami 2001). At higher latitudes, pronounced seasonal fluctuations produce markedly pulsed life history patterns that can translate to episodes of increased food resource availability (Yang et al. 2008). Both freshwater and terrestrial invertebrate abundance can show high seasonal variability within stream reaches. In temperate streams along the Pacific Rim, these prey resources can exhibit temporally offset peaks in availability and use by fishes, with the greatest influence of freshwater invertebrates often occurring in late winter through early summer, followed by terrestrial invertebrates during mid- to late-summer (Wipfli 1997; Nakano and Murakami 2001). Likewise, seasonal migrations of anadromous salmon during early summer through autumn deliver a pulse of high quality nutrients and energy to stream food webs that can increase productivity beyond in-situ background levels (Kline et al. 1990; Chaloner and Wipfli 2002).

The arrangement of diverse habitats within riverine landscapes can produce additional variability in food resource contributions to consumers at multiple spatial scales. In their River Continuum Concept, Vannote et al. (1980) proposed that food webs vary predictably among reaches along a large-scale, upstream-to-downstream continuum. In support, Doucett et al. (1996) used stable isotope analyses to show that downstream Atlantic salmon (*Salmo salar*) populations derived less dietary carbon from terrestrial sources than fish in headwaters. Alternatively, food webs within habitats in close proximity can exhibit more unique properties relative to each other than to those at greater distances upstream or downstream (Poole 2002; Stanford et al. 2005; Thorp et al. 2006). For example, adult female salmon can superimpose their nests when spawning habitat is limited, releasing previously buried eggs in the process (Fukushima et al. 1998). Consequently, even small increases in adult salmon density beyond a certain threshold can drive disproportionately large increases in egg availability and consumption by stream fishes (Moore et al. 2008). In such cases, a patchy distribution of high quality spawning habitat across the river network could overwhelm any longitudinal patterns in resource availability (Wipfli and Baxter 2010). The trophic ecology of fish in relation to complex riverine landscapes has gained some attention (see Bellmore et al. 2015; Costas and Pardo 2015), but empirical studies at large spatial scales are rare.

Many major salmon runs occur in glacially influenced rivers (Dorava and Milner 2000; Augerot 2005; ADF&G 2013), which differ in hydrology and ecology from the temperate snowmelt- and precipitation-dominated systems where the majority of riverine food webs studies have been concentrated. In contrast to these snowmelt/precipitation-dominated regimes where discharge generally peaks in both spring and late fall, peak glacial melt typically occurs during mid-summer with higher air temperatures (Milner and Petts 1994). Before and after the peak

glacial melting period (early spring and late fall, respectively), relatively benign flows and lower turbidity create “windows of opportunity” for benthic algal and macroinvertebrate production, when standing stocks are typically higher (Uehlinger et al. 1998; Burgherr and Ward 2001; Milner et al. 2009). The effect of suspended sediment on benthic communities could control the contribution of freshwater-derived carbon to stream fishes in glacial habitats (Lloyd et al. 1987; Perry et al. 2003), but this process has not been directly compared across multiple glacial and non-glacial (sloughs and tributary mouth) habitats within a system.

As generalist predators, juvenile Pacific salmon (*Oncorhynchus* spp.) are known to capitalize on ephemeral pulses of high quality allochthonous prey (Wipfli 1997; Bilby et al. 1998) in order to maximize their energy intake and growth, and potentially gain a survival advantage before facing size-selective mortality during subsequent life stages (Henderson and Cass 1991; Pearcy 1992; Thompson and Beauchamp 2014). While many studies have quantified the importance of each of these resources to stream salmonids at smaller scales (e.g., Nielsen 1992; Bilby et al. 1998), less is understood about the emergent patterns of resource use over broad temporal scales and across complex riverine landscapes (Fausch et al. 2002; Wipfli and Baxter 2010). Given the cultural and economic impacts of recent fluctuations in Pacific salmon populations in large rivers (NRC 2004; ADF&G 2013), there is a need to more thoroughly understand spatial and temporal variability in the trophic relationships that support their production during the freshwater phase, to put into context how the metapopulation might respond to limitations in any one food resource.

In this study, we investigated how relative contributions of freshwater, terrestrial, and marine-derived food resources to juvenile Chinook and coho (*O. tshawytscha* and *O. kisutch*) salmon vary within a 97-km section of the large, glacial Susitna River in southcentral Alaska,

U.S.A. Specifically, we addressed variability of these resource contributions both spatially, across different macrohabitat types positioned along the river corridor, and temporally, from June to October, 2013-2014. We accomplished this through Bayesian stable isotope diet modeling and stomach content analyses. In addition, we applied a broad-scale $\delta^{13}\text{C}$ analysis to characterize the relative contributions of instream and terrestrial carbon sources to freshwater invertebrate primary consumers. This supplementary analysis was intended to provide additional context for energy and nutrient flow at the base of food webs in the Susitna River, further clarifying resource contributions to fish production.

This research was implemented as a baseline study for the possible construction of a large hydroelectric dam in the upper section of the river and may be used to assess how flow regulation affects downstream trophic processes supporting salmonids. By quantifying contributions of multiple trophic pathways to juvenile salmon across a complex, seasonally dynamic, and relatively pristine glacial river, we aimed to take an important step toward integrating food web and landscape ecology, with implications for improved management of salmon stocks within similar systems.

Methods

Study area

Field sampling took place in 2013 and 2014 on the Susitna River in southcentral Alaska. This 504-km river drains a 52,000-km² catchment headed by several glaciers in the eastern Alaska Range and flows southwest into the Cook Inlet west of Anchorage (Fig. 1). The river has a characteristic glacial melt and snowmelt hydrological regime with low flows and ice cover in winter, peak flow during snowmelt in late May and June, and sustained flows from glacial runoff

throughout summer. Main channel discharge at river kilometer 225 (from the river mouth) peaked on June 2nd ($2,568 \text{ m}^3 \text{ s}^{-1}$) in 2013 and on June 27th ($1,206 \text{ m}^3 \text{ s}^{-1}$) in 2014.

A total of 16 sampling sites were located within four reaches between 129 and 298 river kilometers. Within each reach we selected sites within the glacial-fed main channel and side channel macrohabitats, and one of several predominant off-channel macrohabitats - tributary mouth, side slough, or upland slough (i.e., springbrook) - depending on the reach (Table 1; AEA 2014). The uppermost reach (Reach 4) at river kilometer 296 was located within an approximately 238-m wide bedrock-bounded canyon and contained a main channel, side channel, and tributary mouth sampling site. A set of Class VI rapids, known as “Devils Canyon”, between river kilometer 241 and 259 differentiated this upstream reach from those below it by creating a migration barrier for the majority of anadromous salmon (LGL and ADF&G 2014). Too few juvenile salmon individuals ($n = 3$) were captured within this reach for analysis, so we excluded this reach from further consideration in analyses. The next reach downstream (Reach 3) at river kilometer 227 was located in a wider canyon segment that averages 716 m in width and contained a main channel, side channel, tributary mouth, and upland slough sampling site (Fig. 1). At river kilometer 167, Reach 2 was located within a primarily single-channel floodplain with numerous interconnected off-channel habitats, and had an average active channel width of 344 m. Here, we sampled within a main channel, side channel, tributary mouth, side slough, and upland slough site (Fig. 1). At river kilometer 130, Reach 1 was the study section closest to the river mouth and was located in the highly braided floodplain below the confluence of the Susitna, Chulitna, and Talkeetna Rivers, where the average active width was 951 m. This reach contained a main channel, side channel, tributary mouth, and upland slough site (Fig. 1). To characterize seasonal variation in juvenile salmon diets, we sampled macrohabitats located within each study

reach three times during the open-water period, and designated these periods as spring, summer, and fall (Table 2). Logistical difficulties in 2013 precluded sampling at all study sites during all seasons, however all study sites were sampled in 2014. For this reason, we focused the majority of our analysis on the 2014 sampling year.

Sample collection and preparation

To elucidate large-scale patterns of energy flow to juvenile salmon and primary consumer invertebrates, we collected samples from juvenile Chinook and coho salmon, freshwater and terrestrial invertebrates, and basal carbon sources (periphyton and terrestrial organic matter) for stable isotope analysis (AEA 2014). Freshwater periphyton and terrestrial organic matter (OM) are considered basal resources for aquatic invertebrates (Finlay 2001). We collected three composite periphyton samples per site for stable isotope analysis by brushing the surfaces of five submerged rocks and rinsing with distilled water, then subsequently freezing samples within six hours of collection. We obtained a total of five terrestrial organic matter and invertebrate samples, both from the stream benthos and from the water column (AEA 2014). Benthic samples were collected either with a Hess sampler (250- μ m mesh) when flow was sufficient, or otherwise with a 250- μ m mesh kick net. Seston samples were collected by partially submerging two drift nets (250- μ m mesh) for a period of 45 min to 3 hr when flow was sufficient (AEA 2014). At sites with little or no flow, we collected seston samples by actively moving a 250- μ m net at the surface of the water until enough mass was obtained for stable isotope analysis. We opportunistically obtained spawning salmon carcasses and eggs when they were present to represent marine-derived food sources. If a salmon carcass was reasonably fresh, we excised 2 - 5 g of white muscle tissue. Salmon eggs were stored whole. Because freezing samples was not

possible at these remote sites, we preserved all OM, invertebrate, and marine-derived samples on site in 70% ethanol. The effects of ethanol preservation on stable isotope values have shown mixed results across recent studies, however most reported negligible shifts in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values relative to dried or frozen samples (Feuchtmayr and Grey 2003; Syväranta et al. 2008), especially if the solution did not exceed 70% ethanol (Gloutney and Hobson 1998; Barrow et al. 2008).

To determine juvenile Chinook and coho salmon food sources, we obtained both stomach content and stable isotope samples for use as integrated datasets in a Bayesian stable isotope mixing model. At each site, we aimed to sample eight juvenile Chinook and eight juvenile coho salmon measuring 50 mm fork length or greater, but sometimes fewer fish were collected when abundance was low (AEA 2014). We used a variety of active and passive fish capture methods across macrohabitat types, which included beach seining, backpack electrofishing, and deploying fyke nets and minnow traps. Fish were anesthetized with a clove oil-ethanol solution or AQUI-S 20E® (AquaTactics Fish Health) immediately before sampling. Once individuals began to lose equilibrium, we measured mass and fork length and obtained stable isotope samples from fish by excising a 1-3 cm² portion of the lower caudal fin lobe (Hanisch et al. 2010), then subsequently placed samples in Eppendorf tubes with 70% ethanol. We sampled caudal fin tissue for stable isotope analysis because it is a rapidly regenerating tissue (Hanisch et al. 2010) with a relatively fast turnover time of approximately 13 days for small salmonid fry (Heady and Moore 2013). We used a modified syringe (Culp et al. 1988) to sample stomach contents by non-lethal gastric lavage (stomach flushing) and stored stomach content samples in 70% ethanol to be later enumerated in the laboratory. Once sampling was complete, we allowed fish to recover and released them near their point of capture.

216

217 *Laboratory methods*218 Stable isotopes

219 We rinsed, dried (at least 72 hrs at 60° C), and ground all tissue into a homogenous
220 powder for stable isotope analysis. In preparation, we thawed and filtered periphyton samples
221 and removed invertebrates and other visible contaminants, then fumed periphyton samples in
222 HCl for 4 hrs to remove any carbonates originating from rock substrates (Harris et al. 2001). We
223 examined benthic and seston samples under a dissecting microscope and removed invertebrates,
224 and identified them to a taxonomic level necessary to distinguish between freshwater and
225 terrestrial origin following Merritt et al. (2008). We further identified and separated aquatic
226 invertebrates into functional feeding groups (collectors, grazers, predators, and shredders) to
227 resolve energy flow pathways from basal food web carbon sources (Merritt et al. 2008). After
228 drying and grinding but before analysis, we treated invertebrate, salmon carcass, and egg
229 samples with a 2:1 chloroform-methanol solution to standardize lipid content across a wide range
230 of tissue types as well as invertebrate body sizes and species (Sotiropoulos et al. 2004; Post et al.
231 2007).

232 We weighed one subsample from each sample on a micro-analytical balance (readability
233 = 0.001 mg) and placed them into tin capsules at the Alaska Stable Isotope Facility (University
234 of Alaska Fairbanks). All samples were analyzed via combustion using an elemental analyzer
235 (Costech Analytical) interfaced to an isotope ratio mass spectrometer (DeltaV^{plus} CF-IRMS,
236 Thermo Fischer LLC) in continuous flow mode, and determined mean analytical precision using
237 laboratory standards (Sigma Chemical; mean $\delta^{15}\text{N}$ = 6.95‰ and mean $\delta^{13}\text{C}$ = -15.82‰), which
238 was 0.11‰ for $\delta^{15}\text{N}$ and 0.05‰ for $\delta^{13}\text{C}$.

Juvenile salmon stomach content samples

We identified invertebrate prey items encountered in fish stomach samples to family and life stage (larva, pupa, adult) if possible following Merritt et al. (2008), and by origin (freshwater or terrestrial, with winged stages of aquatic insects classified as freshwater prey). We identified prey fish to the lowest possible taxonomic level, and measured the length (mm) of intact prey items directly. We estimated total length for partially digested prey based on intact items of the same taxon that appeared similar in size, or via the weighted average of lengths of that taxon in the same sample, site, macrohabitat, reach, or season (AEA 2014).

Statistical analyses

Freshwater invertebrate energy sources

We used multiple linear regressions to determine the overall role of terrestrial OM and freshwater periphyton in the diets of the invertebrate collector, grazer, and shredder invertebrate groups. Periphyton $\delta^{13}\text{C}$ can be highly variable within even small reaches and can often overlap with that of terrestrial OM (Finlay 2004), however stable isotope mixing models require distinct endmembers to determine precise dietary contribution estimates. Therefore, using site-specific mixing models to estimate resource contributions of periphyton and terrestrial OM to invertebrate consumers would likely produce unacceptable error in many cases.

Instead, we determined the overall, relative contributions of freshwater algae (periphyton) and terrestrial OM to invertebrate primary consumers using a gradient method, based on patterns of spatial variability in source and consumer $\delta^{13}\text{C}$ (Finlay 2001; Bunn et al. 2003; Rasmussen 2010; Jardine et al. 2014). To quantify energy pathways supporting aquatic invertebrates, we

performed multiple linear regressions between site-specific mean $\delta^{13}\text{C}$ values of primary consumer feeding groups (collectors, grazers, and shredders) and site-specific mean $\delta^{13}\text{C}$ values of their potential food sources (periphyton and terrestrial OM) collected from all locations. Sample material from some consumer feeding groups was limited or not available at certain sampling events, so we pooled all consumer $\delta^{13}\text{C}$ values across seasons. Each data point in the regressions therefore represents the mean $\delta^{13}\text{C}$ value of a consumer group and source collected from a particular site across all seasons in which sample material was available. Because isotopic discrimination of organic carbon from diet to consumer in aquatic organisms is generally small (0.4 – 0.9‰, Vander Zanden and Rasmussen 2001; Post 2002), a slope coefficient close to 1 and a high r^2 value indicates a relatively strong reliance on a particular food source (Finlay 2001; Rasmussen 2010; Jardine et al. 2014).

Prior to conducting analysis on basal carbon sources, we evaluated possible cross-contamination between periphyton and terrestrial OM by comparing their C:N molar ratios with those reported in literature sources. Periphyton C:N typically ranges from 8 (Thorp et al. 1998) to 12 (Wetzel 1983) and terrestrial OM (soil organic matter and terrestrial plants) C:N ranges from 8 to > 50 (Finlay and Kendall 2007) with a mean value of 20 (Sterner and Elser 2002). Both the periphyton and terrestrial OM C:N aligned well with those distributions (mean $\text{C:N}_{\text{periphyton}} = 8.7 \pm 2.8 \text{ SD}$; mean $\text{C:N}_{\text{OM}} = 29.8 \pm 9.4 \text{ SD}$), suggesting these sources were sufficiently represented.

Additionally, we addressed the possibility that periphyton and freshwater invertebrates assimilated marine-derived nutrients (MDN) from spawning salmon via uptake of dissolved nutrients and consumption, respectively (Wipfli et al. 1998; Hicks et al. 2005; Heintz et al. 2010). Because MDN generally show elevated $\delta^{15}\text{N}$ values relative to freshwater biota, we used non-

parametric Kruskal-Wallis analysis of variance tests to compare the $\delta^{15}\text{N}$ values of periphyton and freshwater invertebrates collected where spawning salmon carcasses were present with those where carcasses were absent. Alpha was set to 0.05 ($\alpha = 0.05$).

Juvenile salmon stomach contents

We calculated the composition of freshwater, marine, and terrestrial diet items as well as the most common invertebrate taxa in stomach samples as diet proportions by dry mass (% mean mass), the most applicable metric for energy flow and food web studies (Chipps and Garvey 2007). We determined terrestrial and freshwater invertebrate dry mass using the allometric formula:

$$W = aL^b, \quad (1)$$

where W is the total dry body mass, L is the total body length, and a and b are the constants of the regression between W and L (Ricker 1973). We derived length-mass regression constants a and b from the literature (Rogers et al. 1976, 1977; Smock 1980; Benke et al. 1999; Johnston and Cunjak 1999; Sabo et al. 2002) and from Alaskan stream invertebrates (M. Wipfli, unpublished data). We also used length-mass relationships to estimate the wet mass for prey fish using taxon-specific length and mass measurements (AEA 2014) as well as for salmon eggs using published values (Fleming and Ng 1987). We then used the resulting wet mass of prey fish and salmon eggs to estimate dry mass using percent dry mass values of 24.9% for *Oncorhynchus* spp., 22.5% for sculpins, and 40% for fresh salmon eggs (Ashton et al. 1993; Brey et al. 2010).

Isotopic evidence for site fidelity

Stream fishes may relocate to alternate habitats across the river network in order to find more favorable conditions (Armstrong et al. 2010; Daum and Flannery 2011). Before running diet models, we used stable isotope analysis to investigate the assumption required by this study, that juvenile salmon showed evidence of site fidelity and use of local food sources. To do this, we examined juvenile salmon $\delta^{15}\text{N}$ vs. $\delta^{13}\text{C}$ and invertebrate prey signatures graphically to determine whether salmon showed distinct signatures among macrohabitats in each reach (suggesting some level of site fidelity), or if all salmon sampled within a reach had similar signatures (suggesting widespread movement among habitats). In addition, we evaluated differences in the mean $\delta^{13}\text{C}$ values of invertebrates and juvenile salmon within each macrohabitat type using a nonparametric Kruskal-Wallis test ($\alpha = 0.05$).

Juvenile salmon diet models

We estimated the relative contributions of freshwater, marine, and terrestrial prey to salmon diets from stable isotope and stomach content data using the Bayesian stable isotope mixing model, MixSIAR (Stock and Semmens 2013). This model uses isotopic values of consumers, prey, and trophic enrichment factors as model inputs to estimate the probability distributions of multiple prey contributions to consumers while accounting for the observed variability in consumer, prey, and trophic enrichment isotopic values (Stock and Semmens 2013). The model also allows the incorporation of prior information from another dietary dataset (i.e., stomach content data) to further refine estimates of prey contributions to a consumer (Moore and Semmens 2008; Parnell et al. 2010). We ran models both with and without informative priors to evaluate the degree of influence the stomach content data had on posterior diet estimates. We ultimately used estimates from the informed models to mitigate biases of these two methods and

to obtain more precise estimates when isotope data were relatively weak (Moore and Semmens 2008). We calculated prior values separately for each sampling event by multiplying the diet proportion of each prey type (freshwater, terrestrial, or marine) by the sample size of non-empty stomachs. Correlations between posterior estimates of diet proportions were reported for diagnostic purposes as Pearson's product-moment correlation coefficients (r).

To select appropriate trophic enrichment factors (TEF; Δ) for diet modeling, we qualitatively evaluated consumer isotopic signatures relative to those of the potential prey after adjusting for TEF values from four different literature sources that were based primarily on data from aquatic consumers (Vander Zanden and Rasmussen 2001; Post 2002) or specifically from salmonids (McCutchan et al. 2003; Trueman et al. 2005). We plotted consumer values against those of prey adjusted for each of the sets of TEF values separately to determine if consumer values were within mixing polygons (Parnell et al. 2010). We ultimately chose values from Post (2002) (0.4 ± 1.3 for $\Delta^{13}\text{C}$ and 3.4 ± 1.0 for $\Delta^{15}\text{N}$) because the majority of plots showed that consumers fell within mixing polygons.

To compare salmonid diets among macrohabitat types, seasons, and reaches, we ran unique informed diet models for each sampling event where juvenile salmon were caught and organized the resulting estimates graphically in order to detect dietary patterns. Although MixSIAR allows for up to two covariates and a nested design template, the current version does not simultaneously allow for multiple sets of informative priors to be defined for specific consumer groups; therefore, at the expense of further quantifying variation between consumer groups, we chose to run separate models for each consumer group in order to more specifically define informative priors from stomach content data of each group. When Chinook and coho individuals were caught in the same sampling site, we pooled the two species in the diet model to

reduce the number of variables in the models and to simplify interpretation of large-scale diet patterns. Overall, mean $\delta^{13}\text{C}$ values of all freshwater invertebrate functional feeding groups (collectors, grazers, shredders, and predators) were not significantly different (Kruskal-Wallis H-test; $H = 5.23$, $p = 0.16$); therefore, we combined these functional feeding groups into a single “freshwater” invertebrate prey type for each sampling event for use in stable isotope mixing models. We used the same marine source values for all models within a year, which included any salmon carcass and egg samples collected across the entire river. We report proportional contributions of each prey type as the mean of the posterior distributions (Fig. 4) with 2.5 and 97.5% lower and upper credibility intervals (Table A1). We verified that all models converged using Geweke’s criterion and trace plots given from the MixSIAR model output (Stock and Semmens 2013).

Many fishes exhibit ontogenetic dietary shifts, and larger fish feeding at higher trophic levels generally have higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Kadye and Booth 2012; Costas and Pardo 2015). To evaluate possible ontogenetic effects, we used simple linear regressions to examine site-specific relationships between isotopic values and fork length (mm) of individual juvenile salmon if sample size was adequate. For this analysis, we combined all seasons within each site and only considered data from 2014.

Results

Freshwater invertebrate energy sources

Relatively strong correlations between freshwater invertebrate and periphyton $\delta^{13}\text{C}$ signatures suggested that all freshwater invertebrate feeding groups relied primarily on freshwater, rather than terrestrial sources of carbon (Table 3, Fig. 2). Site-specific mean

periphyton $\delta^{13}\text{C}$ predicted site-specific mean primary consumer $\delta^{13}\text{C}$ better than did terrestrial OM $\delta^{13}\text{C}$ for all freshwater primary consumer groups (Table 3). Multiple linear regressions for collector, grazer, and shredder invertebrate $\delta^{13}\text{C}$ against periphyton $\delta^{13}\text{C}$ were significant ($p < 0.05$) and resulted in relatively high partial r^2 values (range: 0.597 to 0.869), whereas all relationships of invertebrate groups to terrestrial OM were not significant ($p > 0.05$) and had negative partial r^2 values (range: -0.245 to -0.037; Table 3). Collectors appeared to be most reliant on periphyton, followed by grazers and finally by shredders (Table 3, Fig. 2).

Non-parametric analysis of variance tests revealed possible assimilation of MDN by periphyton and freshwater invertebrates. $\delta^{15}\text{N}$ signatures for both sample types were slightly, though significantly, elevated when and where spawning salmon were present. Mean periphyton $\delta^{15}\text{N}$ was elevated by 0.9‰ at spawning sites ($\delta^{15}\text{N}_{\text{PRESENT}} = 2.0 \pm 1.6\text{‰}$; $\delta^{15}\text{N}_{\text{ABSENT}} = 1.1 \pm 1.6\text{‰}$; $H = 8.7$, $p = 0.003$) and mean freshwater invertebrate $\delta^{15}\text{N}$ was elevated by 1.0‰ ($\delta^{15}\text{N}_{\text{PRESENT}} = 3.5 \pm 2.0\text{‰}$; $\delta^{15}\text{N}_{\text{ABSENT}} = 2.4 \pm 1.6\text{‰}$; $H = 51.9$, $p < 0.001$).

Juvenile salmon diet

Stomach contents

In 2013, we sampled 216 juvenile Chinook and coho individuals for stomach contents, but we analyzed samples from only 161 individuals after accounting for empty stomachs and those with entirely unidentifiable prey. Sampling efforts in 2014 yielded 277 non-empty and fully identifiable stomach content samples from a total of 316 juvenile Chinook and coho individuals, collected across a larger number of sites than the previous year.

Diptera larvae and adults were the most prevalent invertebrate prey taxon by mass found in fish stomachs pooled across both years (21.5 and 15.3%, respectively; Table 4). Other

important freshwater invertebrate taxa in fish stomachs were larval and adult Trichoptera, larval and adult Plecoptera, and larval Ephemeroptera. The most prevalent terrestrial taxon by mass was Hymenoptera, followed by Coleoptera, Lepidoptera, Hemiptera, and Diptera (Table 4). Marine-derived diet items were present in stomach samples in the form of salmon eggs, and no salmon carcass material was observed.

Isotopic evidence for site fidelity

Stable isotope values of juvenile salmon relative to site-specific prey signatures suggested that they primarily fed on local invertebrate prey from within their respective sites of capture. For example, invertebrate and fish signatures collected during the summer sampling event (mid-August) within Reach 2 showed distinct macrohabitat-specific groupings, except for three individuals caught within the side channel that had signatures significantly outside of that site's prey polygon (Fig. 3). Across all reaches, periphyton, invertebrate, and juvenile salmon samples collected within the margins of the glacial main and side channels were significantly (Kruskal-Wallis H test; $H = 182.9$; $p < 0.001$) more ^{13}C -enriched compared to those in off-channel tributary mouths, upland sloughs, and the side slough (Fig. 3).

Bayesian stable isotope diet models

a) Overall dietary patterns and model precision

Juvenile salmon were primarily supported by freshwater energy sources while terrestrial- and marine-derived food subsidies were of lesser importance, according to mixing models (Fig. 4). Freshwater prey contributed on average $57.2 \pm 13.1\%$ SD (range: 24.9 to 79.0%) to

assimilated diets across all habitats and seasons, while terrestrial and marine prey contributed $28.3 \pm 12.5\%$ SD (range: 8.4 to 66.2%) and $14.5 \pm 8.6\%$ SD (range: 2.5 to 40.3%), respectively.

Relative to stomach contents, the uninformed models generally underestimated the importance of freshwater energy and overestimated the importance of terrestrial and marine energy for juvenile salmon (Table A1). In the vast majority of cases, including priors in the models resulted in mean diet estimates that were intermediaries of stomach content and uninformed stable isotope estimates (Table A1). Informed model estimates were more precise compared to uninformed models (Table A1), with a mean reduction of 14.8% in the 95% credibility interval range. Many of the terrestrial and freshwater diet estimates with large credibility intervals corresponded to glacial main and side channels, where the overall difference in mean $\delta^{13}\text{C}$ between freshwater and terrestrial invertebrates was smallest relative to differences in other macrohabitat types (difference of mean $\delta^{13}\text{C}$ values: 1.3 and 1.2‰ respectively; Table A1). Terrestrial invertebrate $\delta^{13}\text{C}$ was more variable than expected (range: -35.7 to -22.8‰) and often exhibited the same site-specific isotopic shifts as freshwater invertebrates, which contributed to overlapping isotopic signatures between these two sources within sites (Fig. 3). Including stomach content priors in mixing models generally improved Pearson's correlation coefficients (mean: -0.78, range: -0.32 to -0.97) relative to uninformed models (mean: -0.88, range: -0.6 to -0.98). In cases where sources were highly correlated and the model was unable to discern source contributions from isotope data, prior information from stomach content data were more influential in guiding proportional contribution estimates.

Ontogeny appeared to have varying effects on juvenile salmon isotope signatures across sites. Out of a total of 12 sites, only three showed a significant positive relationship between $\delta^{13}\text{C}$ and fork length (r^2 range: 0.003 to 0.301, p -value range: 0.01 to 0.860) while seven of the 12

sites showed significant size effects for $\delta^{15}\text{N}$ (r^2 range: 0.015 to 0.621, p -value range: <0.001 to 0.570).

b) Seasonal variability

The relative importance of freshwater, terrestrial, and marine energy pathways to juvenile salmon varied across the growing season. Mixing model results for most sites revealed that the importance of freshwater prey either decreased slightly from spring to fall or had the lowest overall contribution during the summer (Fig. 4). Terrestrial prey generally showed opposing seasonal trends relative to freshwater prey, where mean contributions either increased from spring to fall or peaked in summer. These 2014 seasonal patterns were evident for fish populations caught in all macrohabitat types. Seasonal trends of marine contributions were highly variable among sites sampled, however in sites where spawning salmon were observed in relatively higher densities (Reach 3 tributary mouth and upland slough; Reach 1 upland slough), the mean contribution of marine prey sources increased from summer to fall (Fig. 4). Interestingly, 2014 mixing models often estimated peaks in marine contributions in spring, when no eggs were found in stomach samples, followed by a decrease in summer and more variable contributions in fall (Fig. 4).

c) Spatial variability

Juvenile salmon were primarily supported by the freshwater energy pathway regardless of macrohabitat type and study reach (Fig. 4). Overall, the relative contributions of freshwater and terrestrial food resources to juvenile salmon did not differ among glacial-fed (main and side channels) and non-glacial (sloughs and tributary mouths) habitats (Fig. 4), despite generally large

differences in turbidity (Table 1). Exceptions existed for fish rearing in upland sloughs within Reaches 1 and 3 and the Reach 2 side slough (Fig. 4) where the greatest consumption of salmon eggs occurred (see Table A1) during active spawning. While we found lower percentages of salmon eggs in stomach samples within the Reach 3 tributary mouth, mixing models still estimated a relatively large contribution from marine-derived energy (Table A1, Fig. 4). We did not find any evidence of salmon eggs or carcass tissue in the stomach samples of fish collected from glacial-fed main channel habitats in 2014; however, we did find salmon eggs in the stomachs of juvenile salmon captured within the glacial-fed side channel in Reach 2 in 2013 (Table A1).

Hotspots for marine-derived energy contributions varied across the landscape during the two study years. While marine-derived contributions were greatest in tributary mouths in 2013, importance shifted to slough macrohabitats in 2014 (Fig. 5). Finally, we found no patterns to suggest that the importance of energy subsidies varied consistently by reach (Fig. 4).

Discussion

The importance of allochthonous resources to stream communities is well known (Minshall 1967; Fisher and Likens 1973; Baxter et al. 2005), but less is understood about the relative importance of available energy pathways across spatial and temporal scales that are more relevant within large, biophysically complex and dynamic riverine landscapes. Our findings provide a broader, quantitative, spatial and temporal context for the use of local and subsidized energy pathways by juvenile Chinook and coho salmon, while corroborating results from previous diet studies conducted at finer scales.

Freshwater invertebrate energy sources

Despite the availability of terrestrial OM, multiple invertebrate feeding groups in large and glacial-fed rivers are known to rely on freshwater algae, presumably because it is a more labile food source (Gaedke et al. 1996; Zah et al. 2001; Thorp and Delong 2002). Our findings provide additional support for this observation, showing that even shredder invertebrates, which typically specialize on conditioned terrestrial OM (Cummins 1973), relied more on freshwater carbon.

The isotopic signatures of periphyton explained much of the spatial variability in aquatic invertebrate signatures. The remaining variability could be caused by a number of different factors, including invertebrate mobility (Gibbins 2007, 2010), differences in tissue turnover rates (Jardine et al. 2014) and diet-tissue discrimination among invertebrate species (McCutchan et al. 2003; Bunn et al. 2003), within-site $\delta^{13}\text{C}$ variability of periphyton food sources (Finlay 2004), and the assimilation of MDN from spawning salmon tissue by both periphyton and invertebrates (Wipfli et al. 1998; Hicks et al. 2005). Because we found that periphyton and invertebrate $\delta^{15}\text{N}$ signatures were significantly elevated at spawning sites, it is possible that the freshwater energy pathway in diet models represents an additional, but indirect, mode of assimilation of marine-derived energy and nutrients via lower trophic levels within instream food webs. Nevertheless, the relatively strong associations with periphyton signatures indicate that freshwater invertebrates primarily provide autochthonous carbon to juvenile salmon.

*Juvenile salmon diet models*Seasonal variability

As opportunistic predators, juvenile salmon diets likely represent the timing and magnitude of high quality terrestrial and marine resource pulses. Because salmonids are known to selectively forage for terrestrial invertebrates (Hubert and Rhodes 1989; Young et al. 1997; Nakano et al. 1999), the increased contributions of terrestrial invertebrates to juvenile salmon observed during mid-summer might be explained by a large-scale pulse of this prey subsidy to instream habitats. Similarly, other river systems at higher latitudes experience increases in the flux of terrestrial invertebrates during mid-summer when terrestrial productivity can be at its highest and when invertebrates are most active (Chloe and Garman 1996; Wipfli 1997; Bridcut 2000; Nakano and Murakami 2001). The greater influence of high quality marine subsidies during fall may have contributed to this apparent pattern where rearing and spawning overlapped (e.g., Reach 1 and 3 upland sloughs, Reach 2 side slough, and Reach 3 tributary mouth), since salmon eggs are known to be a preferred prey source when available (Bilby et al. 1998; Quinn et al. 2012). This pattern, however, varied between the two study years depending on the magnitude of marine contributions.

The higher marine contribution estimates during the spring sampling event (when no eggs were found in stomach samples) may be an artifact of life history timing, when sampling coincided with outmigrations of larger age 1-2 smolts (R2 and UAF 2015). Mean juvenile salmon $\delta^{15}\text{N}$ was indeed significantly higher during spring sampling events (R2 and UAF 2015), which in turn can be explained by ontogenetic $\delta^{15}\text{N}$ -enrichment and possibly by over-winter storage of MDN that was assimilated by tissues the previous fall. The latter effect was observed for stream-resident Dolly Varden in southcentral Alaska, where evidence from stable isotope and fatty acid analyses suggested that MDN persisted in tissues for at least nine months after feeding

on salmon eggs the previous summer, possibly due to low winter energetic demands that slow tissue turnover (Rinella et al. 2013).

Taken together, evidence from diet models supports the notion that the relative importance of different prey sources for stream fishes can be asynchronous (Wipfli and Baxter 2010), where in many cases freshwater contributions peaked early in the season, followed by terrestrial prey in summer, and finally by marine contributions in the fall where this resource was available. Because the ultimate quality of any one food resource is modified by its timing relative to a consumer's life cycle and to the timing of other resources (Wipfli and Baxter 2010; Yang et al. 2010; Marcarelli et al. 2011), pulses of marine subsidies that occur just prior to overwintering may be more important in conferring a survival advantage than earlier inputs when freshwater and terrestrial food sources are typically more abundant (Bilby et al. 1998).

Spatial variability

We found that juvenile Chinook and coho salmon were supported predominately by freshwater prey across a diverse set of macrohabitat types, however this energy source was supplemented by spatially patchy marine and terrestrial subsidies. Contrary to the conventional wisdom that salmonids avoid rearing in turbid habitats (Lloyd 1987) and despite markedly lower benthic invertebrate densities (R2 and UAF 2014), our isotopic data and mixing model results suggest that juvenile salmon were supported primarily by locally-produced autochthonous prey in glacial-fed main and side channels. Murphy et al. (1989) also captured juvenile Chinook and coho salmon in the margins and braids of the glacial Taku River main channel in Alaska; however, they could not be certain that fish were rearing, rather than simply migrating through these turbid habitats. Laboratory feeding trials have shown that juvenile Chinook salmon can

feed effectively on invertebrates at turbidity levels of up to 150 NTU (Nephelometric Turbidity Units) (Gregory and Northcote 1993), suggesting that the conditions we observed in main channel habitats would not prevent foraging. These findings contrast with a multitude of field studies that observed a range of deleterious effects on foraging (Lloyd 1987) as well as reduced assimilation of autochthonous carbon with increased turbidity (Perry et al. 2003); however, it is likely that different catchments accommodate biota that vary in sensitivity to a given sediment load depending on the background conditions (Lloyd 1987).

We observed a marked decrease in the importance of marine-derived subsidies for juvenile salmon rearing within tributary mouths during the second year of the study, coinciding with findings from a concurrent study of salmon escapement using fish wheel sampling, that fewer adults returned to these macrohabitats (LGL and ADF&G 2014, 2015). Because salmon eggs and carcass tissues are an extremely energy rich food source (Quinn et al. 2012), a shift in the availability of this pulsed subsidy across the landscape could alter the relative qualities of different rearing habitats over time (Wipfli and Baxter 2010). In unaltered, spatially heterogeneous rivers, such variations in the magnitude and distribution of pulsed subsidies at smaller scales are not unusual (Stanford et al. 2005) and when considered in aggregate, have been shown to have a stabilizing effect on meta-community food web dynamics (Bellmore et al. 2015; Schindler et al. 2015).

We found further evidence of this effect when observing variability at a larger scale across study reaches, as the energy pathways supporting juvenile salmon did not change in any consistent or discernable way across reaches. Likewise, others (Poole 2002; Stanford et al. 2005; Thorp et al. 2006) have noted that habitats in close proximity often exhibit more unique properties relative to each other than to those at greater distances along a river's continuum,

therefore producing non-systematic variations that are inconsistent with a longitudinal effect. It is possible that we failed to detect a weak longitudinal trend that was obscured by the uncertainty associated with the mixing model estimates. Regardless, concurrent escapement studies showed that Chinook, coho, chum, and pink salmon spawning habitat in the Susitna River is generally concentrated in larger tributaries throughout the lower and middle reaches (LGL and ADF&G 2014). This patchy distribution of marine subsidies across the landscape would result in a greater apparent variability among macrohabitats compared to the variability between upstream and downstream reaches.

Applying *in situ* stable isotope diet methods to stream fishes is complex, given the great variability in $\delta^{13}\text{C}$ values of instream producers (Finlay 2004) and tissue turnover rates across trophic levels (Jardine et al. 2014), as well as the mobility of fish and their prey (Bradford et al. 2001; Gibbins 2007). The use of diet models in this study required a number of assumptions, perhaps the most important of which is that fish were feeding within their sites of capture for long enough to reach isotopic equilibrium with the local prey. At least a subset of fish likely obtained their isotopic signatures while feeding in other habitats, especially given that some samples were obtained from smolting juveniles that could have already migrated long distances from upstream reaches. Despite this caveat, stable isotope evidence suggested that most juvenile salmon within our study reaches maintained consistent rearing locations long enough to represent distinct, macrohabitat-specific isotopic signatures. To our knowledge, our stable isotope data provides the strongest available evidence of juvenile Chinook and coho salmon rearing and feeding on local freshwater prey within turbid main channel habitats in glacial rivers. Further research is necessary to determine whether this surprising result is a rare occurrence or widespread pattern.

Robust interpretation of stable isotope diet models also required isotope values of site-specific diet sources to be distinct enough in order to differentiate their importance in consumer diets (Moore and Semmens 2008); however, terrestrial invertebrate signatures tended to reflect those of freshwater invertebrates from within the same site. A likely explanation is a reciprocal flow of carbon from freshwater to terrestrial habitats via consumption of exposed periphyton by terrestrial invertebrate herbivores (Bastow et al. 2002) and of local emerging aquatic insects by predatory terrestrial spiders and beetles (Power and Rainey 2000; Paetzold et al. 2006). Similarities between terrestrial and freshwater prey sources led to more uncertainty around mean source contribution estimates in the mixing models and therefore precluded more definitive diet assignments.

In cases where sources were highly correlated and the model was unable to discern source contributions from isotope data, prior information from stomach content data provided greater resolution for proportional contribution estimates (Moore and Semmens 2008). While integrating stomach content data as priors generally improves model estimates, it also incorporates high temporal variability as well as biases towards recent diet items and those that do not easily digest. Regardless, our stomach content estimates generally agreed with other juvenile salmon diet studies in Alaska (Hansen and Richards 1985; Sagar and Glova 1987) and aligned with observations of spawning salmon presence within our sampling sites. Because the uninformed models use *a priori* source contributions that are all equally likely (Moore and Semmens 2008), resulting posterior distributions could have overestimated the influence of marine and terrestrial subsidies and underestimated that of freshwater prey, even after incorporating informed priors in the models. Although it is possible that salmon tissue was consumed but completely digested at the time of sampling, informed model estimates of marine

subsidies should be interpreted with some caution at sites where no salmon eggs were detected in stomach contents.

Freshwater production provides the majority of energy and nutrients to aquatic invertebrates and juvenile salmonids in our study system, and is a potentially limiting food resource. Several studies in Alaska have demonstrated that larval and emerging benthic invertebrates, especially Dipteran chironomids of all life stages, were the primary food source for juvenile salmon (Loftus and Lenon 1977; Hansen and Richards 1985; Sagar and Glova 1987), and when production and availability of benthic invertebrates increased via experimental nutrient fertilization, fish growth and production also increased (Johnston et al. 1990; Harvey et al. 1998). Furthermore, bioenergetics models of the same Susitna River salmonid populations revealed that feeding rate was often the primary factor limiting their growth, while food quality and water temperature were secondary factors (R2 and UAF 2015). Any major reductions in standing stocks of periphyton and benthic macroinvertebrates may then have the greatest overall adverse effects on juvenile salmonids rearing throughout the landscape mosaic. While we found that terrestrial and marine subsidies were of secondary importance, a reduction of these high quality resources could translate to stronger interaction strengths with freshwater prey and lowered resilience to fluctuations in productivity (McCann et al. 1998; Bellmore et al. 2015). Such changes could result from perturbations that reduce or homogenize instream habitat (e.g., variations in flow, temperature, and sediment types) and interactions with floodplains that supply energy and nutrients to instream primary and secondary production (Ward and Stanford 1979; Vinson 2001; Cook et al. 2015).

This study provides an assessment of baseline trophic conditions for rearing salmon below the potential site of a large hydroelectric dam. Flow regulation would likely affect

seasonal hydrological regimes that in turn influence habitat quality as well as the distribution and availability of food sources for stream fishes (Vinson 2001; Holt et al. 2014). These results will assist operators in understanding how proposed dam operations might influence energy flow to juvenile salmon across the landscape, and can help to predict and mitigate for negative effects at multiple scales. Future investigations are needed to test the generality of these findings across other river systems. To appreciate how variable diet patterns contribute to growth and production of salmonids throughout a diverse river system, future studies should incorporate a growth modeling component that accounts for the nutritional quality of all major food sources (including availability and energy density) and environmental conditions. While the latest diet modeling tools can simultaneously consider both stomach content and stable isotope data, other considerations (concentration of essential nutrients; fat content; availability relative to other sources, life history shifts, and body condition) will help to shape a more holistic understanding of the importance of various food resources to consumers. Such information, in conjunction with results from this study, can provide valuable insight into food-driven variables limiting the productivity of Pacific salmon populations at the freshwater rearing stage.

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Tables

Table 1. Key characteristics of macrohabitat types sampled.

Table 2. Dates for spring, summer, and fall sampling events in 2013 and 2014.

Table 3. Results of multiple linear regressions for aquatic invertebrate consumer groups and potential carbon sources (periphyton and terrestrial OM).

Table 4. Overall taxonomic and life stage composition of aquatic and terrestrial invertebrate mass ingested by juvenile Chinook and coho salmon.

Draft

1117 **Table 1.**
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Macrohabitat Type (code)	Connectivity to main channel	Water source	Description			
			Turbidity (NTU)	Mean (range) water velocity (m s ⁻¹)	Mean (range) water temperature (°C)	Typical spawning salmon activity
Upland slough (US)	Disconnected at upstream end; typical backwater connection at downstream end	Substantial contribution of clear water from tributaries or from upwelling groundwater; glacial backwater dependent on glacial main or side channel flows	0.5-11	0.1 (0.0 – 0.6)	7.8 (2.8 – 11.0)	Reach 1: milling, no redds observed Reach 2: None Reach 3: milling, holding; redds and eggs observed
Side slough (SS)	Intermittently connected at upstream end; backwater connection at downstream end	Substantial contribution of clear water from tributaries or from upwelling groundwater; glacial backwater or upstream contribution dependent on glacial main or side channel flows	0.5-46	0.2 (0.0 – 0.9)	5.6 (1.0 – 8.0)	Reach 2: milling, holding; few redds observed
Tributary mouth (TM)	Full	Primary contribution of clear water from tributary flows, influence of glacial main channel, side channel, or slough at downstream end	0.5-5.5	0.5 (0.2 – 1.5)	8.0 (3.0 – 14.0)	Reach 1: milling, holding; few redds observed Reach 2: milling, holding; few redds observed Reach 3: many have been observed holding; redds and eggs observed
Main channel (MC)	-	Primarily glacial	9.5-600	0.46 (0.1 – 1.3)	8.9 (2.5 – 14.0)	No observations
Side channel (SC)	Fully connected at upstream end except during periods of extreme low flows	Primarily glacial	0.5-111	0.4 (0.1 – 1.3)	8.7 (2.0 – 13.0)	No observations

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Table 2.

Year	Sampling Period		
	Spring	Summer	Fall
2013	Jun 11 – Jul 13	Aug 12 – Aug 21	Sept 22 – Oct 2
2014	Jun 10 – Jun 20	Aug 4 – Aug 14	Sept 20 – Sept 30

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Table 3.

Consumer group	Whole model r^2	Periphyton			Terrestrial OM		
		Slope estimate	P	r_{PT}	Slope estimate	P	r_{OM}
Collector	0.783	1.142	< 0.001	0.869	-0.802	0.378	-0.245
Grazer	0.604	1.242	0.001	0.790	-2.603	0.053	-0.526
Shredder	0.483	0.734	0.008	0.655	-0.339	0.730	-0.097

Note: “ r_{PT} ” and “ r_{OM} ” represent partial correlation values of periphyton and terrestrial OM $\delta^{13}\text{C}$, respectively, and consumer group $\delta^{13}\text{C}$. These values show the degree of association between either periphyton and terrestrial OM and the consumer group after removing the effects of the other carbon source.

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1132 Table 4.

Taxon, life stage	%
Aquatic	
Diptera, immature	21.5
Diptera, adult	15.3
Trichoptera, adult	12.7
Plecoptera, immature	9.4
Ephemeroptera, immature	9.3
Trichoptera, immature	3.8
Plecoptera, adult	1.6
Other	2.4
Terrestrial	
Hymenoptera, adult	6.0
Coleoptera, adult	4.1
Lepidoptera, all stages	2.0
Hemiptera, adult	1.8
Diptera, adult	0.1
Other	0.8
Unknown	9.2

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Figures

Figure 1. Study area showing the upper and lower extents of each sampling site, identified by macrohabitat type (TM: tributary mouth, SS: side slough, US: upland slough, SC: side channel, MC: main channel) within study reaches 1-3 (panels a-c). Arrows indicate direction of flow.

Figure 2. Relationships of aquatic invertebrate consumer group $\delta^{13}\text{C}$ with potential food source (periphyton [filled circles] and terrestrial organic matter [open circles]) for 2014. Each data point represents site-specific mean invertebrate $\delta^{13}\text{C}$ vs. site-specific mean source $\delta^{13}\text{C}$ for all seasons combined.

Figure 3. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for juvenile Chinook and coho salmon (open symbols, representing individuals) and their potential prey items (closed circles; means $\pm$ 1 SD) separated by macrohabitat within Reach 2 (rkm 167) during the summer sampling event. Colors of juvenile salmon and invertebrate symbols indicate macrohabitat types in which they were sampled. The isotopic signatures of marine-derived prey (salmon eggs and carcasses) were pooled across all habitat types (black, dotted error bars). Freshwater sources are indicated by solid error bars and terrestrial sources by dashed error bars.

Figure 4. Mean estimated proportional contributions of freshwater, marine, and terrestrial prey to the diet of juvenile salmon in 2014, according to informed MixSIAR Bayesian mixing models. Results are organized by reach, macrohabitat type (TM: tributary mouth, SS: side slough, US: upland slough, SC: side channel, MC: main channel), and season.

Figure 5. Interannual (2013-2014) comparison of mean estimated proportional contributions of freshwater, marine, and terrestrial prey to the diet of juvenile salmon captured in tributary mouths, according to informed MixSIAR Bayesian mixing models. Results are organized by year, reach, and season.

a) Reach 1 (rkm 130)

b) Reach 2 (rkm 167)

c) Reach 3 (rkm 227)

Table A1. Percent mean weight (%MW $\pm$ 1 SD) and mean percent contribution estimates (95% credibility range) of uninformed and informed stable isotope mixing model (SIMM) for a) freshwater, b) marine, and c) terrestrial prey categories of juvenile Chinook (CK) and (or) Coho (CO) salmon captured in study sites.

a) Freshwater prey contributions

Year	Season	Reach	Macrohabitat type	Consumer species (n)	% Freshwater prey		
					Gut contents	SIMM - Uninformed priors	SIMM - informed priors
2013	SP	1	US	CK (7), CO (6)	71.1 $\pm$ 24.9	29.2 (1.5 - 74.3)	58.3 (35.6 - 80.5)
			TM	CK (8), CO (7)	70.7 $\pm$ 28.9	34.8 (5.7 - 67.1)	57.3 (38.0 - 77.7)
			TM	CK (4)	97.2 $\pm$ 5.5	29.6 (3.1 - 62.1)	51.5 (25.2 - 82.0)
	SU	3	TM	CK (2), CO (7)	88.7 $\pm$ 29.0	49.0 (16.2 - 71.8)	60.9 (43.1 - 76.2)
			TM	CK (1), CO (4)	62.2 $\pm$ 46.1	39.7 (1.9 - 87.0)	48.3 (15.3 - 81.0)
			TM	CK (2), CO (21)	64.1 $\pm$ 38.9	42.8 (23.1 - 59.4)	69.0 (51.7 - 84.9)
		3	US	CK (1), CO (13)	93.6 $\pm$ 5.1	44.1 (13.9 - 71.2)	50.9 (38.8 - 63.7)
			SC	CO (9)	41.5 $\pm$ 47.9	44.7 (5.1 - 86.2)	41.0 (18.2 - 65.9)
			TM	CK (3), CO (10)	7.0 $\pm$ 13.5	18.3 (1.3 - 48.0)	31.9 (14.7 - 54.0)
	FA	1	US	CO (3)	34.4 $\pm$ 56.9	32.4 (2.4 - 73.7)	37.6 (7.4 - 74.5)
			TM	CO (23)	19.0 $\pm$ 32.5	34.2 (11.4 - 57.5)	63.0 (34.4 - 91.1)
			US	CO (5)	84.3 $\pm$ 32.1	38.1 (4.1 - 73.4)	31.0 (17.6 - 45.2)
		3	SC	CO (11)	27.4 $\pm$ 28.9	32.7 (2.1 - 72.7)	27.7 (9.3 - 51.5)
			TM	CK (5), CO (7)	26.5 $\pm$ 44.4	36.2 (8.6 - 64.6)	40.5 (20.1 - 60.0)
			US	CO (6)	63.9 $\pm$ 49.9	42.9 (10.6 - 67.6)	66.7 (42.8 - 92.9)
2014	SP	1	TM	CO (4)	90.7 $\pm$ 18.2	44.7 (4.1 - 87.0)	69.7 (37.5 - 93.2)
			SC	CK (5), CO (1)	88.4 $\pm$ 15.1	36 (1.9 - 80.7)	69.6 (41.3 - 91.5)
			MC	CK (3), CO (6)	83.5 $\pm$ 28.7	46.7 (4.6 - 88.3)	79.0 (54.7 - 95.0)
			US	CO (4)	95.5 $\pm$ 9.0	64.7 (45 - 81.0)	68.6 (51.9 - 83.9)
		2	SS	CO (5)	79.9 $\pm$ 27.7	53.3 (21.9 - 80.9)	57.3 (33.9 - 79.4)
			TM	CK (6), CO (10)	74.4 $\pm$ 38.8	56.9 (46.1 - 67.4)	60.0 (50.7 - 70.3)
			TM	CK (1), CO (5)	72.2 $\pm$ 30.5	58.5 (22.4 - 83.5)	61.3 (39.3 - 80.9)
			SC	CK (4), CO (1)	73.7 $\pm$ 36.4	50.7 (5.2 - 89.8)	60.7 (29.9 - 86.5)
		3	MC	CK (8)	90.3 $\pm$ 9.7	46.6 (8.6 - 84.2)	73.1 (48.1 - 92.8)
			US	CK (4), CO (8)	87.5 $\pm$ 23.8	31.0 (12.6 - 49.9)	47.9 (31.1 - 72.3)
			US	CK (4), CO (8)	87.5 $\pm$ 23.8	31.0 (12.6 - 49.9)	47.9 (31.1 - 72.3)
			US	CK (4), CO (8)	87.5 $\pm$ 23.8	31.0 (12.6 - 49.9)	47.9 (31.1 - 72.3)
	SU	1	US	CK (4), CO (8)	87.5 $\pm$ 23.8	31.0 (12.6 - 49.9)	47.9 (31.1 - 72.3)
			US	CK (4), CO (8)	87.5 $\pm$ 23.8	31.0 (12.6 - 49.9)	47.9 (31.1 - 72.3)
			US	CK (4), CO (8)	87.5 $\pm$ 23.8	31.0 (12.6 - 49.9)	47.9 (31.1 - 72.3)

FA	2	TM	CK (6), CO (6)	86.7 ± 24.9	42.9 (24.0 - 63.2)	57.9 (40.3 - 78.3)
		SC	CK (3)	67.9 ± 18.9	40.2 (2.4 - 88.9)	52.1 (17.3 - 85.6)
		MC	CK (8)	66.8 ± 22.9	64.1 (24.0 - 92.4)	48.2 (23.2 - 72.0)
		US	CK (6), CO (7)	91.4 ± 17.7	58.2 (41.9 - 75.4)	69.2 (53.3 - 86.5)
		SS	CK (2), CO (2)	46.9 ± 51.9	17.8 (1.2 - 46.5)	25.4 (6.9 - 53.1)
		TM	CK (2), CO (6)	84.2 ± 24.6	42.6 (18.2 - 64.8)	53.4 (34.9 - 73.5)
	3	SC	CK (7), CO (5)	64.7 ± 42.2	64.7 (17.8 - 92.6)	61.7 (36.9 - 83.5)
		MC	CK (10)	83.3 ± 16.8	55.6 (26.6 - 81.5)	60.8 (41.8 - 79.4)
		US	CK (5)	98.7 ± 2.5	43.7 (6.6 - 72.1)	61.6 (38.8 - 83.2)
		TM	CK (7)	88.2 ± 30.6	40.6 (13.4 - 70.0)	62.9 (39.4 - 87.7)
		SC	CK (8)	83.2 ± 26.4	28.9 (4.1 - 58.4)	48.8 (27.1 - 73.7)
		MC	CK (8)	55.4 ± 31.1	44.9 (15.7 - 75.6)	43.8 (24.0 - 64.0)
	1	US	CO (12)	57.2 ± 39.6	40.7 (16.6 - 67.1)	43.9 (25.7 - 64.1)
		SC	CK (3)	33.3 ± 57.7	41.7 (2.6 - 89.4)	40.0 (8.3 - 78.5)
		MC	CK (6)	94.3 ± 8.0	43.7 (4.0 - 85.9)	61.2 (23.0 - 91.0)
	2	US	CK (1), CO (8)	96.4 ± 16.5	56.8 (30.0 - 79.5)	70.0 (50.3 - 89.3)
		SS	CO (8)	52.7 ± 45.3	38.2 (9.8 - 68.2)	49.0 (29.1 - 68.8)
		TM	CK (8), CO (8)	86.0 ± 26.8	48.7 (28.1 - 69.1)	63.5 (48.4 - 79.4)
		SC	CK (7), CO (5)	68.2 ± 36.8	20.9 (0.7 - 53.4)	45.6 (24.9 - 67.7)
	3	MC	CK (4)	97.1 ± 5.9	46.9 (4.8 - 87.9)	66.7 (36.0 - 92.1)
		US	CK (3)	28.4 ± 30.9	36.6 (2.0 - 85.6)	24.9 (2.1 - 63.8)
		TM	CK (7)	100.0	39.4 (8.5 - 65.5)	57.6 (38.3 - 73.9)
		SC	CK (8)	99.9 ± 0.3	26.5 (3.1 - 62.7)	68.9 (37.8 - 93.9)
		MC	CK (8)	98.3 ± 3.1	39.1 (4.5 - 77.3)	69.1 (43.6 - 90.8)

b) Marine prey contributions

Year	Season	Reach	Macrohabitat type	Consumer species (n)	% Marine prey		
					Gut contents	SIMM - Uninformed priors	SIMM - informed priors
2013	SP	1	US	CK (7), CO (6)	0.0	4.1 (0.1 - 15.5)	3.0 (0.1 - 11.0)
			TM	CK (8), CO (7)	0.0	12.5 (1.0 - 28.8)	9.9 (0.7 - 23.1)
		2	TM	CK (4)	0.0	12.9 (1.6 - 26.9)	11.8 (1.2 - 25.5)
			TM	CK (2), CO (7)	0.0	26.4 (13.1 - 37.6)	23.6 (10.9 - 34.3)
		SU	1	TM	CK (1), CO (4)	19.4 ± 43.4	22.0 (2.2 - 56.2)
			2	TM	CK (2), CO (21)	16.5 ± 36.9	16.1 (4.8 - 26.2)
	SU		US	CK (1), CO (13)	0.0	15.9 (3.5 - 27.8)	23.1 (16.1 - 29.7)

2014	FA	3	SC	CO (9)	11.1 ± 33.3	16.2 (2.1 - 32.4)	15.7 (3.5 - 29.9)	
		TM	CK (3), CO (10)	89.1 ± 27.1	39.9 (24.4 - 54.7)	47.3 (34.0 - 63.7)		
		1	US	CO (3)	0.0	35.6 (9.0 - 60.4)	27.3 (2.1 - 56.6)	
		2	TM	CO (23)	67.9 ± 45.1	37.6 (25.4 - 49.8)	18.9 (1.3 - 39.0)	
		US	CO (5)	12.8 ± 28.6	25.5 (3.7 - 50.4)	40.3 (33.7 - 53.4)		
		SC	CO (11)	32.9 ± 45.9	36.4 (2.2 - 82.9)	35.0 (15.5 - 54.7)		
	SP	3	TM	CK (5), CO (7)	72.0 ± 44.0	37.5 (23.3 - 50.9)	43.6 (31.8 - 57.4)	
		1	US	CO (6)	0.0	32.7 (5.7 - 51.6)	14.3 (0.9 - 37.9)	
		TM	CO (4)	0.0	25.8 (1.7 - 68.8)	15.4 (1.7 - 35.6)		
		SC	CK (5), CO (1)	0.0	26.1 (1.6 - 73.4)	8.1 (0.3 - 22.3)		
		MC	CK (3), CO (6)	0.0	15.9 (0.8 - 52.4)	23.0 (8.6 - 33.6)		
		2	US	CO (4)	0.0	25.0 (10.2 - 36.3)	15.3 (1.8 - 29.6)	
	SU	3	SS	CO (5)	0.0	17.8 (2.7 - 32.3)	15.4 (9.2 - 21.6)	
			TM	CK (6), CO (10)	0.0	17.3 (11.4 - 23.3)	17.6 (4.9 - 30.1)	
			TM	CK (1), CO (5)	0.0	20.2 (5.5 - 34.5)	11.6 (0.7 - 29.6)	
			SC	CK (4), CO (1)	0.0	18.6 (1.1 - 64.1)	10.1 (0.7 - 21.7)	
			MC	CK (8)	0.0	13.9 (2.3 - 26.0)	12.6 (0.5 - 40.8)	
			US	CK (4), CO (8)	0.0	22.3 (5.8 - 36.8)	19.2 (2.9 - 33.6)	
		1	TM	CK (6), CO (6)	0.0	12.9 (4.9 - 20.6)	11.0 (2.6 - 19.0)	
			SC	CK (3)	0.0	23.4 (0.6 - 76.2)	12.4 (0.3 - 45.4)	
			MC	CK (8)	0.0	7.2 (0.4 - 20.2)	11.7 (1.6 - 22.8)	
			2	US	CK (6), CO (7)	0.0	2.3 (0.1 - 8.1)	2.5 (0.1 - 8.1)
			SS	CK (2), CO (2)	0.0	8.3 (0.3 - 24.3)	8.4 (0.4 - 23.6)	
			TM	CK (2), CO (6)	0.0	5.9 (0.2 - 17.5)	6.0 (0.2 - 16.9)	
		2	SC	CK (7), CO (5)	0.0	10.3 (0.7 - 26.4)	5.7 (0.1 - 17.2)	
			MC	CK (10)	0.0	9.4 (1.2 - 19.1)	7.9 (0.9 - 16.4)	
			3	US	CK (5)	0.0	28.8 (6.8 - 47.4)	26.6 (5.3 - 41.6)
			TM	CK (7)	9.7 ± 27.3	13.8 (5.3 - 21.9)	12.0 (4.0 - 20.5)	
			SC	CK (8)	0.0	6.3 (0.4 - 14.8)	7.3 (0.5 - 16.5)	
			MC	CK (8)	0.0	16.9 (6.0 - 26.9)	14.7 (4.1 - 24.2)	
	FA	1	US	CO (12)	12.7 ± 30.6	26.5 (10.5 - 39.9)	25.5 (10.9 - 38.1)	
			SC	CK (3)	0.0	19.2 (0.2 - 74.2)	8.2 (0.1 - 36.9)	
			MC	CK (6)	0.0	21.9 (2.8 - 54.1)	17.8 (1.9 - 40.6)	
			2	US	CK (1), CO (8)	0.0	9.5 (2.1 - 18.2)	8.3 (1.4 - 16.7)
		SS	CO (8)	36.7 ± 50.6	12.2 (0.5 - 33.0)	21.7 (8.6 - 37.9)		
		TM	CK (8), CO (8)	5.8 ± 23.3	4.6 (0.2 - 14.5)	7.6 (1.2 - 16.4)		
SC		CK (7), CO (5)	0.0	19.6 (11.5 - 26.6)	14.6 (4.8 - 22.4)			

3	MC	CK (4)	0.0	20.6 (1.8 - 60.0)	13.5 (1.0 - 30.6)
	US	CK (3)	58.1 ± 50.5	23.7 (0.7 - 75.3)	40.3 (9.3 - 79.1)
	TM	CK (7)	0.0	35.0 (24.0 - 46.9)	32.1 (19.3 - 43.0)
	SC	CK (8)	0.0	3.4 (0.1 - 11.2)	4.2 (0.1 - 17.3)
	MC	CK (8)	0.0	7.8 (0.3 - 26.3)	6.6 (0.2 - 17.6)

c) Terrestrial prey contributions

Year	Season	Reach	Macrohabitat type	Consumer species (n)	% Terrestrial prey		
					Gut contents	SIMM - Uninformed priors	SIMM - informed priors
2013	SP	1	US	CK (7), CO (6)	28.9 ± 24.9	66.7 (19.8 - 96.7)	38.7 (16.7 - 61.1)
			TM	CK (8), CO (7)	29.3 ± 28.9	52.7 (14.3 - 89.2)	32.9 (14.3 - 54.4)
		2	TM	CK (4)	2.8 ± 5.5	57.5 (23.7 - 87.4)	36.7 (7.6 - 65.0)
	SU	3	TM	CK (2), CO (7)	11.3 ± 29.0	24.6 (2.0 - 59.2)	15.4 (2.7 - 34.9)
		1	TM	CK (1), CO (4)	18.4 ± 31.8	33.7 (1.5 - 84.8)	29.7 (5.0 - 64.3)
		2	TM	CK (2), CO (21)	19.4 ± 28.2	33.1 (16.8 - 51.6)	14.9 (1.8 - 33.8)
			US	CK (1), CO (13)	6.4 ± 12.3	39.9 (9.1 - 77.6)	26.0 (14.8 - 38.5)
			SC	CO (9)	47.4 ± 48.6	39.1 (2.5 - 82.1)	43.3 (20.1 - 69.1)
			TM	CK (3), CO (10)	3.9 ± 13.9	41.8 (14.2 - 66.8)	20.7 (3.4 - 39.0)
	FA	1	US	CO (3)	65.6 ± 56.9	32.1 (3.0 - 66.2)	35.1 (7.0 - 71.2)
		2	TM	CO (23)	13.1 ± 33.4	28.2 (9.5 - 49.8)	18.1 (0.8 - 48.8)
			US	CO (5)	2.9 ± 4.2	36.4 (2.2 - 82.9)	26.0 (14.5 - 38.5)
			SC	CO (11)	39.7 ± 33.7	30.6 (1.4 - 74.0)	37.3 (15.5 - 62.0)
			TM	CK (5), CO (7)	1.4 ± 5.1	26.3 (3.2 - 55.5)	15.9 (1.9 - 35.1)
		3	TM	CK (5), CO (7)	1.4 ± 5.1	26.3 (3.2 - 55.5)	15.9 (1.9 - 35.1)
2014	SP	1	US	CO (6)	36.1 ± 49.9	24.4 (1.4 - 72.7)	14.2 (0.7 - 38.8)
			TM	CO (4)	9.3 ± 18.2	29.6 (1.2 - 79.3)	16.0 (1.1 - 45.4)
			SC	CK (5), CO (1)	11.6 ± 15.1	37.9 (2.4 - 85.2)	15.0 (0.8 - 43.3)
		2	MC	CK (3), CO (6)	16.5 ± 28.7	37.4 (1.9 - 86.1)	12.8 (1.1 - 36.2)
			US	CO (4)	4.5 ± 9.0	10.3 (0.5 - 31.7)	8.4 (0.5 - 24.7)
			SS	CO (5)	20.1 ± 27.6	28.9 (2.5 - 65.7)	27.4 (7.0 - 55.4)
		3	TM	CK (6), CO (10)	25.6 ± 38.8	25.8 (15.6 - 36.3)	24.6 (15.4 - 34.1)
			TM	CK (1), CO (5)	27.8 ± 30.5	21.3 (1.5 - 54.2)	21.1 (5.3 - 41.6)
			SC	CK (4), CO (1)	26.3 ± 36.4	30.8 (1.1 - 80.4)	27.7 (5.5 - 59.4)
		SU	MC	CK (8)	9.7 ± 9.7	39.5 (4.4 - 79.0)	16.8 (1.9 - 40.6)
			US	CK (4), CO (8)	12.5 ± 23.8	46.7 (21.7 - 76.3)	32.9 (13.6 - 53.4)
			TM	CK (6), CO (6)	13.2 ± 24.9	44.2 (24.4 - 66.1)	31.2 (13.7 - 48.7)

FA	2	SC	CK (3)	32.1 ± 19.2	36.4 (1.8 - 84.8)	35.5 (6.4 - 72.3)
		MC	CK (8)	33.2 ± 22.9	28.6 (3.0 - 66.1)	40.1 (20.9 - 61.2)
		US	CK (6), CO (7)	8.6 ± 17.7	39.5 (20.6 - 56.9)	28.3 (10.6 - 45.2)
		SS	CK (2), CO (2)	53.1 ± 51.9	74.0 (37.2 - 96.3)	66.2 (34.6 - 89.4)
		TM	CK (2), CO (6)	15.8 ± 24.6	51.5 (24.4 - 78.6)	40.6 (19.5 - 61.3)
		SC	CK (7), CO (5)	35.3 ± 42.2	25.0 (0.9 - 72.0)	32.5 (12.5 - 58.1)
	3	MC	CK (10)	16.7 ± 16.8	34.9 (6.5 - 66.8)	31.3 (12.7 - 52.6)
		US	CK (5)	1.3 ± 2.5	27.5 (0.9 - 74.6)	11.8 (0.5 - 35.9)
		TM	CK (7)	2.1 ± 3.9	45.6 (19.1 - 71.3)	25.1 (3.9 - 46.9)
	1	SC	CK (8)	16.8 ± 26.4	64.8 (31.4 - 93.5)	43.8 (17.9 - 68.7)
		MC	CK (8)	44.6 ± 31.1	38.2 (6.4 - 72.8)	41.5 (21.3 - 65.1)
		US	CO (12)	30.2 ± 32.5	32.8 (7.5 - 64.8)	30.6 (13.0 - 51.7)
		SC	CK (3)	66.7 ± 57.7	39.1 (2.2 - 87.5)	51.7 (16.6 - 85.3)
		MC	CK (6)	5.7 ± 8.0	34.4 (2.0 - 78.6)	21.0 (0.9 - 57.1)
		US	CK (1), CO (8)	3.6 ± 6.5	33.7 (10.8 - 62.2)	21.7 (4.7 - 41.1)
	2	SS	CO (8)	10.7 ± 19.7	49.6 (12.2 - 85.0)	29.3 (7.2 - 54.1)
		TM	CK (8), CO (8)	8.2 ± 16.5	46.6 (22.0 - 69.6)	28.9 (11.2 - 47.1)
		SC	CK (7), CO (5)	31.8 ± 36.8	59.5 (30.3 - 79.4)	39.8 (22.0 - 57.5)
		MC	CK (4)	2.9 ± 5.9	32.5 (2.1 - 74.9)	19.8 (1.9 - 48.5)
		US	CK (3)	13.4 ± 20.1	39.7 (1.9 - 87.7)	34.8 (5.7 - 72.2)
		TM	CK (7)	0.0	25.7 (1.8 - 57.6)	10.3 (0.4 - 28.7)
	3	SC	CK (8)	0.1 ± 0.3	70.1 (33.7 - 93.9)	26.9 (2.3 - 59.6)
		MC	CK (8)	1.7 ± 3.1	53.1 (11.6 - 90.6)	24.3 (4.1 - 51.0)

Note: Season codes: “SP” = Spring, “SU” = Summer, and “FA” = Fall. Macrohabitat type codes: “US” = Upland slough, “SS” = Side slough, “TM” = Tributary mouth, “SC” = Side channel, and “MC” = Main channel. Sampling events where $n \leq 2$ were not considered in analyses and are not included in this table.