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Juvenile salmon body condition in Southeast Alaska is buffered during marine heatwaves

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ABSTRACT: Pacific salmon (*Oncorhynchus* spp.) are ecologically, culturally, and commercially valuable throughout the Pacific Rim. Early marine survival of juvenile salmon is crucial for maintaining population abundance and sustainable fisheries. Climate variability, including multiple marine heatwaves, have recently caused ecosystem-wide changes and stressors with reduced return rates for some salmon populations in the Gulf of Alaska. We examined dietary niche breadth and condition metrics in juveniles of 4 salmon species (chum *O. keta*, coho *O. kisutch*, pink *O. gorbuscha*, and sockeye *O. nerka*), spanning 2010 to 2019, including 2 prominent heatwaves (2015—2016 and 2019). Samples were collected annually in Icy Strait, a major fish migration corridor in the Southeast Alaska archipelago. Analyses included bulk δ^{15}N and δ^{13}C stable isotopes, stomach contents, energy density, and morphometrics to evaluate variability in niche breadth and condition in response to extreme climate events. Interannual variability in stable isotopes was primarily explained by sea surface temperature (SST) anomalies for all species. The inverse relationship between SST and δ^{13}C suggests the potential for increased terrestrial input into the nearshore environment during warmer conditions. We also found weak relationships between interannual variability in stomach contents and SST anomalies for pink salmon and a combination of δ^{13}C, δ^{15}N, SST, and condition for coho. However, fish condition did not show a significant relationship with SST anomalies. We propose that the complex topography and oceanography of northern Southeast Alaska provide marine habitat that temporarily buffers juvenile salmon from declines in body condition during heatwaves prior to migration into the Gulf of Alaska.

KEY WORDS: Marine ecology · Fisheries · Trophic ecology · Stable isotope analysis · Diet analysis · Pacific salmon · *Oncorhynchus*

1. INTRODUCTION

Pacific salmon (*Oncorhynchus* spp.) are ecologically, culturally, and commercially valuable species, with salmon spawning biomass sometimes linked to juvenile abundance (Murphy et al. 2021). In the state of Alaska (USA), juvenile salmon surveys play a crucial role in forecasting adult returns, which are vital for effective fishery management. For instance, juvenile Chinook salmon *O. tshawytscha* abundance estimates from surveys in the Northern Bering Sea are used to forecast adult Chinook returns to the Yukon River; similarly, in Southeast Alaska (SEAK), juvenile salmon abundance is used to forecast adult pink salmon *O. gorbuscha* harvests (Murphy et al. 2022). These forecasts rely on a strong relationship between juvenile salmon survival and subsequent adult returns, emphasizing the importance of monitoring juvenile populations to predict future fishery yields (Murphy et al. 2017). Examining environmental impacts on early life stages is essential for furthering our understanding of juvenile survival and its relationship to adult returns and fisheries management.

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The survival and growth rates of juvenile Pacific salmon have been linked to ocean conditions and food availability at regional scales (Mueter et al. 2002, Malick et al. 2015, Keister et al. 2022). These connections include thermal responses associated with metabolic rates, as well as changes in prey availability and prey quality, among other ecosystem drivers (Farley & Trudel 2009, McKinstry & Campbell 2018). Measurable effects of marine heatwaves and warm ocean temperatures on juvenile salmon vary regionally and have been connected to declines in fish condition across the eastern Pacific and Bering Sea (Botsford & Lawrence 2002, Mueter et al. 2002, Andrews et al. 2009, Daly et al. 2017). In multiple regions of Alaska, warm water has been associated with increased salmon survival rates and improved fish condition (Mueter et al. 2002, Farley et al. 2007, Malick et al. 2015, Kohan et al. 2019, Fergusson et al. 2020).

Recent marine heatwaves in Alaska, however, were notable in being longer lasting and of greater magnitude than previous warm periods, and included warming throughout the water column (Hobday et al. 2018, Walsh et al. 2018, Danielson et al. 2022). This persistent warming reduced the condition and abundance of key prey species (Arimitsu et al. 2021) and led to widespread effects throughout the food web from zooplankton to humans, including commercial salmon harvests (Cavole et al. 2016, Walsh et al. 2018, Suryan et al. 2021) as well as declines in juvenile salmon fish condition observed in western Alaska (Farley et al. 2024). Since the North Pacific marine heatwaves in 2014–2016 and 2019 (Bond et al. 2015, Di Lorenzo & Mantua 2016, Amaya et al. 2020), there is evidence that the relationship between predominant modes of climate variability in the North Pacific and ecosystem responses are shifting as climate warming continues, and warm marine conditions may become less favorable for salmon survival in Alaska (Litzow et al. 2020a,b, Farley et al. 2024).

Following warm temperature anomalies in 2015–2016 and 2019, multiple salmon stocks in the Gulf of Alaska declined (North Pacific Anadromous Fish Commission 2021, Ruggerone et al. 2021), prompting US State and Federal agencies to issue fishery disaster declarations (NOAA Fisheries 2022). Furthermore, adult returns have not been consistent between species or between different stocks within a species, and some stocks of Pacific salmon have shown reduced abundance during and after heatwaves (Peterson et al. 2016, Heinl et al. 2017, Reid et al. 2019, Hagerman et al. 2021, Thynes et al. 2022). Freshwater conditions, including drought-associated low water flows and reduced dissolved oxygen, were a clear impediment to adult salmon spawning success and survival in some locations (Sergeant et al. 2017, von Biela et al. 2022). In other cases, however, declines in adult salmon abundance were best explained by reduced marine survival of juvenile fish (Murphy et al. 2022, Farley et al. 2024).

It is critical for juvenile salmon to find sufficient food during early marine residence (Cooney et al. 2001, Willette et al. 2001) and reach a minimum length and body condition by early fall of their first marine year to survive predation and fasting during winter, a period of limited food availability (Beamish & Mahnken 2001, Malick et al. 2011). During recent heatwaves in some regions, however, nutritional needs of juvenile salmon were not met despite relatively high biomass of prey (Daly et al. 2017, Murphy et al. 2021). In western Alaska, although juvenile salmon biomass increased during warm years, body condition declined due to poor food quality, contributing to overall population declines (Farley et al. 2024). It has been hypothesized that during periods of varying ocean conditions in the Gulf of Alaska, juvenile salmon in the inside waters of the SEAK archipelago were not food-limited (Sturdevant et al. 2012, Fergusson et al. 2020).

SEAK experienced above-average sea surface temperatures (SSTs) during recent marine heatwaves; however, maximum temperatures were consistently lower than those observed in the eastern Gulf of Alaska (EGOA) outer coast region by up to 3°C (Orsi & Fergusson 2016, Fergusson et al. 2018). SEAK includes an abundance of complex oceanography and geography that contribute to unique and diverse marine habitats (Stabeno et al. 2004, Weingartner et al. 2009), with the potential for local processes to partially buffer this region from large-scale marine heatwave impacts observed in the Gulf of Alaska.

We used a 10 yr data set on juveniles of 4 sympatric salmon species obtained in SEAK between 2010 and 2019, which includes 2 marine heatwave periods (2015–2016 and 2019) to assess the effect of marine heatwaves on juvenile salmon dietary niche breadth and condition. We expand on a recent study (Fergusson et al. 2020) that showed a shift in dominant prey species during one heatwave year with minimal effect on juvenile salmon condition. Our study includes 2 additional heatwave years and the addition of stable isotope analysis paired with stomach content analysis to provide a more complete picture of dietary niche breadth during heatwaves. Whereas stomach content analysis used by Fergusson et al. (2020) yields information about specific prey items consumed during the past hours to days, stable isotope analyses provide information integrated over weeks to months (Sakano et al. 2005). We also included a comparison of body condition for fish collected in the EGOA.

Based on declines in juvenile salmon condition and food web changes observed in response to recent marine heatwaves (Arimitsu et al. 2021, Suryan et al. 2021, Farley et al. 2024), we would expect to see SST impacts on fish condition and dietary niche breadth in SEAK — although potentially dampened based on dietary shifts observed in 2015 in shorter local studies (Fergusson et al. 2020) and indications of slightly reduced SST variability. We examined diet shifts in response to changing water temperatures to evaluate whether the inside marine waters of SEAK provide marine habitat that buffers juvenile salmon from declines in body condition during extreme climate events.

2. MATERIALS AND METHODS

2.1. Study region and sample collection

The Southeast Alaska archipelago has unique geography and oceanography that includes glacial and mountainous terrain with substantial freshwater runoff, fjords, and deep, complex bathymetry, as well as a narrow continental shelf (Stabeno et al. 2004, Weingartner et al. 2009). The outer coast typically experiences downwelling-favorable winds as well as eddies and cross-shelf exchange. The oceanography of this region is further influenced by a combination of winds and strong tidal mixing that can include deep mixing of nutrients to the surface (Stabeno et al. 2016). Our primary study region in SEAK has narrow channels and complex physical dynamics controlling mixing and circulation that results in a wide array of unique and diverse marine habitats.

Our study includes samples from juveniles of 4 Pacific salmon species: chum *Oncorhynchus keta*, coho *O. kisutch*, pink *O. gorbuscha*, and sockeye *O. nerka*. Fish samples were obtained during Southeast Coastal Monitoring surveys in August between 2010 and 2019 from 4 stations in Icy Strait in SEAK (Fig. 1). Samples from SEAK include a total of 282 juvenile salmon collected between 2010 and 2019.

A full description of sample collection methods can be found in Fergusson et al. (2020). Briefly, a surface rope trawl was used to collect fish in the upper 20 m, towed from the stern of the survey vessel. Fish samples were sorted and juvenile salmon were identified to species. Fork lengths (±1.0 mm) were measured, and each fish was individually frozen on board the survey vessel and then transferred to −20°C freezers

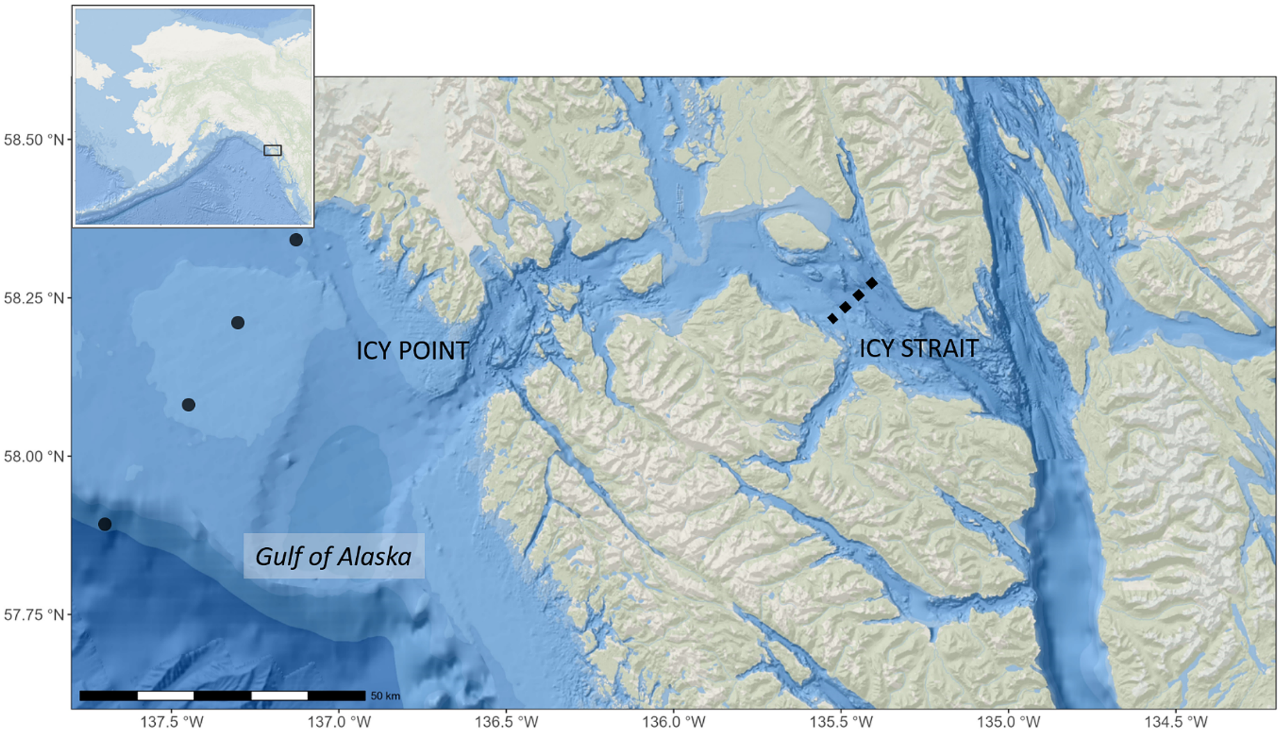

Fig. 1. Sampling stations in Icy Strait in Southeast Alaska (SEAK, black diamonds) and near Icy Point in the eastern Gulf of Alaska (EGOA, black circles)

before laboratory processing and analyses. Within 2 mo of samples arriving at the laboratory, frozen wet mass (±0.1 mg) was measured and stomach contents were removed for later analysis. Whole-body samples (minus stomach contents) were individually wet-homogenized, then a subsample was dried, ground into a fine powder, and stored in small air-tight vials in a desiccator prior to isotope and energy density analyses.

A subset of the data, including 2013–2017 stomach contents and morphometrics, were previously reported by Fergusson et al. (2020); however, our analysis includes an additional 5 years encompassing an additional heatwave and cool years, as well as the inclusion of stable isotope analysis of isotopic niche area and overlap which had not been previously conducted. Our fish collections included both wild and hatchery-raised juvenile salmon which we evaluated for potential biases within the data set. Based on our comparison of wild and hatchery-raised chum salmon (Text S1 and Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m760p135_supp/), we assumed that the metrics used in our study did not differ by origin of sampled fish.

Seawater temperature profiles were routinely sampled across June, July, and August months from SEAK (Fig. 1) using a conductivity-temperature-depth (CTD) profiler (Seabird Scientific SBE 19plus V2 seaCAT Profiler) down to 200 m depth, or within 10 m of the bottom. Annual SSTs were calculated from monthly means integrated down to 20 m surface depth to capture the portion of the water column where juvenile salmon occur and represent temperatures experienced by juvenile salmon throughout their first summer in the marine environment (Fig. 1).

2.2. Stable isotopes

We conducted stable isotopic analysis of 282 archived homogenate samples collected in August between 2010 and 2019 (excluding 2017) from SEAK (Tables S1 & S2). We analyzed up to 10 samples yr^{-1} for chum (2011–2016, 2018–2019), coho (2010–2016, 2018–2019), pink (2013–2016, 2018–2019), and sockeye (2011–2014, 2016, 2018–2019). Data gaps exist due to limited sample availability.

For isotopic analysis, individual dry homogenate samples were weighed to 0.8–1.0 mg at a precision of 0.001 mg and packed into tin capsules. We measured stable carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) isotope ratios using a ThermoScientific FlashSmart Elemental Analyzer coupled to a ThermoScientific Delta V Isotope Ratio Mass Spectrometer, using the approach and methodology detailed by Rogers et al. (2023). Changes in isotope ratios are expressed relative to reference values in units of per mil (‰) using delta notation. Reference values used are Pee Dee belemnite carbonate for carbon isotopes and N_2 in air for nitrogen isotopes. Nitrogen isotopes ($\delta^{15}N$) can indicate relative trophic position of an organism, and carbon isotopes indicate differences in the sources of terrestrial (lower $\delta^{13}C$) or marine-derived (higher $\delta^{13}C$) carbon and prey sources.

Lipid content can bias measured ^{13}C values in aquatic animals irrespective of their carbon source (Kiljunen et al. 2006, Post et al. 2007). To account for this, we used the methodology for lipid corrections detailed by Kiljunen et al. (2006) which has been shown to be effective for Pacific salmon (Lerner & Hunt 2022). We used C:N ratios from elemental analysis to first compute the proportional lipid content (L) of a sample:

$$L = \frac{93}{\{1 + [0.246 \times (\mathrm{C{:}N}) - 0.775]^{-1}\}} \quad (1)$$

where C:N is the carbon to nitrogen ratio of a given sample. We then applied the lipid correction using the following equation:

$$\delta^{13}\mathrm{C} = \delta^{13}\mathrm{C}_{\mathrm{raw}} + \mathrm{D} \times \left[\mathrm{I} + \frac{3.90}{\left(1 + \frac{287}{L}\right)}\right] \quad (2)$$

where $\delta^{13}C$ is lipid corrected, $\delta^{13}C_{raw}$ is the raw measured carbon isotope value, D is the isotopic difference between protein and lipid determined by slope curvature of the lipid normalization model, and I is a constant that defines the model intersection on the x-axis. We used values of D = 7.018 and I = 0.048 as determined by Kiljunen et al. (2006).

2.3. Stomach content diet composition

The mean fork length for each species was determined for each sample year. We then selected up to 10 fish of each species within 1 SD of the mean length for stomach content analysis for each sample month. Stomach content diet composition was determined for the juvenile salmon samples by examining stomach contents, and prey were identified to the lowest possible taxon using a dissecting microscope and weighed (±1.0 mg). Prey were then taxonomically grouped as amphipods, copepods (small and large calanoids), decapods, euphausiids, fish larvae, gastropods, gelatinous prey, and 'other'. For each year and species, mean percent composition by weight was calculated for each prey group.

2.4. Fish condition metrics

Fish condition was characterized as the residuals from log transformed linear regression models for both length and weight residuals and energy density residuals. Length and weight data were obtained as described in Section 2.1. Energy density (kJ g^{-1} dry weight) was measured on dried homogenates using a Parr 6725 semi-microbomb calorimeter as outlined by Siddon et al. (2013).

We found a significant relationship between length and weight for all species ($r > 0.96$, $p < 0.001$). Energy density also had a significant relationship with length for chum, coho, and pink salmon ($r = 0.3$–0.7, $p < 0.003$). To account for these correlative relationships, we natural log transformed the data in linear models to compute length-corrected residuals of weight versus length and energy density versus length. Separate linear models were run for each species for both condition metrics.

2.5. Statistical analyses

Statistical analyses were performed using R Statistical Software v4.2.2 (R Core Team 2022), unless otherwise noted.

2.5.1. Stable isotopes

We used isotopic niche area and overlap to evaluate diet specialization and overlap among species (Graham et al. 2021). We used the R package 'SIBER' v2.1.6 (Jackson et al. 2011) to estimate isotopic niche breadth and overlap among species and years. We estimated summary statistics of Bayesian standard ellipse area, which uses a Bayesian approach and includes multimodal posterior distributions when determining niche area (‰^{2}) for each species, and provides robust estimates of isotopic niche area with variable sample sizes. For these niche area estimates, we specified 20 000 iterations and credible intervals of 95 and 99%.

To test differences in isotopic niche area among species in a given year, we calculated the probability that isotopic niche area posterior distribution was smaller (or larger) by comparing posterior draws for both groups. Niche overlap estimates were computed using the standard ellipse area and a Monte Carlo approach to compute the posterior probability that a given species would be found within the niche of another species, specifying 100 iterations and 95% niche region size as function parameters.

2.5.2. Stomach content diet composition

We used PRIMER version 7 (Anderson et al. 2008) for stomach content diet composition analyses. Prior to statistical testing, the percent composition stomach content data were fourth-root transformed to give less weight to the most prevalent prey items (Clarke & Warwick 2001). Comparisons in interannual variability of the stomach contents of each salmon species were made using a distance-based test for homogeneity of multivariate dispersions (PERMDISP) operating on Bray-Curtis similarity matrices. PERMDISP reports an overall *F*-statistic with associated p-value of statistical significance and the mean (and SD) distance from the centroid for each species tested. Stomach contents were visualized with a heatmap using the R package 'tidyverse' (Wickham et al. 2019), for each year and species.

2.5.3. Fish condition metrics

We used a Shapiro-Wilk test to evaluate normality and homogeneity of variances. The Shapiro-Wilk test results for all species indicated that data were not significantly different from a normal distribution for energy density residuals ($p = 0.136$–0.716) or length–weight residuals ($p = 0.144$–0.330). We tested for significant differences in energy density residuals and length–weight residuals between years within each species with separate ANOVAs for each condition metric within the R built-in 'stats' package and pairwise multiple comparison post-hoc Tukey HSD test in the R package 'emmeans' v1.10.2 (Lenth 2024).

2.5.4. Comparisons and environmental analysis

We defined warm and cool years in SEAK based on whether annual mean SST values were significantly above or below long-term mean SST (10.1°C), respectively, and determined whether above average temperatures were observed in SEAK during marine heatwave years. A Shapiro-Wilk test showed that SST data were not significantly different from a normal distribution ($p = 0.300$). We used ANOVA ($p < 0.001$) and *t*-test statistics that indicated a significant difference between annual mean and long-term mean SST values with a 99% confidence limit (Fig. 2). Cool years (0.6 ± 0.2°C below mean SST) included 2011, 2012, and 2017, and warm years (0.7 ± 0.2°C above mean SST) included 2015, 2016, and 2019 ($p \leqslant 0.001$). Warm years with above-average SST values observed in SEAK were consistent with the marine heatwaves experienced in the Gulf of Alaska during 2015–2016 and 2019 (Bond et al. 2015, Di Lorenzo & Mantua 2016, Amaya et al. 2020).

Z-scores for SST anomalies were calculated using:

$$Z = \frac{x - \mu}{\sigma} \tag{3}$$

where Z is the standardized anomaly, x is the SST for a given year, μ is the long-term mean (1997–2019), and σ is the SD of the long-term mean. We evaluated the correlation between SST anomalies and multiple covariates (length, length–weight residuals, energy density residuals, $\delta^{15}N$, $\delta^{13}C$, and stomach content diet composition) using a random phase test (Ebisuzaki 1997) to avoid over-confidence due to autocorrelation in time-series. This analysis was done using MATLAB (The Mathworks Inc 2020) and functions within the 'WEACLIM' package (Moron 2017). We ran the Ebisuzaki (1997) significance test with 999 iterations to estimate correlation coefficients and determine the likelihood that correlations were not random.

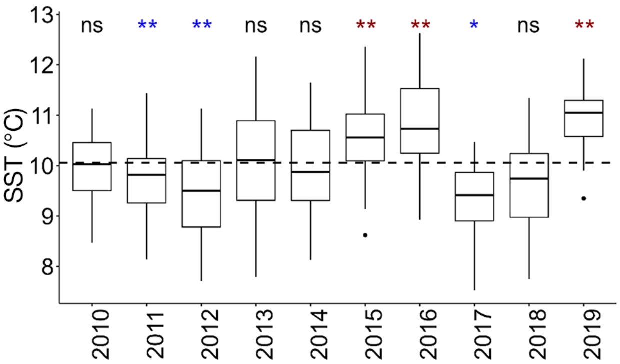

Fig. 2. Mean summer (June–August) sea surface temperature (SST) in Southeast Alaska (SEAK), integrated to 20 m surface depth. Dashed line shows average SST (10.1°C). Statistical differences from the mean SST of a given year from the long-term mean were obtained from a *t*-test: $^{**}p \leqslant 0.0001$; $^{*}p \leqslant 0.001$; ns: $p > 0.04$ (blue and red asterisks indicate relatively cool [2011, 2012, and 2017] and relatively warm periods [2015, 2016, and 2019], respectively). Boxplot midlines indicate annual median values, upper and lower limits of the box reflect the first and third quartiles, and whiskers show 1.5 times the interquartile range. Outliers are indicated as individual points beyond the whiskers. Warm years in SEAK are consistent with marine heatwave years in the Gulf of Alaska

The combination of stable isotope and stomach content diet composition provides a unique and integrated assessment of dietary niche breadth and overlap on multiple timescales (Sakano et al. 2005, Adams et al. 2017), to better evaluate links between environmental variability and fish condition. We used the 'BEST BIOENV' analysis routine in PRIMER version 7 (Clarke & Ainsworth 1993, Anderson et al. 2008) to calculate Spearman rank correlation (ρ_s) between similarity matrices of both stable isotopes and stomach content diet composition with select covariates. This routine uses a D1 Euclidean distance resemblance measure matrix and the resulting correlation values range from 0 to +1; values close to +1 indicate high correlation, while values close to 0 indicate little to no correlation. We used a scale of weak ($\rho_s < 0.4$), moderate ($0.4 \leqslant \rho_s < 0.7$), and strong ($\rho_s \geqslant 0.7$) correlations (Schober et al. 2018).

The covariates used for the stable isotope 'BEST BIOENV' analysis included energy density and length–weight residuals, and SST. The covariates used for the stomach content diet composition 'BEST BIOENV' analysis included energy density and length–weight residuals, SST, $\delta^{15}N$, and $\delta^{13}C$. In both cases, covariates were normalized as *Z*-scores to give equal weight to each variable in the subsequent multivariate analysis. We tested for statistical significance of these results using 999 permutations (global BEST test; Clarke & Warwick 1998) to test the null hypothesis for no relationship between a given set of covariates and both the stomach content diet composition and isotope similarity matrices, respectively.

2.6. SEAK comparison with the EGOA

For a comparison region, additional juvenile Pacific salmon length and weight data were also obtained from 4 Southeast Coastal Monitoring survey stations near Icy Point in the EGOA (Fig. 1). In contrast to the inside and more protected waters of SEAK, the EGOA region is exposed and located on the outer coast, with sampling stations out to 65 km offshore along the outer continental shelf. While above-average SSTs were observed in the inside waters of SEAK during the 2015–2016 marine heatwave years, maximum temperatures were consistently lower than those observed in the EGOA outer coast region by up to 3°C (Orsi & Fergusson 2016, Fergusson et al. 2018).

Length and weight data from the EGOA included a total of 571 juvenile salmon samples from 2010 to 2017 collected annually in August using the same methods described for SEAK sampling (Section 2.1). We compared length–weight residuals between the inside waters of SEAK and the outer coast of the EGOA with a non-parametric Wilcoxon test ('wilcox.test'). Years with samples from both regions include 2010–2016 for coho and pink, 2011–2016 for chum, and 2011–2016 (excluding 2015) for sockeye. There were insufficient length and weight data for statistical comparisons in 2010 and 2014 for coho ($n < 3$ for EGOA) and 2013 for both coho and sockeye (no SEAK data and $n < 3$ for EGOA). Energy density, stomach content diet composition, and stable isotopes were not available to compare from EGOA samples.

Complete sample sizes by species and year with available data metrics are summarized in Table S1. EGOA SSTs were collected in July and August using methods described in Section 2.1 for SEAK SST values. While above-average SSTs were observed in the inside waters of SEAK during the 2015–2016 marine heatwave years, SST values measured in SEAK were less variable and consistently 2.5 ± 1°C lower than those measured in the EGOA (Fig. S2).

3. RESULTS

3.1. Stable isotopes

'BEST BIOENV' multivariate analysis showed that coho and sockeye isotopic values (Fig. 3; Table S2) were more closely correlated with SST than with body condition. This included a moderate relationship with SST for sockeye ($\rho_s = 0.41$, $p = 0.001$) and weak relationship for coho ($\rho_s = 0.12$, $p = 0.042$). We also found weak but significant correlations between isotopic values and a combination of SST and energy density residuals for chum ($\rho_s = 0.12$, $p = 0.011$) and a combination of SST and length–weight residuals for pink ($\rho_s = 0.23$, $p = 0.003$). Both chum and pink also had correlation coefficients with SST alone that were equivalent (chum, $\rho_s = 0.12$) or a close second (pink, $\rho_s = 0.21$). Overall, SST was consistently in the top 3 model results for all 4 species, while energy density and length–weight residuals were not.

We found significant negative correlations (Table 1) between SST and $\delta^{15}N$ for pink ($r = 0.56$, $p < 0.0001$) and sockeye ($r = -0.40$, $p = 0.045$). Similarly, we found significant negative correlations between SST and $\delta^{13}C$ for chum ($r = -0.42$, $p = 0.035$), pink ($r = -0.50$, $p = 0.023$), and sockeye ($r = -0.70$, $p < 0.0001$).

Isotopic niche area was highly variable, with coefficients of variation between 57 and 66% across species (Table 2); however, we did not find a consistent response to SST anomalies. For example, the highest

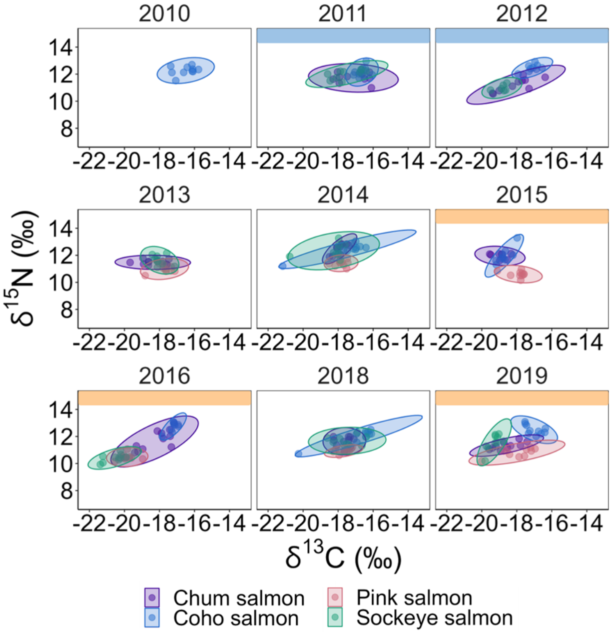

Fig. 3. August stable isotope biplots for $\delta^{15}N$ and lipid-corrected $\delta^{13}C$ (Kiljunen et al. 2006) for Southeast Alaska (SEAK) juvenile salmon with each year separated into an individual panel. Each filled circle represents an individual fish sample from a given year for each species as identified by different colors. The shaded area represents a 95% confidence ellipse for each year and species. The colored strip at the top of each plot panel denotes warm (orange) or cool (blue) years. No data available in 2017

Table 1. Correlation coefficients between sea surface temperature (SST) anomalies and additional correlates (length, length–weight residual [LWR], energy density residual [EDR], $\delta^{15}N$, $\delta^{13}C$, and stomach content diet composition distance from centroid [diet variability]). Statistically significant correlations above a 95% confidence limit are shown in **bold**. Values in parentheses give likelihood (in percentage) that correlations are not random, determined using the Ebisuzaki (1997) significance test

Species	Length	LWR	EDR	$\delta^{15}N$	$\delta^{13}C$	Diet variability
Chum	**+0.73** (97)	−0.09 (71)	−0.05 (63)	−0.01 (54)	**−0.42** (96)	**−0.60** (>99)
Coho	**+0.60** (96)	−0.20 (78)	−0.07 (67)	+0.19 (92)	−0.28 (82)	−0.28 (78)
Pink	**+0.72** (97)	+0.07 (68)	+0.14 (81)	**−0.56** (>99)	**−0.50** (98)	−0.50 (90)
Sockeye	**−0.52** (98)	−0.21 (93)	−0.04 (60)	**−0.40** (96)	**−0.70** (>99)	−0.70 (53)

3 chum area values, all of which were above +1 SD, occurred in 1 heatwave year and 2 non-heatwave years, but the lowest area also occurred in a heatwave year. On average, isotopic niche area for pink salmon was the smallest and least variable (0.33 ± 0.20‰^{2}) relative to the larger average niche area and variability estimates for chum, coho, and sockeye (0.61 ± 0.35‰^{2}, 0.53 ± 0.35‰^{2}, and 0.56 ± 0.33‰^{2}, respectively).

We did not find a statistically significant relationship between SST anomalies and isotopic overlap (Table S3), although we did see reduced overlap estimates for all species combinations in both 2016 and 2019 (with the exception of pink and sockeye in 2016).

3.2. Stomach content diet composition

Stomach contents were variable and species-dependent, with occasional overlaps between species (Fig. 4). Generally, chum stomach contents switched between gelatinous prey and euphausiids; coho stomach contents predominantly consisted of fish or decapods; pink stomach contents included a combination of gelatinous prey, gastropods, and euphausiids; and sockeye stomach contents included a combination of all non-fish prey types.

'BEST BIOENV' multivariate analysis indicated a weak relationship for stomach content shifts and variability with SST for pink (ρ_s = 0.22, p = 0.001) and sockeye (ρ_s = 0.09, p = 0.045), and a combination of SST, δ^{13}C, δ^{15}N, and length–weight residual for coho (ρ_s = 0.20, p = 0.001). The most consistent covariate in the top 3 coho models was δ^{13}C with roughly equivalent correlation values (ρ_s ± 0.01). No significant correlations were found for chum (p = 0.134) stomach contents with any of the covariates tested.

All species showed a negative correlation between SST anomalies and distance from centroid (Table 1), indicating reduced stomach content variability in warmer years, although this was only significant for chum (r = −0.6, p < 0.001). All species were least variable in heatwave year 2015 when euphausiids were the dominant prey for all species (Table 3). Heatwave year 2019 also had low stomach content diet variability with synchronous prey focus on amphipods.

3.3. Fish condition metrics

Fish length but not condition was correlated to SST anomalies for all 4 species (Table 1). We found a positive correlation indicating increased lengths with warmer SST anomalies for chum (r = 0.7, p = 0.031), coho (r = 0.6, p = 0.037), and pink (r = 0.07, p = 0.031), and a negative correlation, indicating shorter lengths with warmer SST, for sockeye (r = −0.5, p = 0.020). In contrast, although energy density residuals (Fig. 5) were significantly different among years for chum (ANOVA $F_{7,69}$ = 4.6, p < 0.001), coho (ANOVA $F_{7,71}$ = 3.5, p = 0.003), and pink (ANOVA $F_{5,54}$ = 24.08, p < 0.0001), the post hoc Tukey HSD test did not reveal significant groupings across our warm and cool year designations. Consistent with this, neither energy density residuals nor length–weight residuals were correlated with SST anomalies for any of

Table 2. Isotope niche area (‰^{2}) for each species computed using the Bayesian standard ellipse area. Mean estimated values and 95% confidence/credible intervals of the posterior distribution of isotopic niche ellipse area are included. Isotopic niche area estimates greater or less than 1 SD away from the record mean are denoted in **bold**. Highlighted rows indicate relatively warm (orange) and cool (blue) years. –: years with no data available for a given species

Year	Chum	Coho	Pink	Sockeye
2010	–	0.51 (0.26, 1.06)	–	–
2011	**0.92 (0.48, 1.85)**	0.32 (0.17, 0.65)	–	0.65 (0.32, 1.32)
2012	**0.94 (0.49, 1.93)**	0.25 (0.12, 0.52)	–	**0.20 (0.08, 0.51)**
2013	0.39 (0.20, 0.77)	–	0.36 (0.18, 0.72)	0.37 (0.19, 0.73)
2014	0.28 (0.14, 0.57)	**1.10 (0.58, 2.22)**	0.20 (0.11, 0.43)	**1.20 (0.60, 2.40)**
2015	0.29 (0.11, 0.67)	0.41 (0.19, 0.78)	0.30 (0.15, 0.57)	–
2016	**1.20 (0.65, 2.46)**	0.20 (0.10, 0.39)	0.28 (0.15, 0.57)	0.37 (0.19, 0.74)
2017	–	–	–	–
2018	0.42 (0.22, 0.85)	**1.06 (0.55, 2.15)**	0.16 (0.08, 0.32)	0.68 (0.37, 1.51)
2019	0.46 (0.22, 0.89)	0.41 (0.21, 0.80)	**0.71 (0.33, 1.41)**	0.43 (0.23, 0.88)
Mean ± SD	0.61 ± 0.35	0.53 ± 0.35	0.33 ± 0.20	0.56 ± 0.33
CV (%)	57	66	61	59

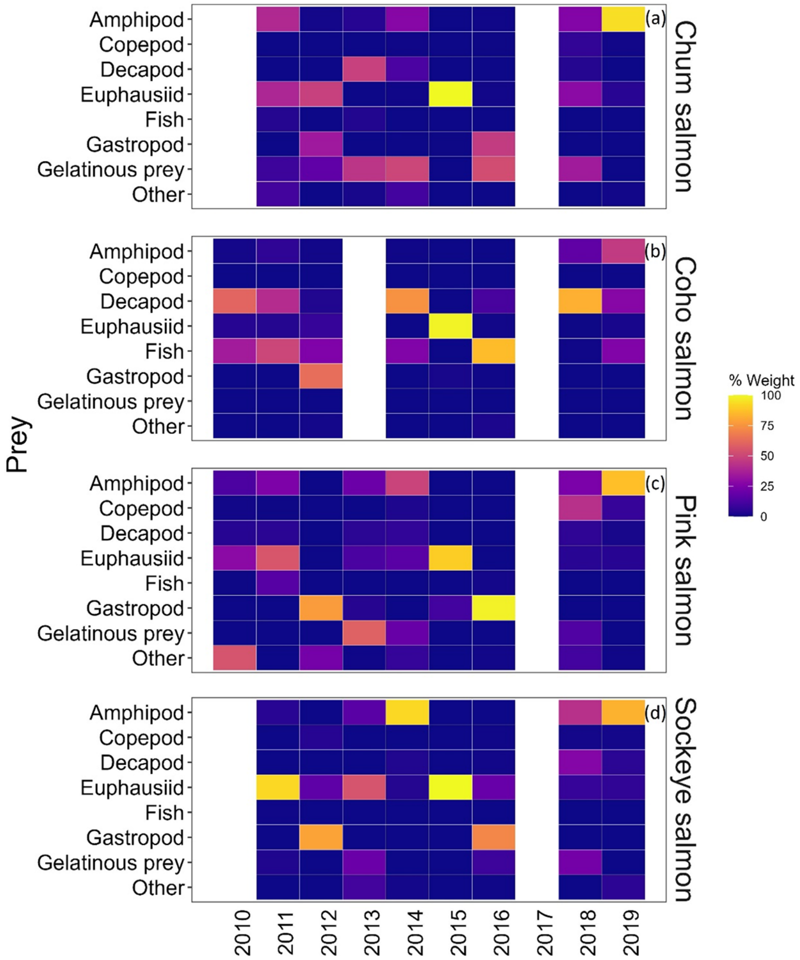

Fig. 4. Percent composition by weight of prey items from juvenile salmon stomach contents from Southeast Alaska (SEAK) for each species in August: (a) chum, (b) coho, (c) pink, and (d) sockeye

the salmon species ($p \geqslant 0.192$). Additionally, neither energy density residuals nor length–weight residuals showed consistent significant relationships with stable isotope or stomach content diet variability.

3.4. SEAK comparison with the EGOA

Fish condition, as indicated by length–weight residuals, was either higher in SEAK compared to the EGOA, or not statistically significant across species during 2010–2016, with the exception of 2013 (Fig. 6; Table S4). Length–weight residuals in SEAK were higher by a mean of 0.06 ± 0.02 in years with significant differences between the 2 regions. Differences between regions were an order of magnitude higher for sockeye and chum during 2014 (warm year in the EGOA) and 2015 (warm year in both regions), with sockeye length–weight residuals in SEAK higher than in the EGOA by 0.14 ($p = 0.007$) in 2014, and chum length–weight residuals in SEAK higher than those in the EGOA by 0.16 ($p < 0.001$) in 2015. The one year when length–weight residuals in SEAK were significantly lower than those in the

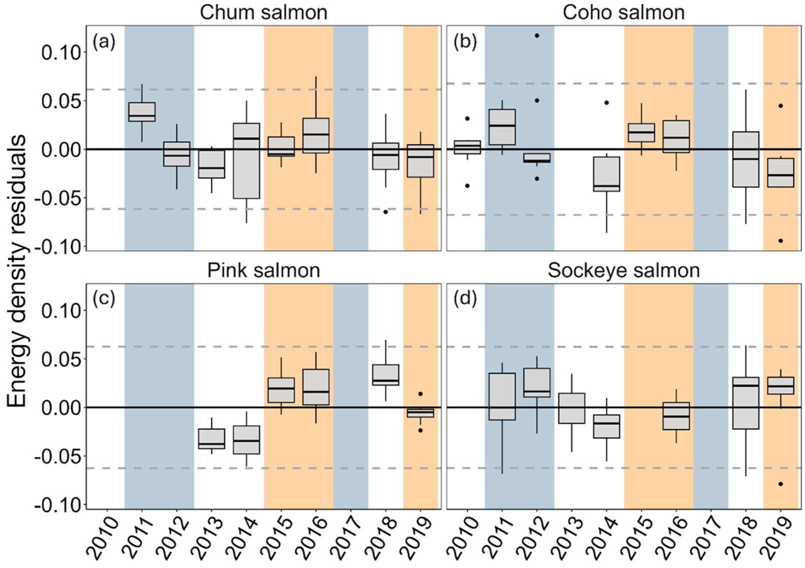

Fig. 5. Energy density length-corrected residuals from August in Southeast Alaska (SEAK) for (a) chum, (b) coho, (c) pink, and (d) sockeye salmon. Shaded regions indicate warm (orange) and cool (blue) years. Boxplot midlines indicate median values, upper and lower limits of the shades box reflect the first and third quartiles, respectively, whiskers show 1.5 times the interquartile range, and individual points show outliers beyond 1.5 times the interquartile range. The energy density residuals for each species vary above and below the zero line (solid line), but the interquartile range remains within 95% confidence intervals (gray-dashed lines)

Table 3. Variability of stomach content diet composition of salmon species from a distance-based test for homogeneity of multivariate dispersions (PERMDISP). Mean distance from centroid is reported for each year. —: years that do not have samples for a given species. Highlighted rows indicate relatively warm (orange) and cool (blue) years. Pseudo-*F* is reported for each species as a summary row; **bold** values are significant at $\alpha = 0.05$

Year	Chum	Coho	Pink	Sockeye
2010	–	22.63	27.76	–
2011	35.53	31.07	19.97	7.59
2012	38.05	26.05	15.83	21.04
2013	35.49	–	30.28	43.06
2014	28.27	23.58	24.42	14.98
2015	3.72	5.41	4.14	0.00
2016	21.23	19.37	6.83	23.38
2017	–	–	–	–
2018	–	–	–	–
2019	14.77	30.91	21.59	22.65
Pseudo-*F*	**9.88**	**3.01**	**5.24**	**5.69**

EGOA for both chum (−0.053, p = 0.039) and pink (−0.067, p = 0.008) was 2013, a neutral SST year in both regions.

4. DISCUSSION

We demonstrated that juvenile salmon in SEAK consumed a wide diversity of prey with variation in whole body isotopic values being more consistently related to ocean temperature than diets from stomach content analysis. Both methods, however, did show reduced dietary niche breadth during heatwave years. Although juvenile salmon body size was related to temperature, body condition was not related to temperature or diet, suggesting that foraging conditions in SEAK were sufficient to buffer fish from potential declines in body condition during heatwave years, in contrast to other regions of the Northeast Pacific. Sockeye salmon, in particular, showed the least variability in body condition, with no significant differences in energy density residuals among years.

We found that SST could best explain significant shifts in isotope values in all 4 species. This pattern generally indicated lower $\delta^{13}C$ in years with warmer SST across species, as well as lower $\delta^{15}N$ in years with warmer SST for pink and sockeye. Chum and pink isotopes also showed weak but significant relationships with energy density residuals and length–weight residuals, respectively. SST was the most consistent covariate present in the top 3 model results across species. The inverse relationship between SST and $\delta^{13}C$ could indicate an increase in terrestrial input into the nearshore environment in warmer years, and the inverse relationship between SST and $\delta^{15}N$ for pink and sockeye could point to the consumption of prey at lower trophic levels during warmer years; however, the mechanism of these relationships remain unclear. Additional explanations could include changes in outmigration patterns, a decrease in nearshore prey sources, or shifts in isotopic baselines (Cabana & Rasmussen 1996, Vander Zanden & Rasmussen 1999), and this is difficult to discern without additional isotope data from the marine environment.

The relationships between salmon tissue isotopes and SST found in this study are indicative of prey switching or changes in prey availability, which is supported by the stomach content analyses. Additionally, all species had significantly lower stomach

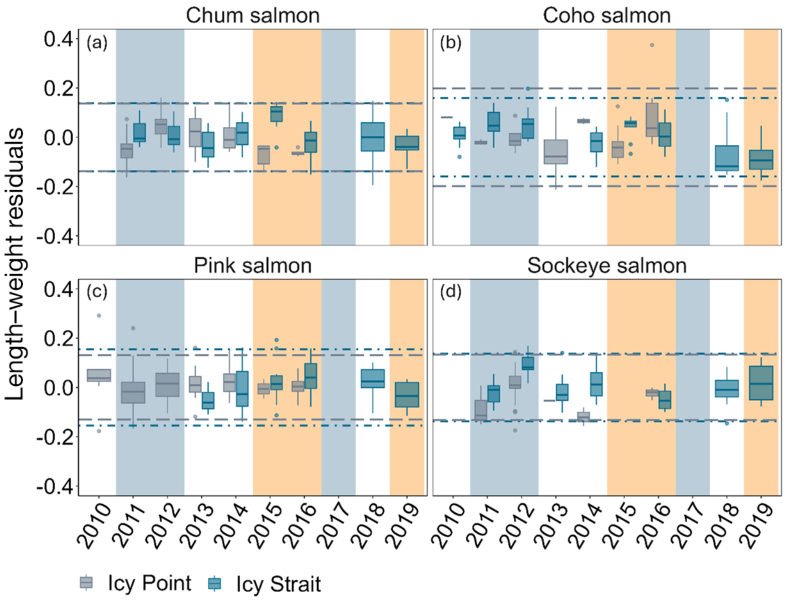

Fig. 6. Length–weight residuals of juvenile salmon in August, comparing the inside waters of Icy Strait, Southeast Alaska (SEAK), and the outside waters of Icy Point, eastern Gulf of Alaska (EGOA) for (a) chum, (b) coho, (c) pink, and (d) sockeye salmon. Shaded regions indicate warm (orange) and cool (blue) years. Boxplot parameters as in Fig. 5; 95% confidence intervals are included for both SEAK (blue dot-dash lines) and EGOA (gray dashed lines). Where comparison data are available, SEAK length–weight residuals are consistently higher or show no significant difference from EGOA values

content variability in heatwave year 2015 and collectively indicate temperature-mediated changes in prey availability across years. This is consistent with previous findings in which, during the onset of the 2014–2016 marine heatwave, juvenile salmon in SEAK appeared to compensate for the presence of low nutritional quality zooplankton by supplementing their diets with larger euphausiid prey (Fergusson et al. 2020), which at the time were in low abundance in the Gulf of Alaska (Arimitsu et al. 2021).

Niche area and overlap can reflect diet specialization or generalization in response to environmental variability (Gladics et al. 2014, Graham et al. 2021). Our results are consistent with these studies, finding greater niche overlap in years with improved prey availability (non-heatwave years) versus lower niche overlap and greater specialization in years of limited prey (heatwave years). Low niche overlap during the heatwave years was primarily reflected in our isotope analyses and less so with stomach contents. For example, stomach contents indicated high diet overlap with consumption of euphausiids and amphipods during two of the heatwave years. This apparent discrepancy is likely explained by stomach contents representing a short-term feeding opportunity of locally abundant prey on the day the fish were collected, in contrast to isotope results representing a more integrated metric of prey consumption over weeks and months due to tissue turnover rates (Sakano et al. 2005).

We did, however, find some notable species-specific variability in diet specialization and niche overlap. Pink salmon showed larger isotopic niche area during the heatwave year of 2019, but a similar pattern was not observed in heatwave years 2015–2016. Chum showed larger isotopic niche area during both non-heatwave years and heatwave years of 2015–2016. Coho stomach content analysis showed high specialization in fish and decapod prey items, which was also reflected in higher δ^{15}N isotope values observed in coho relative to the other species. However, we also observed higher isotopic niche area suggesting less specialization in years preceding warm SST anomalies. In addition to high nitrogen isotope values, coho δ^{13}C values were higher than the other species, indicating a stronger signal from marine-derived carbon sources. Sockeye followed a similar pattern in isotopic niche area to coho, with the addition of expanded niche area in 2019, likely due to added variability from generalized feeding that sockeye tend to exhibit. Sockeye also had the lowest δ^{13}C values across species pointing to potential contributions from more terrestrially derived carbon. Sockeye juveniles typically overwinter in freshwater, and terrestrially derived carbon has lower δ^{13}C values relative to nearshore marine carbon sources, thus a delayed marine entry can expand the range of observed δ^{13}C with a lingering terrestrial carbon signal. Isotopic overlap was also low between chum and coho and between chum and pink in 2015, even with stomach content analysis showing coinciding consumption of euphausiids as the dominant prey item.

Changes in body condition and size associated with anomalous temperature conditions can in part be due to changes in prey abundance or changes in nutritional value of prey items for juvenile salmon. We found that warmer temperatures were significantly connected to longer lengths in all species except sockeye in SEAK. This finding is consistent with other studies (Andrews et al. 2009, Wechter et al. 2017, Thalmann et al. 2020), and we would expect warmer temperatures to support faster growth rates. The negative correlation between temperature and length in sockeye was somewhat unexpected, and may be due to a change in the outmigration timing during warm years when juvenile sockeye may enter saltwater the year they hatch rather than spending a winter in freshwater (Gustafson & Winans 1999), which is known to occur in the region (Orsi & Fergusson 2017). Remarkably, sockeye in SEAK showed no significant differences in energy density residuals among years and had the most consistent condition of all 4 species.

While we observed evidence of variability in isotopic niche area and overlap as well as diet specialization or prey switching, we did not see evidence of SST impacts on condition in SEAK. This result is in contrast with previous studies from various regions which have shown both reduced condition (Botsford & Lawrence 2002, Andrews et al. 2009, Daly & Brodeur 2015, Farley et al. 2024) and higher condition (Farley et al. 2007, Kohan et al. 2019) in response to warm SST anomalies. In SEAK, higher energy densities and longer lengths have been observed in juvenile chum during periods with warmer SST values in years leading up to recent marine heatwaves (Kohan et al. 2019). While we did see a positive correlation in fish lengths with SST anomalies, we did not find higher fish condition significantly related to SST anomalies, indicating that the fish were allocating energy to growth and not storage. Furthermore, the lack of a clear and consistent relationship with SST anomalies in both energy density residuals and length–weight residuals points to something other than SST alone as a dominant driver for these condition metrics for juvenile salmon in SEAK.

Although marine heatwaves did negatively affect future adult salmon returns in this region (North Pacific Anadromous Fish Commission 2021), we found that juvenile salmon condition in SEAK did not decline during the heatwaves. This, in addition to detecting reduced body condition from fish collected in the EGOA, indicates that survival was compromised after juvenile salmon entered the Gulf of Alaska during marine heatwave years. It is possible that juvenile salmon experienced stressors in SEAK that were not measurable until after they reached the Gulf of Alaska. For example, studies of juvenile sand lance *Ammodytes hexapterus* in both Prince William Sound in Alaska and in Haro Strait off the coast of British Columbia (Canada) showed that increased metabolic demands of warm periods are not expressed immediately, and instead found decreased body condition in subsequent winter months or the following year (von Biela et al. 2019, Robinson et al. 2024). However, this is unlikely to be the case in our study because of the relatively transient nature of juvenile salmon migration through our sampling area in Icy Strait, SEAK. Instead, we suggest that negative impacts from marine heatwave conditions contributing to low adult salmon returns (Heinl et al. 2017, Reid et al. 2019, Thynes et al. 2022) occurred after the juveniles left SEAK.

The lack of a clear and significant link between fish condition and SST anomalies is likely attributable to the unique geography and oceanography of SEAK inland waters relative to the Gulf of Alaska. The mountainous region of SEAK is known for abundant freshwater input from snowmelt, glacial rivers, and rainfall that have pronounced seasonal patterns (Curran & Biles 2021, Harley et al. 2023). This high volume of freshwater discharge especially in the spring and summer melt periods coincides with the initial period of juvenile salmon in the marine environment, and it has been shown to be associated with abundance of juvenile chum salmon (Kohan et al. 2019). The complexity of narrow channels, deep fjords and bathymetry, and strong tidal mixing contribute to both deep mixing that transports nutrients to the surface and uniquely diverse marine habitats (Weingartner et al. 2009, Stabeno et al. 2016). The SEAK region contrasts with the broader Gulf of Alaska as well as the adjacent EGOA region, which is somewhat more typical of nearshore marine habitat for juvenile salmon in the North Pacific, and generally experiences higher SST relative to SEAK (Fig. S2). The higher interannual variability and higher mean SST in the EGOA, in addition to differences in habitat, could in part explain some of the observed differences in juvenile condition between these 2 regions.

We propose that the cold inside waters of northern SEAK provide a marine habitat that buffers juvenile salmon from marine heatwave-induced declines in condition prior to migration into the Gulf of Alaska. Our results provide further evidence that a robust and diverse prey community as well as the unique geography and oceanography in SEAK inside waters supported diet plasticity that allowed juvenile salmon to prevent declines in body condition that were observed in other regions of the northeast Pacific Ocean during recent marine heatwaves. Improving our understanding of underlying factors that influence juvenile salmon resilience to environmental change adds to our ability to predict and manage these important species (Malick et al. 2011, Murphy et al. 2017, 2022), especially during a period of increasing marine heatwave frequency.

Data availability. The data that support the findings of this study are available in Supplements 1 & 2 at www.int-res.com/articles/suppl/m760p135_supp/.

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