Critical periods in the marine life history of juvenile western Alaska chum salmon in a changing climate

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ABSTRACT: Recent precipitous declines in western Alaska chum salmon *Oncorhynchus keta* returns followed unprecedented warming in the northern Bering Sea ecosystem. To better understand the role of anomalous events on the early marine ecology of juvenile chum salmon in the northern Bering Sea, we utilized time-series observations over a 17 yr period (2003—2019) of sea surface temperature (SST) and juvenile chum salmon size (length and weight), diet, energy density, and relative abundance. Particular attention was paid to more recent (2014—2019) years in which there was unprecedented loss of sea ice in the northern Being Sea in comparison to previous warm (2003—2005) and cold (2006—2013) periods. Our findings indicate significant correlations between SST and juvenile chum salmon relative biomass (positive) and energy density (negative). We found that juvenile chum salmon were larger during warm periods than during cold periods; however, there was no significant difference in their length and weight between the warm periods. Juvenile chum salmon fed on lower quality prey during warm periods than during cold periods, with an increase in the proportion of lower quality prey during the recent warm period. Consequently, the energy density of juvenile chum salmon was also lower during warm periods than during cold periods, with the lowest values occurring during the recent warm period (2014—2019). These results identify a shift in energy allocation and/or prey quality of juvenile chum salmon with temperature and illustrate how marine ecosystems have altered the nutritional condition of juvenile chum salmon prior to winter, when energy reserves are considered critical to survival.

KEY WORDS: Chum salmon · Western Alaska · Energetics · Critical life history stages

1. INTRODUCTION

Marine environments in the Arctic regions (including the northern Bering, Chukchi, and Beaufort seas) are experiencing accelerated warming and extremes in seasonal sea ice extent (Frey et al. 2014, Stabeno & Bell 2019, Baker et al. 2020b, Danielson et al. 2020, Thoman et al. 2020). Unprecedented reductions in seasonal sea ice occurred during the winter of 2017—2018 in the northern Bering Sea and this was followed by an increase in warm southerly winds during February 2019 and an early ice retreat (Stabeno & Bell 2019, Thoman et al. 2020). The ecosystem response to these extreme events was rapid, with anomalously warm spring and summer sea temperatures, reduction in the size of the cold pool (extremely cold bottom water that acts as a natural benthic barrier between the southern and northern Bering Sea), expansion of subarctic fish species into the northern Bering and southern Chukchi seas, a reduction in high lipid prey, and

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an increase in seabird die-offs (Duffy-Anderson et al. 2019, Huntington et al. 2020, Kimmel et al. 2023). In addition, adult run abundance of western Alaska chum salmon *Oncorhynchus keta* declined to record low levels during 2020–2022 (see Clark 2022, Jallen et al. 2022, Smith et al. 2022) (Fig. 1) following these record low seasonal sea ice and anomalously warm sea temperature events. Here, we examine biological characteristics (size, diet, energy density [ED], and relative abundance) of juvenile chum salmon from a 17 yr (2003–2019) time series of surface trawl and ecosystem surveys (see Murphy et al. 2021) to better understand how recent warming of western Alaska habitats has altered the early marine ecology and how that may have impacted the survival of chum salmon in this region.

Chum salmon spawn in freshwater during the summer and fall months but spend the majority of their life history in the marine environment (Urawa et al. 2018). Chum salmon fry emerge from their gravel nests (redds) during the following spring and begin their downstream migration to the ocean. In western Alaska, juvenile (first ocean year) chum salmon enter the marine waters of the northern Bering Sea from mid-June to mid-July (Vega et al. 2017) and spend their first summer at sea, feeding and growing along the northern Bering Sea shelf (Farley et al. 2005). During late fall and early winter, western Alaska juvenile chum salmon migrate out of the Bering Sea and into the Gulf of Alaska (GOA) and spend 1–4 more years migrating between the GOA during winter and GOA and the

Bering Sea during summer before maturing and returning to spawn (Myers et al. 2009).

The first year in the ocean is a critical survival period for Pacific salmon. During this life-history stage, juvenile Pacific salmon must grow quickly to escape size-selective predation (Pearcy 1992, Willette et al. 1999). Juvenile Pacific salmon must also accumulate sufficient energy reserves to improve their probability of survival during their first winter (Beamish & Mahnken 2001, Howard et al. 2016). Energy allocation, first to rapid growth and then to lipid storage, is a strategy juvenile fishes use to maximize survival during their first year and winter (Mogensen & Post 2012). Fish condition is often used to evaluate survival potential and recruitment success (Heintz et al. 2013) and is often expressed in terms of ED (kJ g^{-1}), which is driven by lipid content of fishes (Van Pelt et al. 1997, Anthony et al. 2000). Within the eastern Bering Sea, there is evidence of a significant positive relationship between juvenile Pacific salmon size and ED (Andrews et al. 2009, Moss et al. 2009, 2016, Farley et al. 2011). However, eastern Bering Sea juvenile Pacific salmon energy reserves tend to be negatively correlated with sea temperatures (Andrews et al. 2009, Farley et al. 2011, Wechter et al. 2017), indicating potential interactions among sea temperature and prey quality and quantity that can affect energy accumulation during summer months (Heintz et al. 2013).

To explore potential explanations for declines in western Alaska chum salmon adult run abundances, we describe patterns of interannual variation in biological characteristics including relative biomass, size (length and weight), diet, and energetic status of juvenile chum salmon in the northern Bering Sea based on 17 yr of fishery-independent survey data. The period examined (2003–2019) was characterized as warm (2003–2005), cold (2006–2013), and anomalously warm (2014–2019) (Kimmel et al. 2023), allowing us to consider potential effects of the recent warming event on the biological characteristics of western Alaska chum salmon. Our findings build on previous studies of the early marine ecology of northern Bering Sea juvenile chum salmon (Farley et al. 2005, Farley & Moss 2009, Moss et al. 2009, 2016, Wechter et al. 2017) to provide insight into how warming Arctic conditions may affect juvenile survival and thus impact adult returns of western Alaska chum salmon.
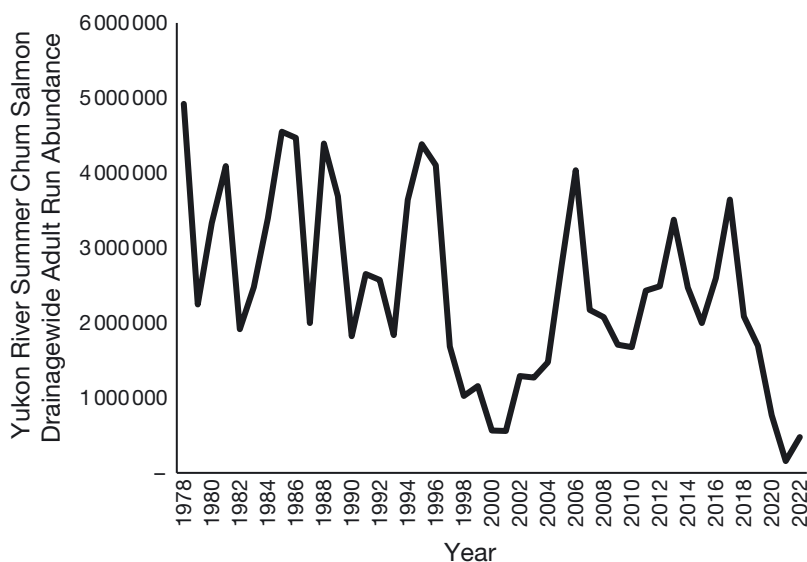

Fig. 1. Yukon River summer chum salmon drainage-wide adult run abundance from 1978 to 2022

2. MATERIALS AND METHODS

2.1. Study area and sampling protocols

Stations along the northern Bering Sea shelf were sampled during late August through September 2003−2019 (except 2008; Fig. 2) following methods described in Murphy et al. (2021). The sampling at each station included physical oceanographic measurements (surface to near bottom depths) and the collection of fishes. The spatial extent of the northern Bering Sea survey has varied over time but, in general, the survey covers a sampling grid from 60−65° N based on latitude and longitude coordinates, with a latitude grid distance of 0.5° (55.56 km) and a longitude grid from nearshore west to 171° W with a distance of 1°. The timing of the survey has also varied among years; therefore, we included day-of-year in the modeling for biological characteristics to account for the annual differences in survey timing (see Wechter et al. 2017).
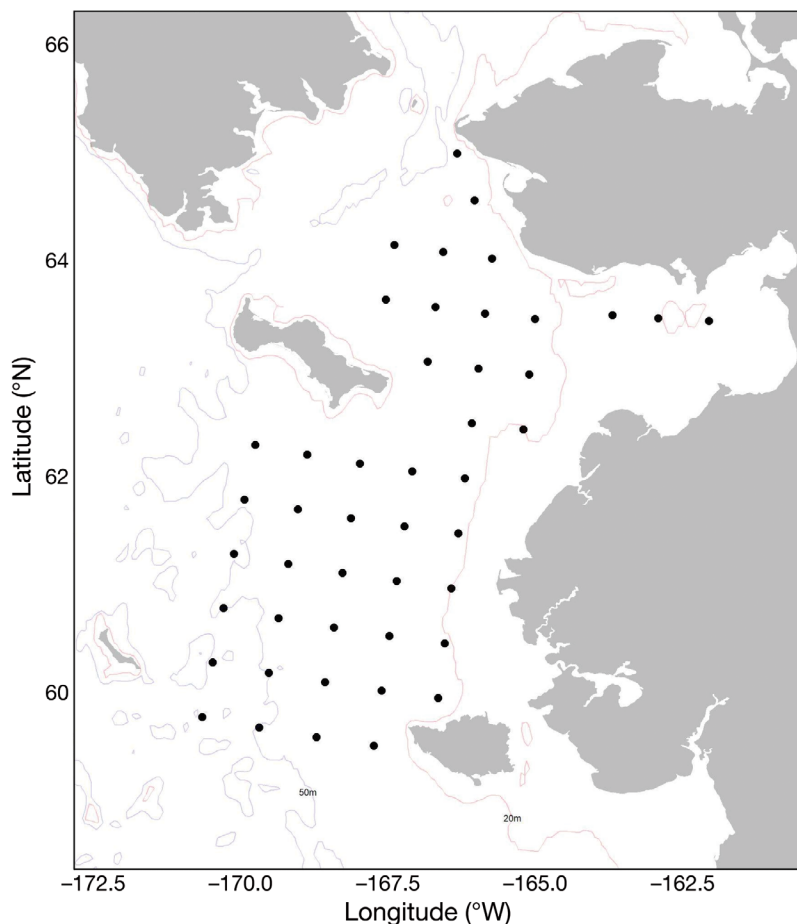
The juvenile chum salmon captured at each station were counted and a total weight was taken. A random subsample of juvenile chum salmon was selected (maximum 50) and fork length (nearest 1.0 mm) and body weight (nearest 1.0 g) were measured. Onboard, weights were measured with Marel M1100 or M2000 motion-compensated scales. All juvenile chum salmon were weighed and measured if the catch was less than 50 individuals. At each station, up to 3 juvenile chum salmon were frozen whole and taken back to the laboratory for energetics analyses, and up to 10 juvenile chum salmon (per station) were randomly selected for stomach content analyses.

Sea surface temperatures (SST; defined as the average from near-surface to 10 m depth) taken from conductivity, temperature, and depth (CTD) casts at each station in the sampling grid were averaged by year (Fig. 3) and used for correlation analyses. These average SSTs, taken during late August to early September, were used to represent the SSTs that juvenile chum salmon would have experienced during their first summer at sea (July to September). Data were also categorized into years as 'Warm 1' (2003−2005), 'Cold' (2006−2013), and 'Warm 2' (2014−2019) periods, as these periods, defined by sea ice extent on the northern Bering Sea shelf, have been related to shifts in zooplankton communities that may impact the food web available to higher trophic level species (Kimmel et al. 2023). In addition, we summarized time-series data as standardized anomalies for the period 2003−2019. We calculated anomalies as Z-scores using the following equation:

$$Z = \frac{(x-\mu)}{\sigma} \qquad (1)$$

where Z is the standardized anomaly, x is the value for a given year, μ is the long-term (2003−2019) mean, and σ is the standard deviation of the long-term mean. We did this to visualize the relative changes in the variables of interest over time.

2.2. Juvenile chum salmon relative biomass

Relative biomass (kg km^{-2}) of juvenile chum salmon was estimated by dividing the total catch weight (kg) of

Fig. 2. Survey stations (black dots) typically sampled within the northern Bering Sea during 2003−2019
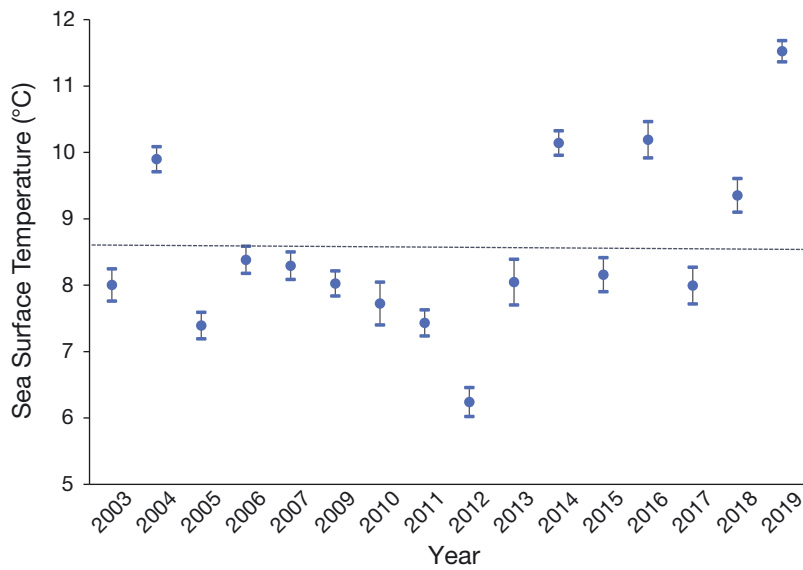
Fig. 3. Annual average and 95% confidence limits and overall average (8.57°C, dashed line) for sea surface temperature (top 10 m of the water column) from conductivity-temperature-depth (CTD) data collected in the northern Bering Sea surveys during 2003–2019

juvenile chum salmon caught at each station by area swept, which was equal to the distance traveled (km) when the trawl net was fishing and multiplied by the estimated trawl net opening (km) during fishing operations. We used the log of relative biomass to stabilize the variance in these measurements throughout the survey area.

2.3. Energy density

The ED of juvenile chum salmon was determined using bomb calorimetry on dried samples of homogenized whole fish tissues following procedures modified from Fergusson et al. (2010). We used ED (cal g^{-1}) because this metric was used in previous analyses of these chum salmon data (Wechter et al. 2017) and because it is associated with lipid content in fishes (Trudel et al. 2005, Siddon et al. 2013). Samples through 2015 were dried to constant mass by heating at 55°C in a drying oven, and samples from 2016 to 2019 were dried by heating at 135°C in a LECO Thermogravimetric Analyzer 701. The 2 drying methods are known to yield moisture estimates differing by less than 1% (Vollenweider et al. 2011) and thus had negligible effects on dry mass ED estimates. Calorimetry data accuracy was verified using benzoic acid and internal fish tissue standards, and precision was verified using sample replicates. Calorimetry sample dry mass ED values were multiplied by percent dry

mass to report ED values on a wet mass basis. ED values in J g^{-1} wet weight were divided by 4.184 to convert to cal g^{-1} wet weight. ED data were available for all years except 2013.

2.4. Stomach content analysis

Stomach contents were evaluated with methods developed for estimating diets at sea (Chuchukalo & Volkov 1986, Volkov et al. 2007, Moss et al. 2009, Coyle et al. 2011). Typically, the contents of up to 10 stomachs from randomly sampled juvenile chum salmon were combined from each station. Contents were removed from the esophagus to the pylorus. Prey taxa were identified to the lowest possible resolution using a dissecting microscope. Prey composition was recorded as a stomach content index (SCI) and a stomach fullness index (SFI). Each prey taxa at a given station was assigned an SCI, calculated as:

$$\text{SCI}_{i,x} = (\text{Prey}_{i,x} / \text{JuvChum}_i \times 10000) \quad (2)$$

where $\text{Prey}_{i,x}$ is the weight (g) of prey taxa x at station i and JuvChum_i is the total weight (g) of all juvenile chum salmon at station i. The SFI_i is the sum of all SCI values from all prey taxa at a given station i. Stomach content data were pooled into broader categories prior to calculating the percent SCI composition. In effect, this normalizes prey weight to predator body weight, removing the effect of predatory capacity due to juvenile chum salmon size across years. These broad categories included fishes (mostly sand lance *Ammodytes hexapterus*, age-0 walleye pollock *Gadus chalcogrammus*, and capelin *Mallotus villosus*), Euphausiacea, Amphipoda, and gelatinous prey, which were further separated into *Oikopleura* spp. and Cnidaria, as these prey items appeared most often in juvenile chum salmon stomachs. Categories that represented less than 10% of the total SCI across all years were grouped together. Prey items that could not be grouped within a taxonomic or functional group were combined into an 'Other' category. Unidentified prey items were removed from the analysis. We grouped years by Warm 1, Cold, and Warm 2 periods and compared the percent of SCI between these periods. Prey categories are summarized as the percent contribution to the total SFI, which is mathematically equivalent to the percent weight of each category.

Dietary comparisons between warm and cold periods were made using PRIMER version 7 (Clarke et al. 2014). SCI values were fourth-root transformed prior to statistical testing to give less weight to the most prevalent prey items prior to calculating similarity measures (Clarke et al. 2014). Dietary composition comparisons were made among the Warm 1, Cold, and Warm 2 periods using the analysis of similarities routine (ANOSIM).

Estimates of the caloric content of prey items were used to provide context to potential shifts in prey quality (see Davis et al. 1998, Moss et al. 2009). These estimates were fishes (1334 cal g^{-1} wet weight; average of sand lance, capelin, and walleye pollock), Euphausiacea (1117 cal g^{-1} wet weight), *Oikopleura* spp. (759 cal g^{-1} wet weight), Amphipoda (589 cal g^{-1} wet weight), and Cnidaria (136 cal g^{-1} wet weight). Fishes, Euphausiacea, and *Oikopleura* spp. were classified as higher quality prey species and amphipods and cnidarians were classified as lower quality prey species.

2.5. Relationships between sea temperature and size, ED, and relative biomass

Annual indices of relative biomass, ED, and size were estimated using a single-species spatio-temporal model with the VAST package (version 3.10.0) in R (version 4.1.3) and RStudio (version 2022.02.3) (Thorson et al. 2015, Thorson 2019, R Core Team 2022). We used the VAST package to account for spatially unbalanced sampling across years. Spatial and spatio-temporal variation for both encounter probability and positive catch rate components were specified at a spatial resolution of 500 knots. We used a Poisson-link, or conventional, delta model and a gamma distribution to model positive relative biomass (Thorson 2019). In addition, day-of-year was added as a normalized covariate with a spatially constant and linear response to account for changes in the timing of the survey among years (see Wechter et al. 2017). The VAST models provided n = 500 extrapolation points per year for log-relative biomass, length, weight, and ED. These estimates were used in subsequent analyses. Non-adjusted estimates of mean relative biomass, ED, and size, as well as parameter estimates for VAST models, are provided in Tables S1—S6 in the Supplement at www.int-res.com/articles/suppl/m726p149_supp.pdf. The VAST model fit parameters and relationship between the distributions of the observed and predicted factors (VAST model estimates) are provided in Figs. S1 & S2 in the Supplement.

Pearson correlation coefficients and p-values were estimated to test the relationships among annual averages of SST and estimates of VAST-adjusted log relative biomass, length, weight, and ED. ANOVA (fixed effects, α = 0.05) was performed to test for significant differences in estimates of VAST-adjusted log relative biomass, length, weight, and ED among years and among warm and cold periods.

3. RESULTS

3.1. Juvenile chum salmon relative biomass

Juvenile chum salmon relative biomass *Z*-scores were consistently negative during the Warm 1 and Cold periods and positive (with the exception of 2017) during the Warm 2 period (Fig. 4A). Year had a significant effect (ANOVA, $F_{15,7984} = 308.5$, p < 0.001) on chum salmon biomass. When comparing individual years, post hoc testing found that juvenile chum salmon had the highest relative biomass during 2014 and the lowest during 2005 (see Table 1 for values). In addition, the ANOVA found that period had a significant effect ($F_{2,7997} = 829.0$, p < 0.001) on juvenile chum salmon biomass. When comparing among the warm and cold periods, post hoc testing found no significant difference in juvenile chum salmon relative biomass between the Warm 1 and Cold periods, but significant differences (p < 0.05) in their relative biomass between Warm 1 and Warm 2 and between Cold and Warm 2 periods (Fig. 5A). The correlation analysis found that juvenile chum salmon relative biomass was positively (p = 0.05) related to SST (Fig. 6). These results illustrate the positive effect that the Warm 2 period had on relative biomass of juvenile chum salmon.

3.2. Energy density

Juvenile chum salmon ED differed significantly among years (ANOVA, $F_{14,7485} = 288.8$, p < 0.001); post hoc testing found that juvenile chum salmon had the highest ED during 2015 and the lowest ED during 2019 (Table 1). Negative and positive *Z*-scores of ED were found throughout the time series, with more negative *Z*-scores occurring during the warm periods (Fig. 4B). Juvenile chum salmon ED differed significantly (ANOVA, $F_{2,7497} = 202.4$, p < 0.001) among the warm and cold periods, with lowest values occurring during the Warm 2 period and highest values during the Cold period (Fig. 5B). In addition, juvenile chum salmon ED
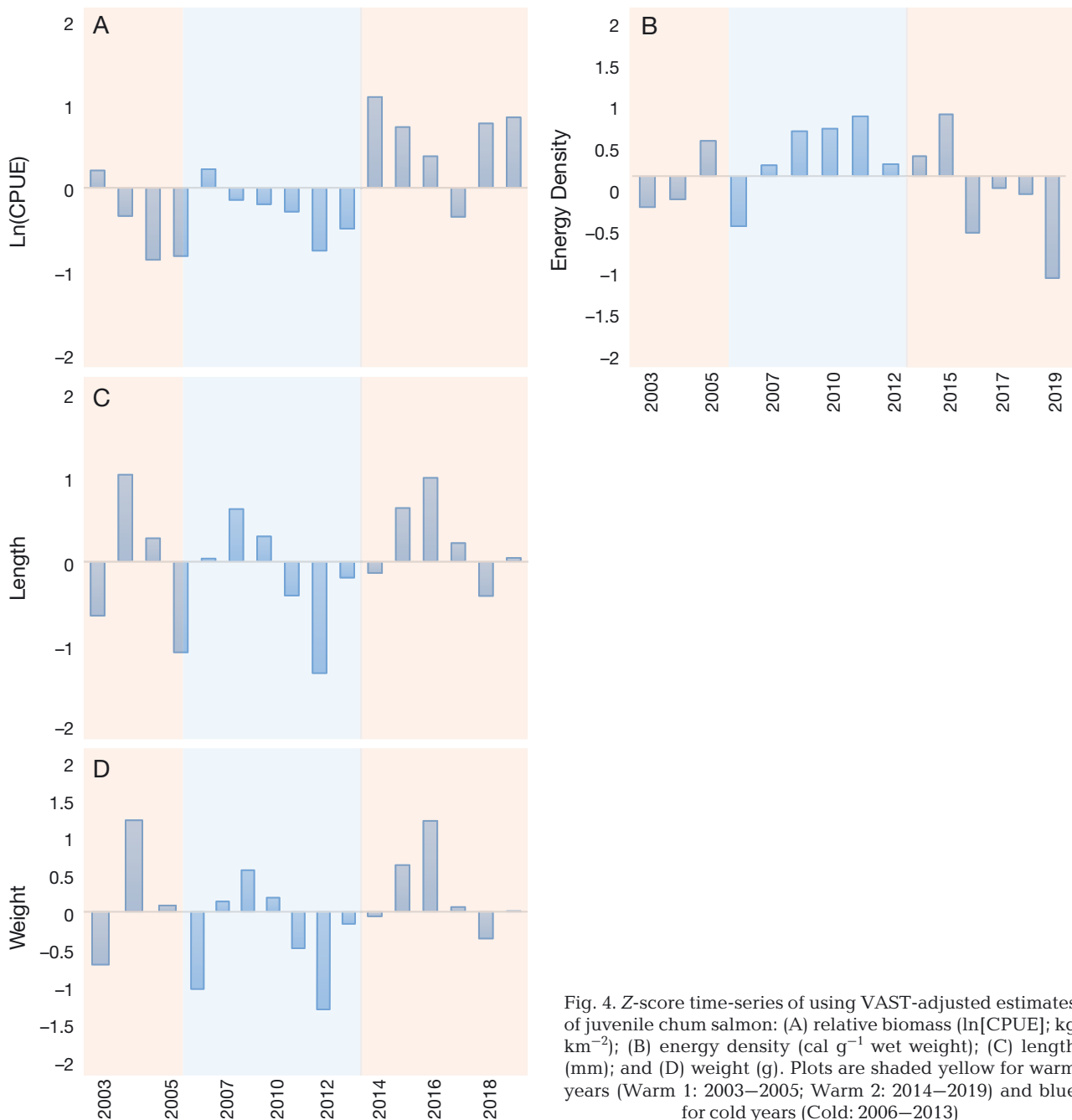
Fig. 4. *Z*-score time-series of using VAST-adjusted estimates of juvenile chum salmon: (A) relative biomass (ln[CPUE]; kg km^{-2}); (B) energy density (cal g^{-1} wet weight); (C) length (mm); and (D) weight (g). Plots are shaded yellow for warm years (Warm 1: 2003–2005; Warm 2: 2014–2019) and blue for cold years (Cold: 2006–2013)

was negatively related to SST (p = 0.05; Fig. 6), but not significantly related to their size (p > 0.05).

3.3. Size

Juvenile chum salmon length and weight differed significantly over time (Table 1; ANOVA, length: $F_{15,7984}$ = 390.6, p < 0.001; weight: $F_{15,7984}$ = 478.8, p < 0.001); post hoc tests found that the largest juvenile

chum salmon was recorded during 2004 (195.8 mm, 83.7g) and smallest was recorded during 2012 (160.3 mm, 38.5g). In general, negative *Z*-scores occurred more often during the cold period than during the warm periods (Fig. 4C,D). Juvenile chum salmon length and weight were significantly smaller (ANOVA, length: $F_{2,7997}$ = 279.1, p < 0.001; weight: $F_{2,7997}$ = 308.6, p < 0.001) during the Cold period than the Warm 1 and 2 periods; no significant difference in weight or length was found between the 2 warm

Table 1. VAST-adjusted (for day-of-year) mean estimates and standard deviation (SD) of juvenile chum salmon catch per unit effort (ln[CPUE]; kg km^{-2}), length (L; mm), weight (W; g), and energy density (ED; cal g^{-1} wet weight) in the northern Bering Sea. n = 500 estimates for each year (except 2008). (−) ED estimates were not available for 2013

Year	CPUE	SD	L	SD	W	SD	ED	SD
2003	1.61	0.72	170.6	8.4	48.9	7.2	1160.5	83.3
2004	1.14	0.46	195.8	13.3	83.7	20.2	1170.6	66.3
2005	0.70	0.45	184.4	7.8	63.2	9.6	1245.9	73.6
2006	0.74	0.61	164.0	6.9	43.0	5.3	1136.0	59.9
2007	1.62	0.70	180.8	18.7	64.1	20.5	1214.4	144.9
2009	1.31	0.81	189.7	10.8	71.7	13.7	1258.3	61.8
2010	1.26	0.74	184.8	7.5	65.0	8.2	1261.6	61.6
2011	1.19	0.83	174.2	11.8	52.9	11.5	1277.6	89.2
2012	0.79	0.83	160.3	7.7	38.5	5.6	1215.9	73.6
2013	1.02	0.70	177.4	7.9	58.8	8.8	−	−
2014	2.35	0.65	178.2	16.5	60.6	16.2	1226.1	97.1
2015	2.05	0.49	189.8	12.1	72.9	15.0	1280.1	93.0
2016	1.75	0.74	195.3	13.2	83.6	16.8	1127.5	60.2
2017	1.14	0.38	183.6	12.8	62.8	13.1	1185.1	67.1
2018	2.08	0.61	174.1	9.0	55.2	9.5	1177.4	87.9
2019	2.15	0.81	180.9	11.2	61.8	11.6	1069.1	34.5

periods (Fig. 5C,D). There were strong positive correlations between juvenile chum salmon average length and weight (Fig. 6) but non-significant (p > 0.1) correlations with SST, relative biomass, and ED.
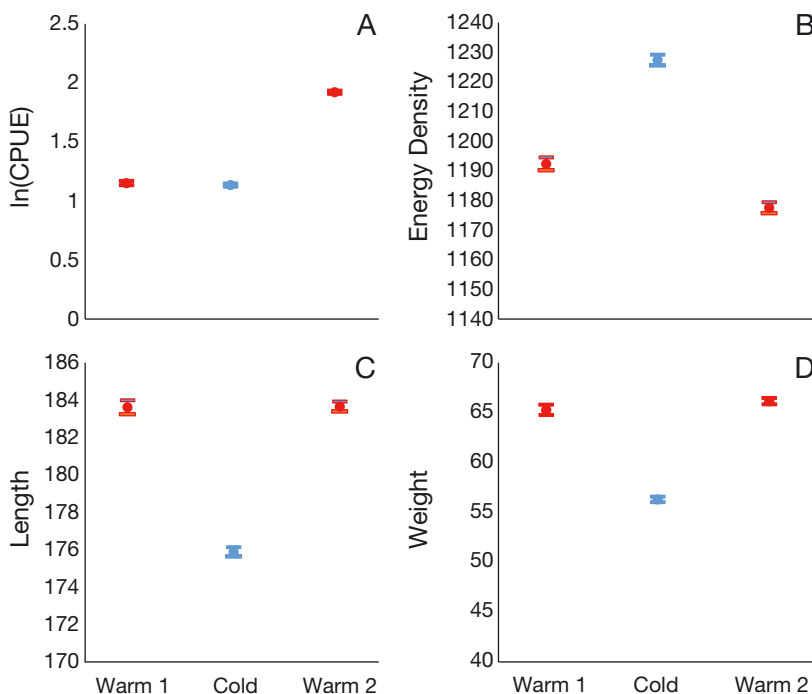

Fig. 5. Time-period mean ±1 SE for VAST-adjusted juvenile chum salmon (A) relative biomass (ln[CPUE]; kg km^{-2}); (B) energy density (cal g^{-1} wet weight); (C) length (mm); and (D) weight (g). Periods are defined as Warm 1 (2003–2005), Cold (2006–2013), and Warm 2 (2014–2019)

3.4. Juvenile chum salmon diet

Juvenile chum salmon dietary composition had consistent overlap among all periods but was still significantly different among all periods (R = 0.138, p = 0.01). Pairwise comparisons for combinations of the Warm 1, Cold, and Warm 2 periods were significant for all combinations (p = 0.01). Juvenile chum salmon stomach contents reflected a change in diets between warm and cold periods (Fig. 7). In both periods, fish and gelatinous prey were the dominant prey species, but *Oikopleura* spp. was the dominant prey item during the Cold period, fishes were dominant during the Warm 1 period, and Cnidaria was the dominant prey during the Warm 2 period. The proportional contributions of higher quality prey (including fishes, Euphausiacea, and *Oikopleura* spp.) were greater during the cold period, comprising >80% of the prey consumed on average, but were lower during the warm periods, comprising approximately 55% during the Warm 1 period and 45% during the Warm 2 period. The contribution of lower quality cnidarian prey increased from an average of approximately 29% during the Warm 1 period to an average of 35% during the Warm 2 period.

4. DISCUSSION

The northern Bering Sea has experienced 3 distinct sea temperature periods over the past 20 yr: a warm period during 2003–2005, a cold period during 2006–2013, and an exceptionally warm period during 2014–2019. These temperature periods have had varying impacts on the biological characteristics of juvenile chum salmon. The Warm 1 and Warm 2 periods (2003–2005 and 2014–2019, respectively) led to conditions that mostly favored larger size but lower ED of juvenile chum salmon, whereas the opposite was true for the Cold period (2006–2013). We also found no difference in the relative biomass of juvenile chum salmon between
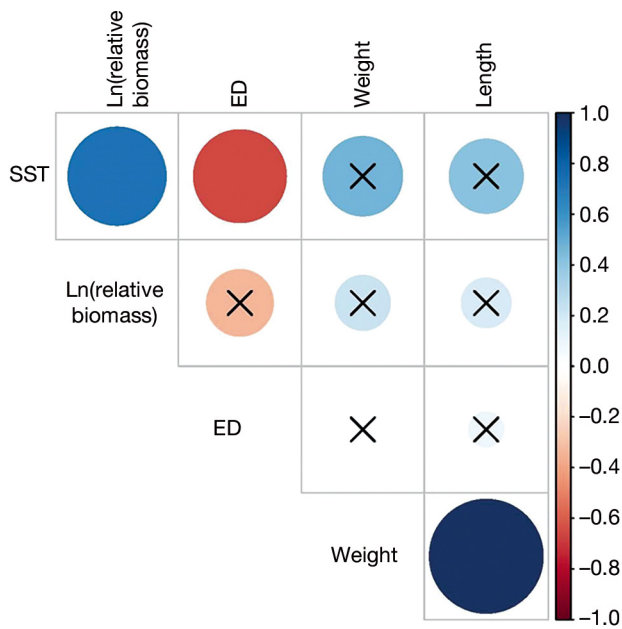
Fig. 6. Pearson correlation coefficients (p = 0.05) relating indices of summer sea temperatures (SST; °C), and VAST-adjusted body weight (weight; g), body length (length; mm); energy density (ED; cal g^{-1} wet weight), and log relative biomass (ln[CPUE]; kg km^{-2}) of juvenile chum salmon in the northern Bering Sea during summer. The size and color of each circle illustrate the strength of the correlation (blue: positive; red: negative); × indicates lack of significance

the Warm 1 (2003–2005) and Cold (2006–2013) periods but there was a significant increase in their relative biomass during the Warm 1 (2014–2019) period. In addition, when we related the biological character-istics of the juvenile chum salmon to SST, there were significant positive effects with relative biomass and significant negative effects with ED.

Juvenile chum salmon in the eastern Bering Sea tend to allocate energy to somatic growth early in their life history and then to lipid storage later in the season (Moss et al. 2016, Burril et al. 2018). This 2-stage energy allocation strategy aligns with the critical size and period hypothesis for juvenile Pacific salmon, whereby faster growth rates early on reduce size-selective mortality (Pearcy 1992) and large juvenile Pacific salmon that also attain sufficient energy reserves at late summer—early fall typically have a higher probability of survival over winter (Beamish & Mahnken 2001, Howard et al. 2016). During late summer and early fall months on the eastern Bering Sea shelf, significant positive relationships between size and ED have been found for juvenile chum salmon (Moss et al. 2016, Wechter et al. 2017); however, when ED and size data from the Warm 2 period (2014–2019) were included, the relationship was no longer significant. This result, which is a function of reduced ED in relation to the size of juvenile chum salmon during the Warm 2 period, indicates that they were not allocating as much energy to lipid storage but instead continued to allocate energy to somatic growth. Thus, given the importance of late summer—early fall lipid storage to juvenile Pacific salmon over-winter survival, a critical aspect of our results is understanding potential drivers that contributed to the recent decline in late summer energy storage for juvenile chum salmon.

Prey quality may play a key role in the variability of juvenile chum salmon ED in the northern Bering Sea. Size and ED are a function of sea temperature, metabolic rates, and prey quality in young fishes on the eastern Bering Sea shelf (Heintz et al. 2013, Siddon et al. 2013). Increased proportional consumption of low-quality prey is known to reduce the lipid content of juvenile chum salmon (Kaga et al. 2013). Juvenile chum salmon feed on a variety of prey species but the percentage of lower quality prey increased during warmer periods, especially during the Warm 2 period. Prey species within Phylum Cnidaria (jellyfish) are of particular importance since they have approximately half the caloric value of other prey species (Davis et al. 1998). Species identification of gelatinous
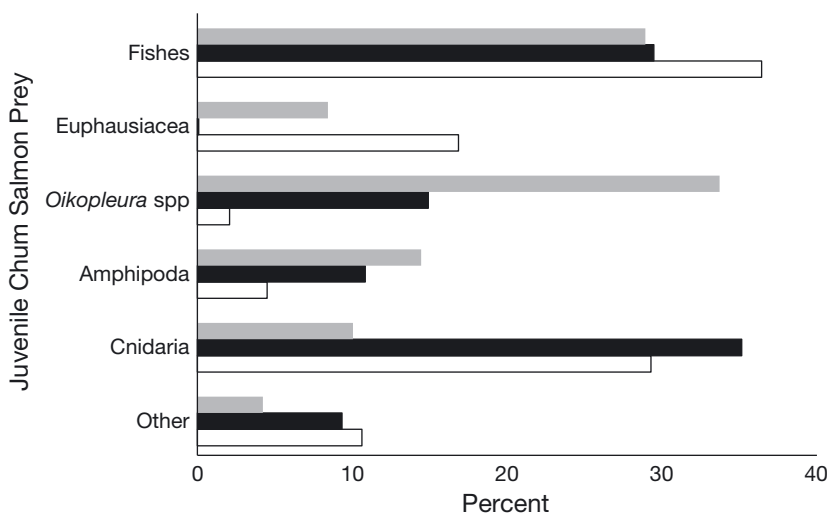

Fig. 7. Percent contribution for each prey category to total stomach fullness index for juvenile chum salmon in the northern Bering Sea during Warm 1 (white bar; 2003–2005), Cold (gray bar; 2006–2013), and Warm 2 (black bar; 2014–2019) periods. Prey categories are listed in order of quality from highest to lowest, with the 'Other' category included at the bottom of the list

prey like Cnidaria can be quite difficult and, consequently, they are often reported as broad species groups like Cnidaria or gelatinous prey. However, one cnidarian species, *Aglantha digitale*, a small hydrozoan species that is common throughout the North Pacific (Shiota et al. 2012), is a particularly important species for chum salmon within the cnidarian prey group. Cnidaria were present in the diet of juvenile chum salmon during the Warm 1 period but were proportionally more dominant in the stomach contents during the Warm 2 period. In addition to the increased proportion of Cnidaria in the stomach contents, the fullness of juvenile chum salmon in the northern Bering Sea generally declines with SST (Murphy et al. 2021), with the lowest fullness values being observed during the Warm 2 period. The combination of reduced fullness and an increase in the proportion of poor-quality prey may be key factors in the reduced ED of juvenile chum salmon.

The increased composition of Cnidaria in juvenile chum salmon diets is consistent with an increase in cnidarian biomass within the northern Bering Sea during warm periods (Kimmel et al. 2023). Asexual and sexual reproduction increase with temperature in many cnidarian species, allowing these zooplankton to quickly respond to changing SST conditions (Purcell 2005). Kimmel et al. (2023) also noted that prey fields differed in their response to warm and cold periods, with a limited response between the Warm 1 and Cold period and a larger response (increase) of smaller-bodied zooplankton during the Warm 2 period. Much of the variability in the northern Bering Sea zooplankton community was associated with a minimum threshold in ice extent and timing of ice retreat and provides context to the cascading effects through upper trophic level species that were evident in the recent warm period (Huntington et al. 2020). Therefore, the decline in juvenile chum salmon late-summer ED was likely a response to the unprecedented loss of seasonal sea ice that led to widespread changes in the northern Bering Sea ecosystem.

Although the ED of chum salmon has declined with warming temperatures, their biomass in the northern Bering Sea increased during the Warm 2 period. This was an interesting result, as the relative biomass of juvenile chum salmon was not significantly different between the Warm 1 and Cold periods. There are a number of possible explanations for the recent increase in relative biomass of juvenile chum salmon. There is evidence that warming freshwater environments improved the survival of young pink salmon *Oncorhynchus gorbuscha* in the northern Bering Sea (Farley et al. 2020). Given that chum salmon have similar freshwater life history traits, the warmer freshwater environments could have improved the freshwater survival of young chum salmon, leading to more juveniles in the study region.

Another possibility is that rapid growth during their early marine life history (and larger overall size) could reduce size-selective mortality and, in turn, lead to greater numbers of juvenile Pacific salmon during their first year at sea. Rapid growth rates for juvenile chum salmon reared at high temperatures were found given sufficient prey resources (Iino et al. 2022). However, it is difficult to discern through our analysis whether conditions during early marine residence could have led to reduced size-selective mortality. For instance, juvenile chum salmon were large during the Warm 1 period, but their relative biomass was significantly lower than during the Warm 2 period. Moreover, an earlier analysis examining their relative abundance, size, and growth rate potential in the northern Bering Sea suggested that size-selective mortality early on after these chum salmon entered the ocean was not likely occurring (Farley & Moss 2009).

Alternatively, the increase in relative biomass of juvenile chum salmon during the Warm 2 period may reflect an increased contribution of stocks outside of the northern Bering Sea. Unfortunately, chum salmon exhibit extremely shallow genetic structure throughout much of western Alaska, and those stocks originating in river systems that empty into the northern Bering Sea (i.e. Yukon River and Norton Sound systems) are not genetically distinguishable from other Western Alaska river systems, except for the relatively small Yukon River fall chum salmon populations (DeCovich et al. 2012, Kondzela et al. 2016). However, we have seen an increased prevalence of southern Bering Sea-origin juvenile Chinook salmon (i.e. Kuskokwim River and Bristol Bay stocks) utilizing northern Bering Sea habitats in years with warmer SSTs during their first summer at sea (Murphy et al. 2021), and a similar temperature-mediated migration shift could also occur for Western Alaska chum salmon.

The abundance of juvenile Pacific salmon can provide key information on the underlying production dynamics of Pacific salmon when combined with adult assessment data over periods of high and low productivity (Murphy et al. 2017). For example, significant positive relationships between juvenile and adult abundance have been identified in Yukon River Chinook salmon (Murphy et al. 2017, Howard et al. 2016). Significant positive relationships between juvenile and adult abundance have also been found

for northern Bering Sea pink salmon (Farley et al. 2020) and southeast Alaska pink salmon (Orsi et al. 2016). Yukon River Chinook salmon spend 2–4 more years in the ocean after their first summer at sea (Riddel et al. 2018), whereas pink salmon spend 1 yr in the ocean after their first summer at sea (Radchenko et al. 2018). Given the marine life history of these Pacific salmon, the relationships identify that the second critical marine period (first winter) has not contributed as much to the annual variation in survival as the early life history stages, including freshwater and early marine (Howard & von Biela 2023).

While a relationship between juvenile chum salmon abundance and adult returns to rivers in the northern Bering Sea has not been established, the expectation was that the higher relative biomass seen in the recent warm period would herald higher adult run abundance to the region 3–4 yr later. This was not the case for these chum salmon and suggests that subsequent marine life history periods, after their first summer at sea, may have contributed substantially to the recent annual variation in survival. Given that western Alaska chum salmon spend their first winter at sea in the GOA, it is possible that the combination of anomalously warm events in the northern Bering Sea (which contributed to poor prey quality and reduced ED [lipid] during the Warm 2 period) and GOA (which was experiencing the second marine heat wave in 2017–2019; see Amaya et al. 2020) may be contributing to poor survival of chum salmon.

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