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Diet and Energy Density Assessment of Juvenile Chinook Salmon from Northeastern Bering Sea Trawl Surveys, 2004–2017

by

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and

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March 2021

Alaska Department of Fish and Game **Divisions of Sport Fish and Commercial Fisheries**

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Weights and measures (metric)	
centimeter	cm
deciliter	dL
gram	g
hectare	ha
kilogram	kg
kilometer	km
liter	L
meter	m
milliliter	mL
millimeter	mm

Weights and measures (English)	
cubic feet per second	ft^3/s
foot	ft
gallon	gal
inch	in
mile	mi
nautical mile	nmi
ounce	oz
pound	lb
quart	qt
yard	yd

Time and temperature	
day	d
degrees Celsius	°C
degrees Fahrenheit	°F
degrees kelvin	K
hour	h
minute	min
second	s

Physics and chemistry	
all atomic symbols	
alternating current	AC
ampere	A
calorie	cal
direct current	DC
hertz	Hz
horsepower	hp
hydrogen ion activity (negative log of)	pH
parts per million	ppm
parts per thousand	ppt, ‰
volts	V
watts	W

General	
Alaska Administrative Code	AAC
all commonly accepted abbreviations	e.g., Mr., Mrs., AM, PM, etc.
all commonly accepted professional titles	e.g., Dr., Ph.D., R.N., etc.
at	@
compass directions:	
east	E
north	N
south	S
west	W
copyright	©
corporate suffixes:	
Company	Co.
Corporation	Corp.
Incorporated	Inc.
Limited	Ltd.
District of Columbia	D.C.
et alii (and others)	et al.
et cetera (and so forth)	etc.
exempli gratia (for example)	e.g.
Federal Information Code	FIC
id est (that is)	i.e.
latitude or longitude	lat or long
monetary symbols (U.S.)	$, ¢
months (tables and figures): first three letters	Jan,...,Dec
registered trademark	®
trademark	™
United States (adjective)	U.S.
United States of America (noun)	USA
U.S.C.	United States Code
U.S. state	use two-letter abbreviations (e.g., AK, WA)

Mathematics, statistics	
all standard mathematical signs, symbols and abbreviations	
alternate hypothesis	H_A
base of natural logarithm	*e*
catch per unit effort	CPUE
coefficient of variation	CV
common test statistics	(F, t, χ^2, etc.)
confidence interval	CI
correlation coefficient (multiple)	R
correlation coefficient (simple)	r
covariance	cov
degree (angular)	°
degrees of freedom	df
expected value	*E*
greater than	>
greater than or equal to	≥
harvest per unit effort	HPUE
less than	<
less than or equal to	≤
logarithm (natural)	ln
logarithm (base 10)	log
logarithm (specify base)	$\log_2$, etc.
minute (angular)	′
not significant	NS
null hypothesis	H_O
percent	%
probability	P
probability of a type I error (rejection of the null hypothesis when true)	α
probability of a type II error (acceptance of the null hypothesis when false)	β
second (angular)	″
standard deviation	SD
standard error	SE
variance	
population	Var
sample	var

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ABSTRACT

The northeastern Bering Sea (NBS) is the rearing habitat for juvenile Norton Sound and Yukon River Chinook salmon (*Oncorhynchus tshawytscha*). In 2002, a marine survey was initiated by the National Oceanic and Atmospheric Administration to study the marine ecology of western Alaska Chinook salmon stocks. Information on the autumn diet (2004–2017) and energetic status (2006–2017) of juvenile Chinook salmon have been collected annually during these surveys to investigate how their feeding and condition respond to changes in the marine environment. During the years observed, juvenile Chinook salmon in the NBS primarily ate fish, including sand lance (Ammodytidae), capelin (*Mallotus villosus*), and other species, along with smaller proportions of decapods and other invertebrates. Annual average piscivory across all project years ranged from 69% to 96% by mass. Diet composition was size-dependent, and higher proportions of decapods and invertebrates were eaten by smaller juvenile Chinook salmon (<160 mm). Although fish are generally higher-quality prey, the relatively high energy content of NBS decapods may provide adequate energy reserves for smaller juvenile Chinook salmon to survive their first marine winter. Diets also varied with sea surface temperature, with higher proportions of sand lance and decapods in warmer years and higher proportions of capelin in colder years. Warm ocean temperatures led to reduced diet mass and lower piscivory, yet the energy density of juvenile Chinook salmon was higher in warmer years than colder years. Changes in diet and energy density between warm and cold years suggest ocean temperatures influence the feeding and condition of juvenile Chinook salmon. Continued annual monitoring of juvenile Chinook salmon size, condition, and diet will enable further investigation of the relationship between ocean conditions, fish condition, and marine survival.

Key words: Chinook salmon, *Oncorhynchus tshawytscha*, energy density, stomach content, diet, marine survey, pelagic trawl, juvenile, Bering Sea, Norton Sound, Yukon River

INTRODUCTION

The early marine life stage is a critical time for juvenile salmon due to high mortality rates following their marine entry (Hartt 1980; Pearcy 1992; Beamish and Mahnken 2001; Farley et al. 2007a). Size-selective juvenile salmon mortality occurs during 2 critical periods in the marine environment (Beamish and Mahnken 2001, Beamish et al. 2004). The first critical period occurs shortly after marine entry when smaller juvenile salmon experience intense predation pressure. Juvenile salmon grow rapidly throughout the first critical period (Brodeuer 1991; Howard et al. 2019), which aids in evading predators and increasing energy reserves before winter (Farley et al. 2007a). The second critical period occurs during their first winter at sea when smaller individuals have insufficient energy reserves to avoid starvation (Pearcy 1992; Beamish and Mahnken 2001; Moss et al. 2005). Successful feeding and assimilation are integral to growth and survival at a time when juveniles are vulnerable to predation and starvation.

Larger, well-fed juvenile salmon with higher energy stores are more likely to survive their first marine winter than smaller, leaner individuals (Farley et al. 2007b). Juvenile salmon achieve high growth rates by intense feeding (Weitkamp and Sturdevant 2008) on high-energy prey items in the marine environment (Brodeur 1991; Davis et al. 1998; Daly et al. 2009). As juvenile salmon grow, they are able to feed on larger prey due to increased gape size, swimming speed, and visual acuity, resulting in higher energy intake (Brodeur 1991; Nunn et al. 2012). Attaining a larger size also reduces predation risk due to gape-limitations of potential predators (Duffy and Beauchamp 2008). Additionally, larger juveniles can survive longer periods of starvation than their smaller conspecifics, due to greater energy stores and lower mass-specific metabolic rates (Beamish et al. 2004).

The feeding ecology and energetic condition of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) have been well-studied from northern California to the eastern Bering Sea (Brodeur et al. 2007; Trudel et al. 2007; Weitkamp and Sturdevant 2008; Farley et al. 2009; Duffy et al. 2010; Hertz et al. 2015). Across their range, juvenile Chinook salmon consume mainly fish but also eat decapods, hyperiid amphipods, euphausiids, and cephalopods (Brodeur et al. 2007). The dominant fish species in juvenile Chinook salmon diets vary by region: juvenile rockfish in California, northern anchovy (*Engraulis mordax*) and smelt in Oregon and Washington, Pacific herring (*Clupea pallasii*) in British Columbia, Pacific herring and Pacific sand lance (*Ammodytes hexapterus*) in Southeast Alaska, and capelin and walleye pollock in the southeastern Bering Sea (Hertz et al. 2015), which suggested diet may be driven by prey availability rather than prey preference (Brodeur et al. 2007; Weitkamp and Sturdevant 2008; Hertz et al. 2015). Juvenile Chinook salmon energy density also varies regionally, highlighting the importance of prey quality to building energy stores (Trudel et al. 2007). Region-specific diets that foster rapid growth and increased energy storage during early marine residence may promote overwinter marine survival.

The northeastern Bering Sea (NBS) is the primary rearing habitat of Norton Sound and Yukon River-origin juvenile Chinook salmon during their first summer at sea (Murphy et al. 2009). To assess juvenile salmon following their first few months at sea, fish were collected in the NBS annually during the autumn of 2002–2017. Beginning in 2004, juvenile Chinook salmon stomachs were collected to assess diet composition. Then, in 2006, juvenile Chinook salmon were collected whole to determine energy density before entering the critical winter period. In 2017, diet data were analyzed separately for 2 size classes of juvenile Chinook salmon, which allowed inferences about size effects on diet. Finally, the influence of temperature on diets and energy density were assessed to better understand how environmental variables may affect marine survival as climatic conditions change.

OBJECTIVES

1. Quantify diet composition and energy density of juvenile Chinook salmon caught in the northeastern Bering Sea through stomach content analyses (2004–2017) and bomb calorimetry (2006–2017).
2. Determine the effect of juvenile Chinook salmon size on diet in 2017.
3. Assess how ocean temperatures influence diet composition (2004–2017) and energy densities (2006–2017).

METHODS

JUVENILE CHINOOK SALMON COLLECTIONS

Juvenile Chinook salmon collections from the NBS occurred between late August and early October from 2002 to 2017 (Table 1; Farley et al. 2009; Murphy et al. 2017; Howard et al. 2019). Fish were collected on a grid from 60°N north to the Bering Strait and from Norton Sound west to -170°W with stations at 30 nmi intervals (Figure 1), and typical bottom depths of 18–55 m. Fish were collected in 30-minute tows using a Cantrawl 400/601 rope trawl (Cantrawl Pacific Ltd., Richmond, B.C.) from 2003 to 2017.

The protocol for sampling juvenile Chinook salmon for diet and energy density analyses was the same at each station. After the trawl catch was separated by species, the total length (mm) and weight (g) were measured for each juvenile Chinook salmon caught. Stomachs were removed from up to 10 fish at each station and either analyzed on-board the vessel (2004–2011) or processed in the laboratory (2012–2017). Beginning in 2006, at least 2 Chinook salmon were frozen whole from each station and analyzed for energy density (Table 1).

SEA SURFACE TEMPERATURE

Sea surface temperature data (Jeanette Gann, Alaska Fisheries Science Center, Auke Bay Laboratories, NMFS, NOAA; personal communication) were collected using Sea-Bird Electronics SBE911 CTD deployed at each station. The average autumn sea surface temperature (SST) for a given year was the average of all CTD temperature measurements from the upper 10 meters of the water column in that year within 60–64.5°N latitude in the Bering Sea (Table 1).

STOMACH CONTENT ANALYSIS

For stomach content analysis, juvenile Chinook salmon stomach contents were pooled by station and weighed to the nearest 0.001 g. Prey items were identified to the lowest possible taxa using a dissecting microscope and weighed to the nearest 0.001 g when analyzed in the laboratory and were visually assigned proportions when the analysis was completed onboard. Intact prey items were enumerated and measured to the nearest mm. To simplify reporting, prey items were grouped into 6 categories: (1) capelin (*Mallotus villosus*), (2) sand lance (*Ammodytidae*), (3) walleye pollock (*Gadus chalcogrammus*), (4) other fish, (5) decapods, and (6) other invertebrates (Appendix A1).

As an index of feeding intensity, a stomach fullness index (SFI) was calculated at each station where juvenile Chinook salmon stomach contents were analyzed. The SFI for a given prey type (x) was calculated for the station (i) as:

$$\mathrm{SFI}_{i,x} = [\, P_{i,x}/\mathrm{C}_i * 100 \,], \tag{1}$$

where $P_{i,x}$ was the weight (g) of prey taxa group (x) at station (i) and C_i was the weight (g) of juvenile Chinook salmon sampled at station (i). The number of juvenile Chinook salmon analyzed for stomach contents from a given station was not necessarily proportional to the total catch of juveniles at that station. Therefore, to account for disproportional sampling, prey weights for each taxa were weighted by the number of juvenile Chinook salmon caught at each station as a proportion of the total number caught across all stations in that year. The weighted SFI (WSFI) for a given prey type was calculated for the station (i) as:

$$\mathrm{WSFI}_{i,x} = [\, P_{i,x}/\mathrm{C}_i * 100 \,] * [\, \frac{n_i}{\sum_{i=1}^{I} n_i} \,], \tag{2}$$

where n_i was the number of juvenile Chinook caught at that station, I was the total number of stations sampled in that year, and $\sum n_i$ was the total number of juvenile Chinook salmon caught across all stations in that year. The WSFIs were then summed across all stations and all taxa groups (6 total groups) to get a total WSFI for a given year:

$$\mathrm{WSFI}_{\mathrm{TOT}} = \sum_{i=1}^{I} \sum_{x=1}^{6} \mathrm{WSFI}_{i,x}. \tag{3}$$

To assess the importance of specific prey items to Chinook salmon, the diet proportion (D), contributed by each prey taxa group (x) for a given year, was calculated as:

$$D_x = [\, \sum_{i=1}^{I} \mathrm{WSFI}_{i,x} \,]/\ \mathrm{WSFI}_{\mathrm{TOT.}} \tag{4}$$

Stomach contents were analyzed from 2004 to 2017, except 2008 when no fish collection occurred. Due to the small sample size, stomach contents from 2012 (42 juvenile Chinook salmon stomachs from 6 stations) were not included in the results. Due to unequal variance in the WSFI time series, Welch's ANOVA was used to compare among yearly juvenile Chinook WSFIs and post-hoc Games-Howell pairwise comparisons were used to identify specific year differences (Welch 1951; Games and Howell 1976; Day and Quinn 1989). Beta regression models (Cribari-Neto 2004) were used to assess whether SST influenced diet proportions and WSFI.

Juvenile Chinook salmon diet composition was assessed separately for 2 size classes for 2017 data only: yearling juvenile Chinook salmon (>160 mm) and presumed subyearling Chinook salmon (<160 mm). All presumed subyearlings were assessed for stomach content separately in 2017, which allowed for diet comparison by size. The smaller size class was expected to represent the minority subyearling life history type, because coded-wire-tagged juveniles from the Whitehorse Hatchery in Canada that emigrate out of the river as subyearlings are typically less than 160 mm when captured. Very few small juvenile Chinook salmon (<160 mm) were available for stomach content analysis in 2017 (n = 17) and even fewer contained prey items in their stomachs (n = 13).

ENERGY DENSITY ANALYSIS

Energetic condition (energy density, ED) of juvenile Chinook salmon from the NBS was obtained using bomb calorimetry on dried samples of homogenized whole fish tissues (Fergusson et al. 2010). From 2006 to 2015, samples were heated at 75°C in a drying oven and manually re-weighed until mass was constant. Starting in 2016, the method of sample drying and moisture determination before bombing was changed. Since 2016, samples were heated at 135°C to dryness using a LECO Thermogravimetric Analyzer 601. Moisture values obtained by the 2 methods were known to differ by less than 1% (Vollenweider et al. 2011).

Comparing annual average ED required the use of weighted least squares in Welch's ANOVA (Welch 1951; Day and Quinn 1989) due to unequal variances among years, and post-hoc Games-Howell pairwise comparisons (Games and Howell 1976; Day and Quinn 1989) to identify specific years that differed. Testing for differences in ED among years while controlling for fish size was accomplished using 1-way ANCOVA and post-hoc Tukey's pairwise comparisons. Due to unequal variances among years, ANCOVA results were compared to results from a rank-based Kruskal-Wallis test performed on the residuals from a simple linear regression of ED against length, followed by Tukey's pairwise comparisons on the ranked residuals.

Multiple linear regression models were used to test for the effects of fish length and SST on annual average ED. The small-sample corrected form of the Akaike Information Criteria (AICc) was used to compare annual average ED models with SST versus without:

$$\mathrm{AICc} = -2\ln(L) + 2K + 2K(K + 1)/(n - K - 1), \qquad (5)$$

where L is the likelihood, K is the number of parameters in the model, and n is the number of observations. The model yielding the lowest AICc score was considered best and models scoring up to 2 points higher than the best model were strongly supported (Burnham and Anderson 2004).

RESULTS AND DISCUSSION

TRENDS IN DIETS

NBS juvenile Chinook salmon primarily ate fish but also consumed decapods, zooplankton, cephalopods, and insects (Table 2), consistent with previously reported prey items for juvenile Chinook salmon (Brodeur 1991; Weitkamp and Sturdevant 2008; Daly et al. 2009; Farley et al.

2009). Juvenile Chinook salmon were primarily piscivorous and 69%–96% of their diet was comprised of fish. No single fish species consistently dominated Chinook salmon diets in the NBS, which suggested juvenile Chinook salmon are opportunistic predators whose diets may change in response to changes in the available prey field (Beamish et al. 2003; Duffy et al. 2010; Figure 2). Juvenile Chinook salmon diets also appeared to be influenced by their size and ocean temperature, which was consistent with previous studies (Trudel et al. 2007; Daly et al. 2009).

Diets in 2017 differed between the larger (>160 mm) yearling Chinook salmon and the smaller (<160 mm) presumed subyearlings. Chinook salmon <160 mm ate more decapods and other invertebrates than their larger counterparts (Figure 3). Chinook salmon >160 mm had 89% fish prey in their stomachs compared to 53% for Chinook salmon <160 mm. Increased piscivory with increasing length has been documented for juvenile Chinook salmon in other parts of their range (Daly et al. 2009; Duffy et al. 2010). Size alone may influence diet, but spatial differences could also play a role; Chinook salmon <160 mm were generally caught closer to the Yukon River Delta, where prey may have differed from those offshore. Most of the fish prey in Chinook salmon <160 mm stomachs were not identifiable to species, making it difficult to distinguish nearshore versus offshore prey fish distributions. Future stomach content analyses should continue to sample presumed subyearling stomachs separately from the yearling juveniles to allow further size class comparisons.

Small juvenile Chinook salmon may compensate for lower piscivory by eating relatively high energy invertebrate prey. In 2017, minimally digested sand lance and larval crabs (*Chionoecetes* spp. megalopae) were sampled from juvenile Chinook salmon stomachs for ED. On average, sand lance wet mass ED was approximately 25% higher than larval crabs (4.85 kJ/g versus 3.78 kJ/g). However, compared to other zooplankton (e.g., amphipods and copepods; Foy and Norcross 1999), the larval crabs sampled from the NBS exhibited fairly high energy densities. Although Chinook salmon <160 mm may be eating a higher proportion of decapods relative to their larger counterparts, the comparatively high ED of larval crabs, coupled with the presumed lower energetic costs of pursuing and capturing them, may be enough to foster marine growth necessary for surviving their first winter.

In addition to the effects of size, diet composition appeared to shift with ocean temperature. Diet proportions of sand lance, decapods, capelin, and fish prey in the autumn were significantly affected by SST (Figure 4). Higher SST was associated with greater proportions of sand lance (pseudo-R^2 = 0.43, p = 0.002, slope = 0.695; Figure 4a) and decapods (pseudo-R^2 = 0.32, p = 0.002, slope = 0.516; Figure 4b) in juvenile Chinook salmon diets, which suggested these prey items may be more abundant in warmer years, or their distribution may overlap more frequently with that of juvenile Chinook salmon. Capelin proportions in juvenile Chinook salmon diet decreased with increasing SST (pseudo-R^2 = 0.46, p = 0.02, slope = -0.665; Figure 4c), corresponding with decreased capelin biomass in the NBS during warmer years (Andrews et al. 2016). Piscivory decreased with increasing autumn SST, because fewer fish were consumed during warmer years (pseudo-R^2 = 0.25, p = 0.02, slope = -0.344; Figure 4d). Warmer SSTs may decrease prey quality and quantity, such as decreased lipid content of age-0 pollock (Moss et al. 2009) and lower biomass of capelin and Pacific herring (Andrews et al. 2016), but temperature effects may not be consistent across all fish species, as evidenced by higher proportions of sand lance in warmer SSTs. These results provided evidence that juvenile Chinook salmon diet composition in the NBS was not consistent across the range of temperatures analyzed in this study.

Ocean temperature not only affected diet composition, but also the amount of prey consumed. WSFIs varied within and across years but were lower during warmer years in the NBS. Average annual WSFIs differed significantly across years (Welch's ANOVA, $F = 3.33$, $R^2 = 7.4\%$, $p = 0.002$), but post-hoc tests did not identify a specific year that differed significantly from other years (Figure 5). Average WSFIs decreased with increasing SST, which suggested juvenile Chinook salmon were feeding less in warmer temperatures (pseudo-$R^2 = 0.52$, $p < 0.0001$, slope = -0.426; Figure 6). Juvenile Chinook salmon require more food and more frequent feeding due to increased metabolic demands in warmer temperatures (Daly and Brodeur 2015). During warm SSTs in the NBS, juvenile Chinook salmon generally ate higher proportions of sand lance (Figure 4a), which have high lipid content (Robards and Piatt 1999). Consuming high-energy prey, such as sand lance, may require less intense feeding to grow and build energy stores. Juvenile Chinook salmon from the North California Current (NCC) had the highest survival in a year with low stomach fullness, but the diets contained high proportions of Pacific sand lance (Daly et al. 2009). These results, in conjunction with those from the NCC, suggest the combination of high prey quality and lower prey quantity consumed during warm periods may still be favorable for juvenile Chinook salmon survival.

TRENDS IN ENERGETIC CONDITION

The energetic condition of NBS juvenile Chinook salmon varied across the 10 years of available data (Figure 7), partially driven by differences in fish size. Average ED (kJ/g dry tissue mass) differed significantly among years (Welch's ANOVA, $F = 11.47$, $R^2 = 18.3\%$, $p < 0.001$), and 2016 was the highest and 2011 was the lowest. Fish size also differed among years (Welch's ANOVA, $F = 24.74$, $R^2 = 20.9\%$, $p < 0.001$). When all data was pooled across years, linear regression analysis indicated energetic condition of juvenile Chinook salmon increased with fish size expressed in terms of length (slope = 0.0242, $p < 0.001$; Figure 8). This positive relationship to size was not unexpected, because energetic condition commonly increases with size in fishes that must store energy prior to winter (Post and Parkinson 2001) and has been previously observed in juvenile Chinook salmon (Murphy et al. 2014). However, less than half of the variation in individual ED was explained by fish size alone. Including year and length increased the explained variation to 52.8%, with a significant effect of year after controlling for length (ANCOVA, $F_{9,\ 473} = 10.85$, $p < 0.001$; Table 3). Mean size-adjusted energetic condition overlapped significantly among years but was lowest in 2011 and highest in 2017 (Table 4). Similar results regarding yearly comparisons were obtained using a rank-based test and comparisons of ranked residuals from the regression fit of ED versus length (Kruskal-Wallis test, $H = 79.7$, $p < 0.001$; Table 5). Monitoring yearly differences in autumn energetic condition may help researchers understand and predict juvenile survival, because cohorts that are able to store more energy prior to their first winter are more likely to survive (Sogard and Olla 2000).

Differences in ED among years may also be driven by annual differences in SST. Temperature alone accounted for 45.8% of the variation in annual average ED (slope= 0.298; $F_{1,9} = 6.77$, $p = 0.032$; Figure 9) in a simple linear regression model, and average length alone accounted for 57.7% (slope = 0.0276; $F_{1,9} = 10.89$, $p = 0.011$; Figure 10). Temperature combined with length in a multiple regression model explained 74.8% of the variation in average ED ($\text{slope}_{\text{SST}} = 0.198$, $\text{slope}_{\text{LEN}} = 0.0212$; $F_{2,8} = 10.41$, $p = 0.008$). The effect of SST on ED was marginally not significant ($p = 0.065$) in that model and was potentially weakened by collinearity with length due to the non-significant but positive influence of SST on length (slope = 4.72, $F_{1,\ 9} = 1.42$; $R^2 = 15\%$, $p = 0.267$). The 17.1% improvement in fit versus length alone justified the inclusion of the SST term in the model (AICc = 0.798). The positive relationship between NBS juvenile Chinook salmon energetic condition and temperature may be expected of fish near the northern limit of their distribution where temperatures are probably lower than optimal for growth and condition. Given the typical bell-shaped responses of fish growth and condition to temperature, increasing temperatures up to a species-dependent optimum should have a positive effect (Beauchamp et al. 2007; Laurel et al. 2016). Warmer temperatures support higher survival of northern stocks of pink (*O. gorbuscha*), chum (*O. keta*), and sockeye salmon (*O. nerka*), potentially through indirect effects on prey production, though the mechanism is unclear (Mueter et al. 2002). It is difficult to resolve whether temperature influences ED directly by affecting metabolic rates or indirectly by affecting prey quality or quantity. However, the higher energetic condition we observed in association with warmer temperatures may contribute to improved survival for NBS Chinook salmon.

Higher ED in warmer years suggested that juvenile Chinook salmon energetic condition for this period generally was not limited by food. Due to greater metabolic costs at higher temperatures (Gillooly et al. 2001), increasing fat storage or growth at higher temperatures should only be possible with prey of sufficient quantity and quality. Juvenile Chinook salmon may adapt to decreased availability of capelin in warm years (Andrews et al. 2016) by eating more sand lance and early-stage decapods. Diet differences in warmer versus colder years make it difficult to strictly distinguish temperature effects from diet effects on energetic condition. However, despite eating fewer fish and less prey overall in warmer years, NBS juvenile Chinook salmon diets were adequate to support higher energetic condition than in cooler years.

CONCLUSIONS

This study found that juvenile Chinook salmon diets and energy density in the NBS were influenced by size and temperature. Larger juvenile Chinook salmon were more piscivorous and had higher energy density than their smaller conspecifics. Additionally, warm years in the Bering Sea resulted in juvenile Chinook salmon with lower stomach fullness but higher energy density than in cold years. Although metabolic costs increase with temperature, the higher energy density in warmer years suggested that prey quality and quantity in the NBS were sufficient for growth and energy storage. This study demonstrated that larger juveniles have higher energy reserves, which was expected to increase the likelihood of surviving their first winter at sea. Although the warm periods in the northern Bering Sea have been favorable for the condition of juvenile Chinook salmon thus far, it is unclear how the fish will respond if warming trends continue as predicted (Wang et al. 2012). If further warming continues to decrease prey consumption, prey quality may not be sufficient to compensate for reduced prey quantity. Reduced prey quality and quantity, coupled with increased metabolic demands in warmer temperatures, may result in insufficient energy stores prior to the onset of winter. Continued monitoring of juvenile Chinook salmon diets and energy density will help researchers understand changes as warming trends continue in the Bering Sea.

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REFERENCES CITED

Andrews, A. G. III, W. W. Strasburger, E. V. Farley Jr., J. M. Murphy, and K. O. Coyle. 2016. Effects of warm and cold climate conditions on capelin (*Mallotus villosus*) and Pacific herring (*Clupea pallasii*) in the eastern Bering Sea. Deep Sea Research II 134:235–246.

Beauchamp, D. A., A. D. Cross, J. L. Armstrong, K. W. Myers, J. H. Moss, J. L. Boldt, and L. J. Haldorson. 2007. Bioenergetic responses by Pacific salmon to climate and ecosystem variation. North Pacific Anadromous Fish Commission Bulletin 4:257–269.

Beamish, R. J., and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Progress in Oceanography 49:423–437.

Beamish, R. J., I. A. Pearsall, and M. C. Healey. 2003. A history of the research on the early marine life of Pacific salmon off Canada's Pacific coast. North Pacific Anadromous Fish Commission Bulletin 3:1–40.

Beamish, R. J., C. Mahnken, and C. M. Neville. 2004. Evidence that reduced early marine growth is associated with lower marine survival of coho salmon. Transactions of the American Fisheries Society 133:26–33.

Brodeur, R. D. 1991. Ontogenetic variations in the type and size of prey consumed by juvenile coho, *Oncorhynchus kisutch,* and Chinook, *O. tshawytscha*, salmon. Environmental Biology of Fishes 30:303–315.

Brodeur, R. D., E. A. Daly, M. V. Sturdevant, T. W. Miller, J. H. Moss, M. E. Thiess, M. Trudel, L. A. Weitkamp, J. Armstrong, and E. C. Norton. 2007. Regional comparisons of juvenile salmon feeding in coastal marine waters off the west coast of North America. American Fisheries Society Symposiums 57:183–203.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference understanding AIC and BIC in model selection. Sociological Methods and Research 33:261–304.

Cribari-Neto, F. 2004. Beta regression for modelling rates and proportions. Journal of Applied Statistics 31:799–815.

Daly, E. A., and R. D. Brodeur. 2015. Warming ocean conditions relate to increased trophic requirements of threatened and endangered salmon. PLoS One 10: e0144066. DOI: 10.1371/journal.pone.0144066.

Daly, E. A., R. D. Brodeur, and L. A. Weitkamp. 2009. Ontogenetic shifts in diets of juvenile and subadult coho and Chinook salmon in coastal marine waters: important for marine survival? Transactions of the American Fisheries Society 138:1420–1438.

Davis, N. D., K. W. Myers, and Y. Ishida. 1998. Caloric value of high-seas salmon prey organisms and simulated ocean growth and prey consumption. North Pacific Anadromous Fish Commission Bulletin No. 1:146–162.

Day, R. W., and G. P. Quinn. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecological Monographs 59:433–463.

Duffy, E. J., and D. A. Beauchamp. 2008. Seasonal patterns of predation on juvenile Pacific salmon by anadromous cutthroat trout in Puget Sound. Transactions of the American Fisheries Society 137:165–181.

REFERENCES CITED (Continued)

Duffy, E. J., D. A. Beauchamp, R. M. Sweeting, R. J. Beamish, and J. S. Brennan. 2010. Ontogenetic diet shifts of juvenile Chinook salmon in nearshore and offshore habitats of Puget Sound. Transactions of the American Fisheries Society 139:803–823.

Farley Jr., E. D., J. H. Moss, and R. J. Beamish. 2007a. A review of the critical size, critical period hypothesis for juvenile pacific salmon. North Pacific Anadromous Fish Commission Bulletin No. 4:311–317.

Farley Jr., E. D., J. M. Murphy, M. D. Adkison, L. B. Eisner, J. H. Helle, J. H. Moss, and J. Nielsen. 2007b. Early marine growth in relation to marine-stage survival rates for Alaska sockeye salmon (*Oncorhynchus nerka*). Fishery Bulletin 105:121–130.

Farley Jr., E. D., J. M. Murphy, J. Moss, A. Feldman, and L. Eisner. 2009. Marine ecology of western Alaska juvenile salmon. American Fisheries Society Symposium 70:307–329.

Fergusson, E. A., M. V. Sturdevant, and J. A. Orsi. 2010. Effects of starvation on energy density of juvenile chum salmon (*Oncorhynchus keta*) captured in marine waters of Southeastern Alaska. Fishery Bulletin 108:218–225.

Foy, R. J., and B. L. Norcross. 1999. Spatial and temporal variability in the diet of juvenile Pacific herring (*Clupea pallasii*) in Prince William Sound, Alaska. Canadian Journal of Zoology 77:697–706.

Games, P. A., and J. F. Howell. 1976. Pairwise multiple comparison procedures with unequal n's and/or variances: A Monte Carlo study. Journal of Educational and Behavioral Statistics 1:113–125.

Gilooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. Effects of size and temperature on metabolic rate. Science 293:2248–2251.

Hartt, A. C. 1980. Juvenile salmonids in the oceanic ecosystem: the critical first summer. Pages 25–57 [*In*]: Salmonid ecosystems of the North Pacific. W. J. McNeil and D. C. Himsworth, editors. Oregon State University Press, Corvalis, OR.

Hertz, M., M. Trudel, R. D. Brodeur, E. A. Daly, L. Eisner, E. V. Farley Jr., J. A. Harding, R. B. MacFarlane, S. Mazumder, J. H. Moss, J. M. Murphy, and A. Mazumder. 2015. Continental-scale variability in the feeding ecology of juvenile Chinook salmon along the coastal northeast Pacific Ocean. Maine Ecology Progress Series 537:247–263.

Howard. K. G., S. Garcia, J. Murphy, and T. H. Dann. 2019. Juvenile Chinook salmon abundance index and survey feasibility assessment in the northern Bering Sea, 2014–2016. Alaska Department of Fish and Game, Fishery Data Series, No. 19-04, Anchorage.

Laurel, B. J., M. Spencer, P. Iseri, and L. A. Copeman. 2016. Temperature-dependent growth and behavior of juvenile Arctic cod (*Boreogadus saida*) and co-occurring North Pacific gadids. Polar Biology 39(6):1127–1135.

Moss, J. H., D. A. Beauchamp, A. D. Cross, K. Myers, E. V. Farley Jr., J. M. Murphy, and J. H. Helle. 2005. Higher marine survival associated with faster growth for pink salmon (*Oncorhynchus gorbuscha*). Transactions of the American Fisheries Society 134:1313–1322.

Moss, J. H., E. V. Farley Jr., A. M. Feldmann, and J. N. Ianelli. 2009. Spatial distribution, energetic status, and food habits of eastern Bering Sea age-0 walleye pollock. Transactions of the American Fisheries Society 138:497–505.

Mueter, F. J., R. M. Peterman, and B. J. Pyper. 2002. Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (Oncorhynchus spp.) in northern and southern areas. Canadian Journal of Fisheries and Aquatic Sciences 59(3):456–463.

Murphy J. M., W. D. Templin, E. V. Farley, and J. E. Seeb. 2009. Stock-structured distribution of western Alaska and Yukon juvenile Chinook salmon (Oncorhynchus tshawytscha) from United States BASIS surveys, 2002–2007. North Pacific Anadromous Fish Commission Bulletin No. 5:51–59.

Murphy, J., K. Howard, A. Andrews, L. Eisner, J. Gann, W. Templin, C. Guthrie, J. Moss, D. Honeyfield, K. Cox, and E. Farley. 2014. Yukon River Juvenile Chinook Salmon Survey. AKSSF Project 44606 Final Report.

REFERENCES CITED (Continued)

Murphy, J., K. Howard, J. Gann, K. Cieciel, W. Templin, and C. Guthrie. 2017. Juvenile Chinook salmon abundance in the northern Bering Sea: Implications for future returns and fisheries in the Yukon River. Deep-Sea Research II 135:156–167.

Nunn, A. D., L. H. Tewson, and I. G. Cowx. 2012. The foraging ecology of larval and juvenile fishes. Reviews in Fish Biology and Fisheries 22:377–408.

Pearcy, W. G. 1992. Ocean ecology of the North Pacific salmonids. Seattle, WA: University of Washington Press.

Post, J. R., and E. A. Parkinson. 2001. Energy allocation strategy in young fish: allometry and survival. Ecology 82(4):1040–1051.

Robards, M. D., J. A. Anthony, G. A. Rose, and J. F. Piatt. 1999. Changes in proximate composition and somatic energy content for Pacific sand lance (*Ammodytes hexapterus*) from Kachemak Bay, Alaska relative to maturity and season. Journal of Experimental Marine Biology and Ecology 242:245–258.

Sogard, S. M., and B. L. Olla. 2000. Endurance of simulated winter conditions by age-0 walleye pollock: effects of body size, water temperature and energy stores. Journal of Fish Biology 56(1):1–21.

Trudel, M., M. E. Thiess, C. Bucher, E. D. Farley Jr., R. B. MacFarlane, E. Casillas, J. Fisher, J. F. T. Morris, J. M. Murphy, and D. W. Welch. 2007. Regional variation in the marine growth and energy accumulation of juvenile Chinook salmon and coho salmon along the west coast of north America. American Fisheries Society Symposium 57:205–232.

Vollenweider, J. J., R. A. Heintz, L. Schaufler, and R. Bradshaw. 2011. Seasonal cycles in whole-body proximate composition and energy content of forage fish vary with water depth. Marine Biology 158:413–427.

Wang, M., J. E. Overland, and P. Stabeno. 2012. Future climate of the Bering and Chukchi seas projected by global climate models. Deep-Sea Research Part II: Topical Studies in Oceanography 65–70:46–57.

Weitkamp, L. A., and M. V. Sturdevant. 2008. Food habits and marine survival of juvenile Chinook and coho salmon from marine waters of southeast Alaska. Fisheries Oceanography 17:380–395.

Welch, B. L. 1951. On the comparison of several mean values: an alternative approach. Biometrika 38:330–336.

TABLES AND FIGURES

Table 1.–Marine survey start and end dates, number of stations sampled, total number of juvenile Chinook salmon caught, number assessed for diet and energy density, and annual sea surface temperature from northeastern Bering Sea surface trawl surveys, 2004–2017.

Year	Start date	End date	Number of stations sampled	Number of juvenile Chinook salmon caught	Number of stomachs sampled	Number assessed for energetic density	Average autumn sea surface temperature (°C)
2004	9/10	9/28	45	168	128	0	9.86
2005	9/17	10/6	37	142	69	0	7.44
2006	9/3	9/19	43	103	87	10	8.31
2007	9/12	10/3	48	271	98	49	8.61
2008	–	–	–	–	–	–	–
2009	9/1	9/12	39	130	46	17	8.06
2010	9/10	10/1	54	133	69	95	8.60
2011	8/29	9/17	57	314	111	41	7.47
2012	9/10	9/25	38	90	42	31	6.58
2013	9/10	9/24	42	521	174	–	8.20
2014	9/4	9/22	45	267	205	87	10.38
2015	9/1	9/16	37	322	180	69	8.93
2016	8/28	9/12	32	216	93	36	10.75
2017	8/27	9/9	35	195	148	49	9.03

Note: There was no northeastern Bering Sea survey in 2008.

Table 2.–Weighted diet compositions from juvenile Chinook salmon caught during the northeastern Bering Sea surface trawl surveys, 2004–2017.

	Percent contribution						
Year	Capelin	Sand lance	Walleye pollock	Other fish	Decapod	Other invertebrates	Percent piscivory
2004	26.7%	34.9%	13.1%	7.4%	16.4%	1.6%	82.1%
2005	34.6%	2.3%	20.7%	11.2%	21.2%	10.0%	68.8%
2006	10.5%	29.2%	10.1%	38.8%	9.0%	2.4%	88.6%
2007	45.5%	7.2%	2.6%	22.1%	21.1%	1.6%	77.4%
2008	–	–	–	–	–	–	–
2009	27.7%	27.3%	0.0%	38.0%	3.1%	4.0%	93.0%
2010	70.5%	5.0%	0.0%	17.8%	2.1%	4.6%	93.3%
2011	42.8%	24.4%	0.0%	28.7%	2.3%	1.9%	95.9%
2012	–	–	–	–	–	–	–
2013	72.5%	10.4%	0.0%	8.1%	4.1%	4.9%	91.0%
2014	3.0%	56.5%	7.1%	13.7%	16.4%	3.4%	80.3%
2015	4.4%	68.9%	3.9%	9.4%	11.7%	1.8%	86.6%
2016	0.9%	61.5%	3.6%	3.2%	30.7%	0.2%	69.2%
2017	2.5%	38.6%	4.2%	43.0%	7.8%	3.9%	88.3%

Note: No survey was conducted in 2008 and stomach contents were not representative of trawl catch in 2012.

Table 3.–Results from ANCOVA of energy density (covariate: length) by year, for juvenile Chinook salmon caught during the northeastern Bering Sea surface trawl surveys, 2006–2017.

Source	DF	Seq SS	Contribution	Adj SS	Adj MS	F-Value	P-Value
Length (mm)	1	242.95	43.00%	194.82	194.82	345.12	0.000
Year	9	55.11	9.75%	55.11	6.12	10.85	0.000
Error	473	267.00	47.25%	267.00	0.56		
Lack-of-fit	312	180.30	31.91%	180.30	0.58	1.07	0.310
Pure error	161	86.71	15.34%	86.71	0.54		
Total	483	565.06	100.00%				

Table 4.–Grouping information from post-hoc Tukey pairwise comparisons (95% confidence) of energy density (covariate: length) by year, ordered by mean value, for juvenile Chinook salmon caught during surface trawl surveys from the northeastern Bering Sea, 2006–2017.

Year	N	Mean energetic density (kJ/g)	Grouping				
2017	49	22.266	A				
2010	95	22.199	A	B			
2016	36	22.195	A	B	C		
2014	87	21.921	A	B	C	D	
2007	49	21.714			C	D	
2006	10	21.653	A	B	C	D	E
2012	31	21.597				D	E
2009	17	21.588		B	C	D	E
2015	69	21.584				D	E
2011	41	21.134					E

Note: Years that share a common letter do not significantly differ (95% confidence).

Table 5.–Grouping information from post-hoc Tukey pairwise comparisons of ranked residuals from simple linear regression of energy density versus length, ordered by mean rank, for juvenile Chinook salmon caught during the northeastern Bering Sea surveys, 2006–2017.

Year	N	Mean rank	Grouping		
2017	49	317.30	A		
2016	36	307.20	A		
2010	95	304.00	A		
2014	87	245.00	A	B	
2007	49	215.60		B	C
2012	31	202.80		B	C
2006	10	194.40	A	B	C
2015	69	181.30		B	C
2009	17	181.10		B	C
2011	41	150.80			C

Note: Years that share a common letter do not significantly differ (95% confidence).

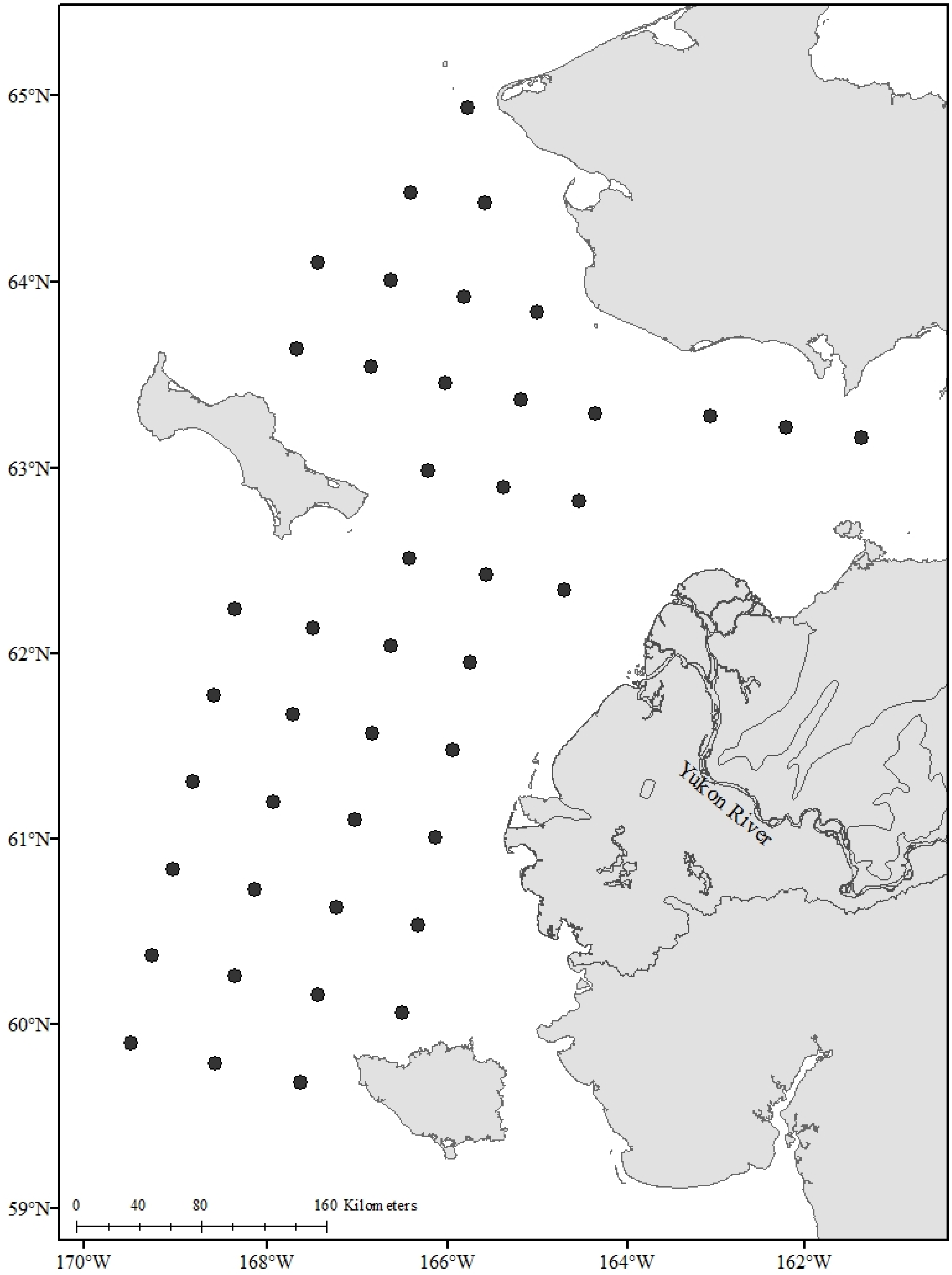

Figure 1.–Stations typically sampled during the northeastern Bering Sea marine surveys.

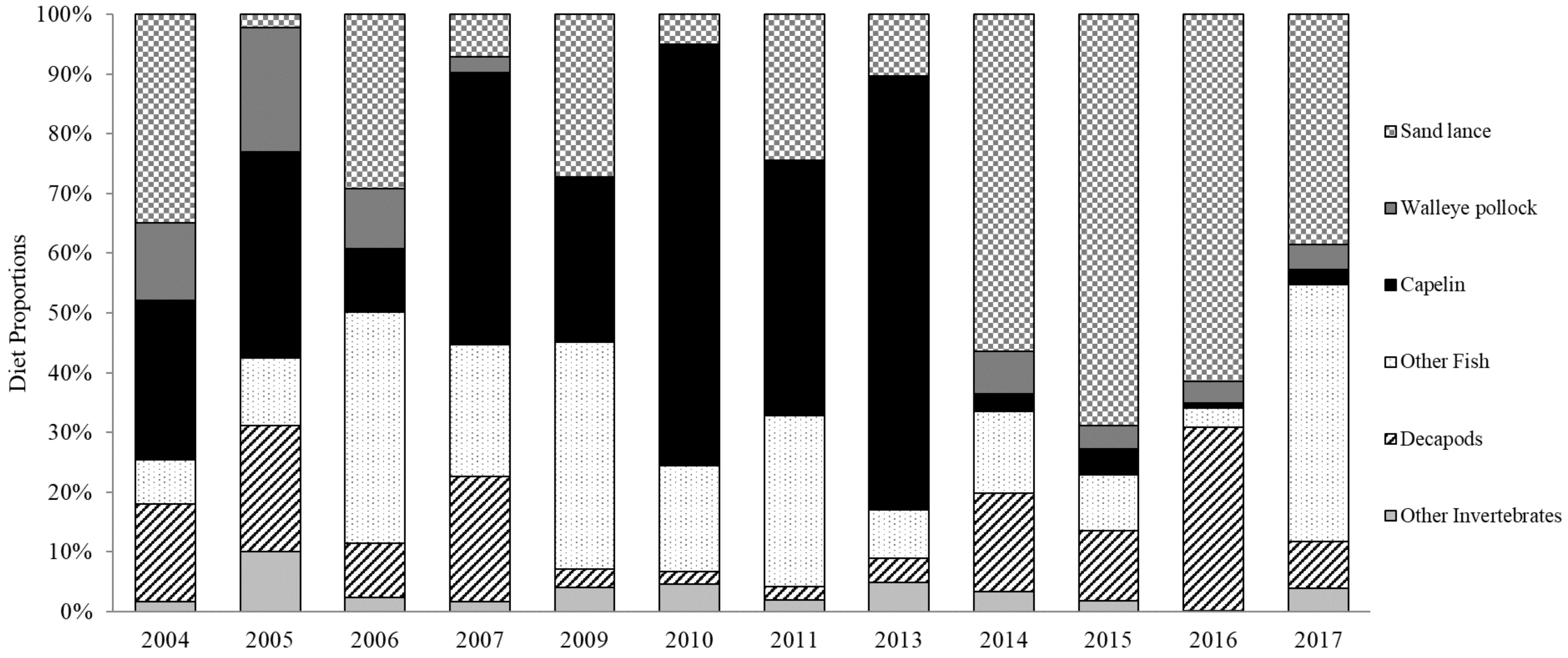

Figure 2.–Weighted diet proportions from juvenile Chinook salmon caught during the northeastern Bering Sea surface trawl surveys, 2004–2017.

Note: No survey in 2008, and 2012 samples were deemed not representative.

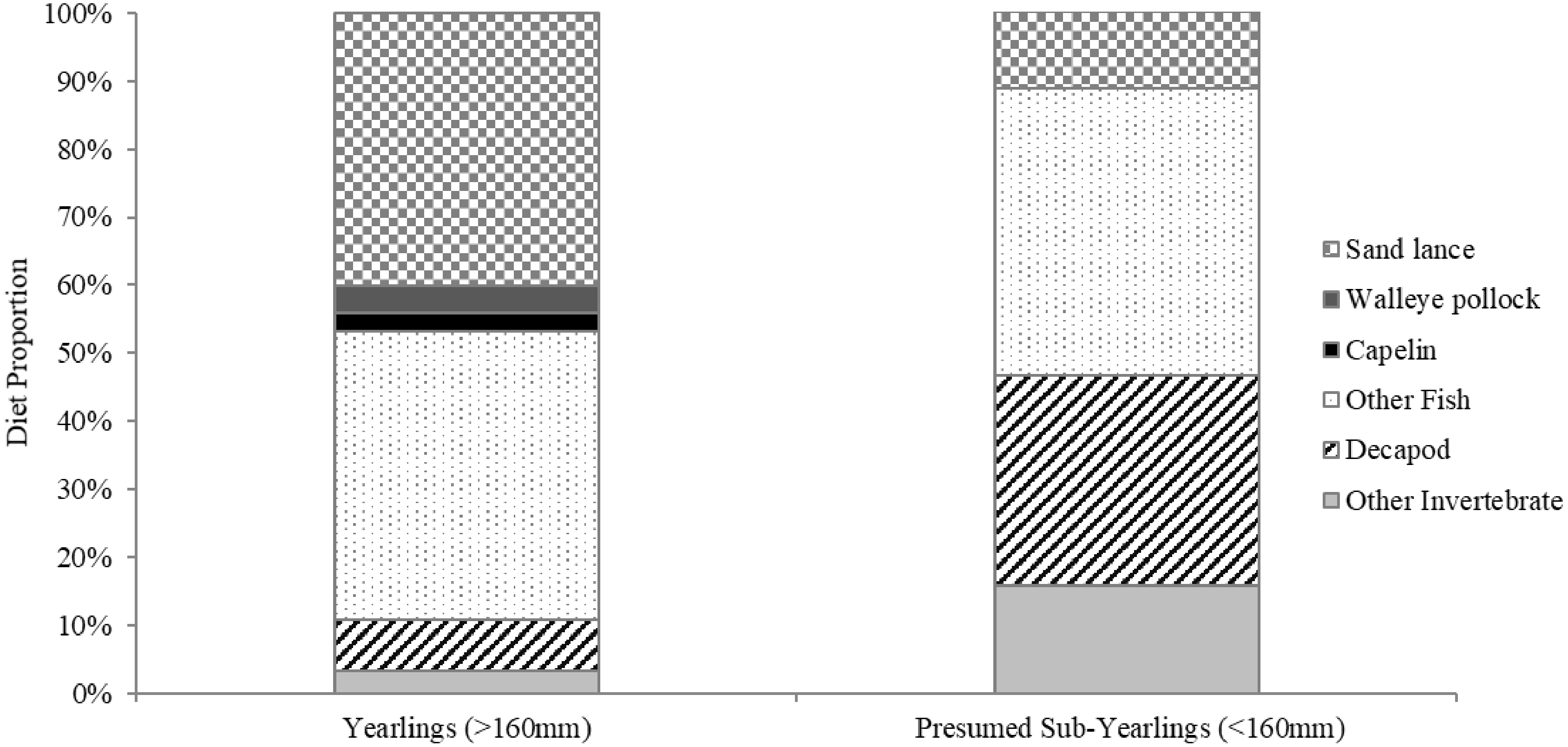

Figure 3.–Chinook salmon weighted diet compositions for yearling (>160 mm) and presumed subyearling (<160 mm) fish caught during the northeastern Bering Sea surface trawl survey aboard the F/V *Northwest Explorer*, 2017.

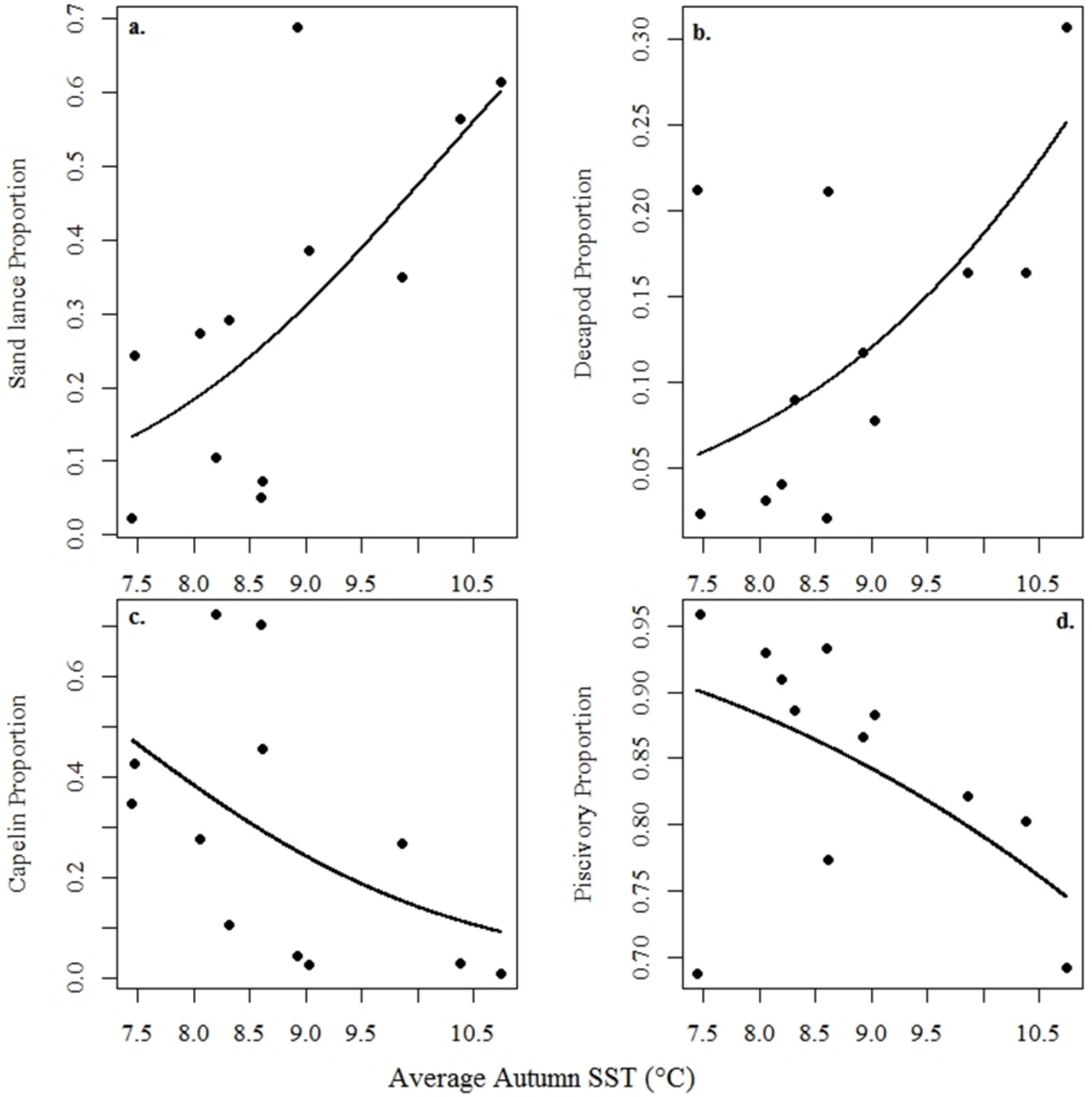

Figure 4.–Sand lance (a), decapod (b), capelin (c), and piscivory (d) proportions (by mass) in juvenile Chinook salmon diets by autumn sea surface temperature in the northeastern Bering Sea, 2004–2017.

Note: Black circles are data points and black lines indicate predicted values from fitted beta regression models. No survey occurred in 2008, and 2012 stomach content data were not included due to low sample size.

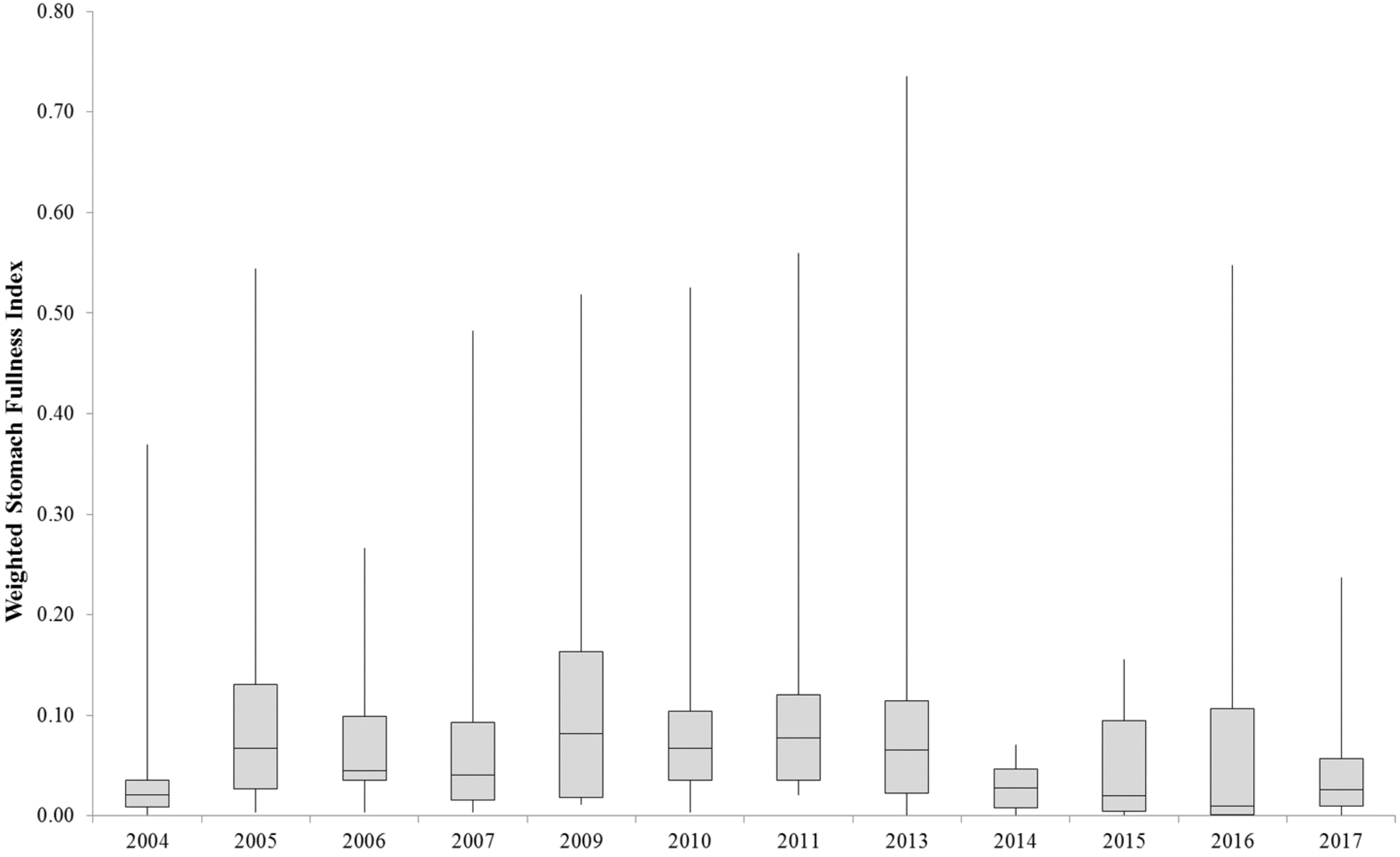

Figure 5.–Weighted stomach fullness indices for juvenile Chinook salmon caught during surface trawl surveys in the northeastern Bering Sea, 2004–2017.

Note: Boxplot whiskers represent minimum and maximum stomach fullness for each year, black line represents the median, and the boxes represent the 25th and 75th percentile.

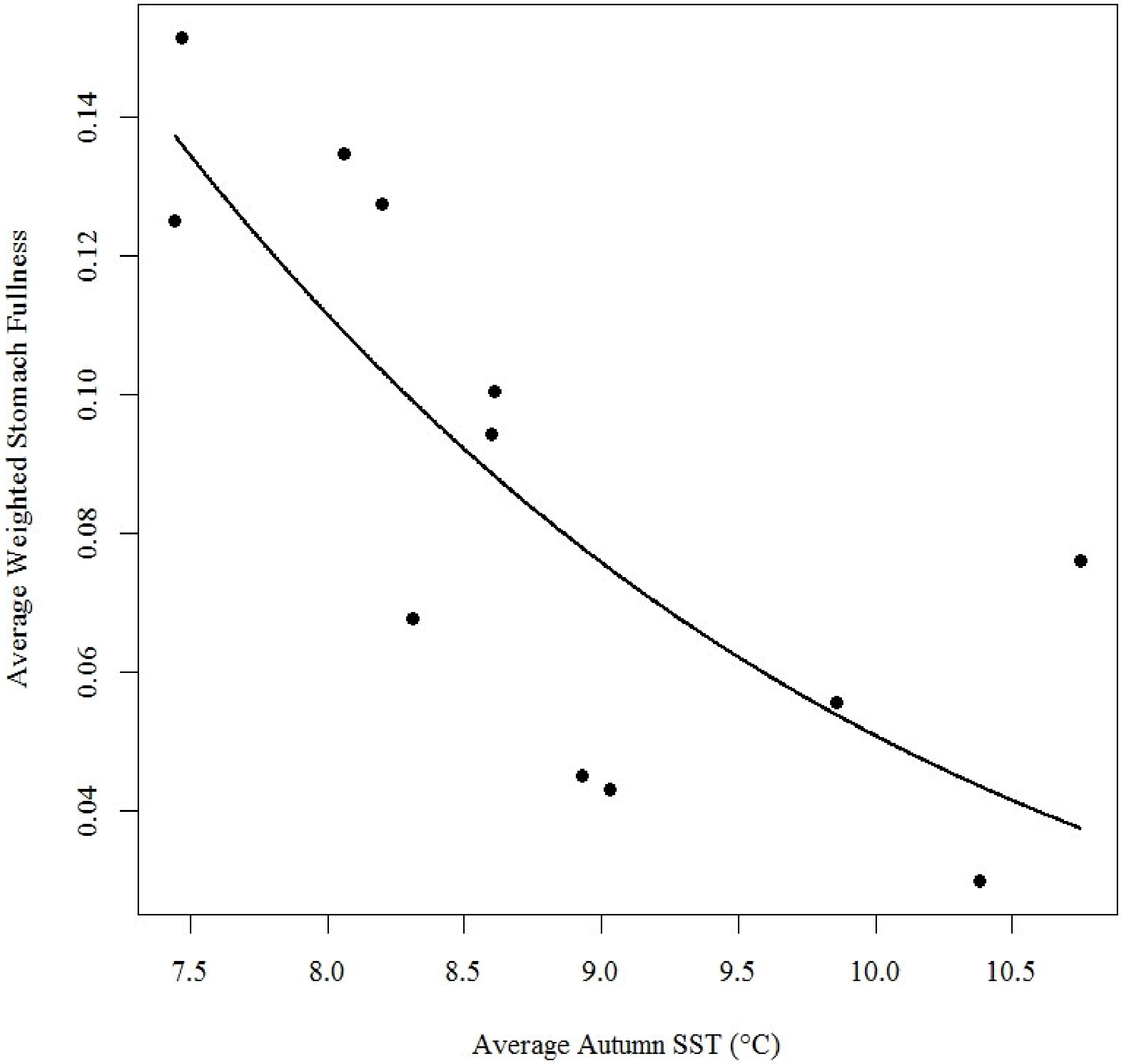

Figure 6.–Average weighted stomach fullness indices from juvenile Chinook salmon by autumn sea surface temperature in the northeastern Bering Sea, 2004–2017.

Note: Black circles are data points and black line indicates predicted values from fitted beta regression model. No survey occurred in 2008, and 2012 stomach content data were not included due to low sample size.

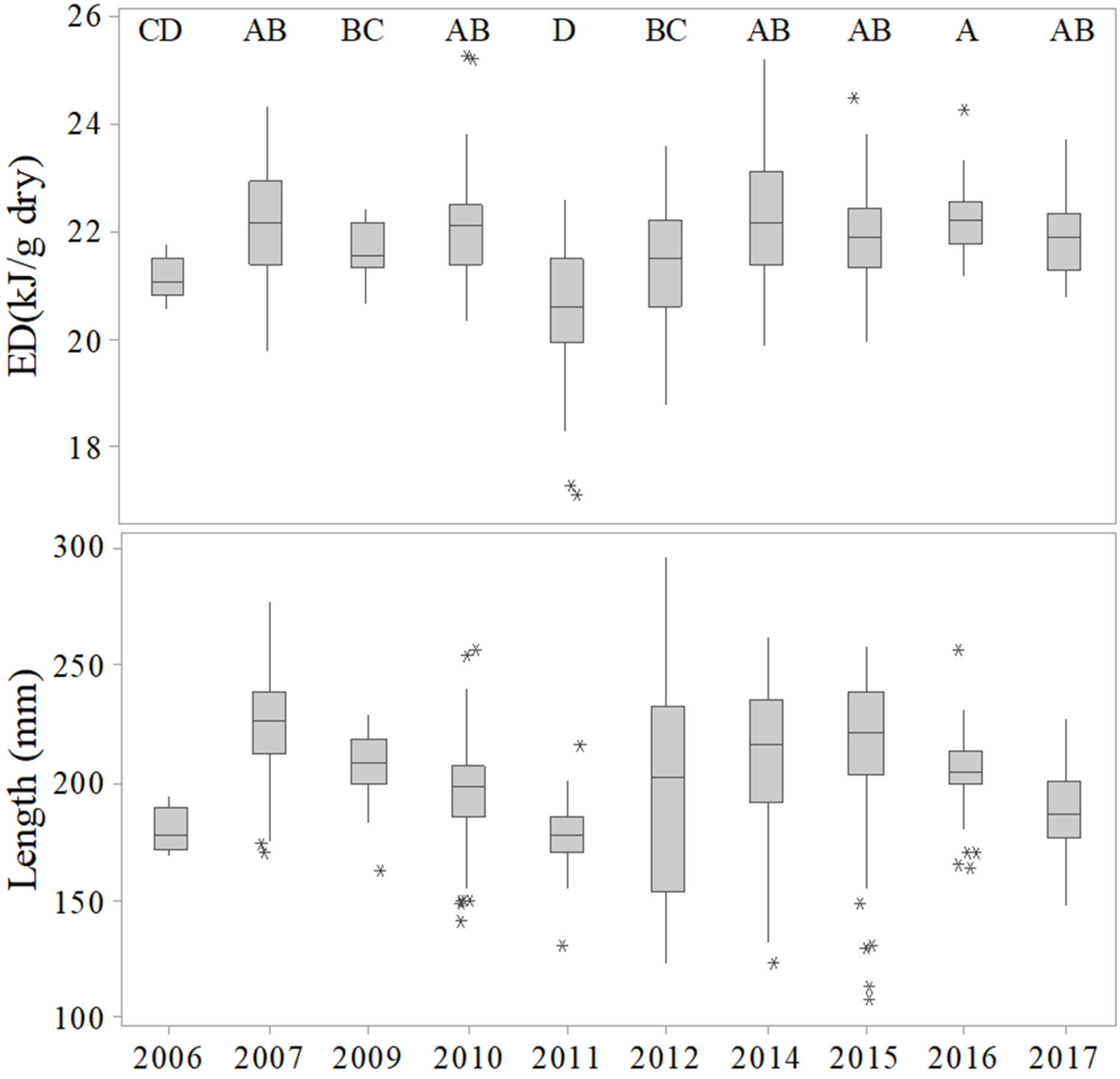

Figure 7.–Energy density of dry tissue mass (top panel) and fork length (bottom panel) of juvenile Chinook salmon caught during surface trawl surveys in the northeastern Bering Sea, 2006–2017.

Note: *n* = 484. Data unavailable for 2008 and 2013. Letters at top indicate groups of similar years from Games-Howell pairwise comparisons of energy density. Medians, interquartile ranges (IQR), whiskers (≤1.5 IQR), and outliers (*, >1.5 IQR) are shown.

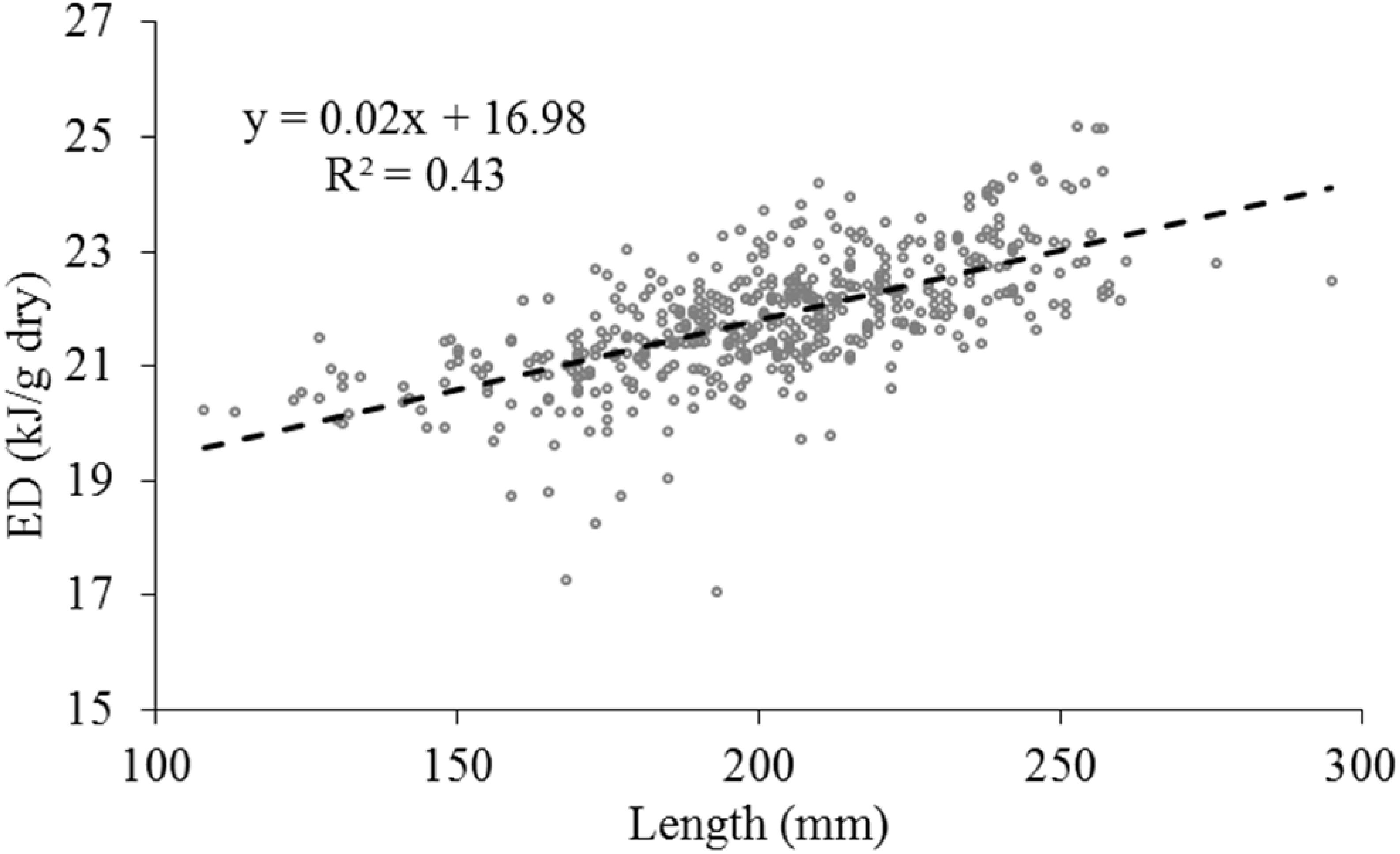

Figure 8.–Energy density (kJ/g) of dry tissue mass by fork length (mm) of juvenile Chinook salmon caught during surface trawl surveys in the northeastern Bering Sea (2006 – 2017).

Note: Simple linear regression model fit shown by dashed line (*n* = 484).

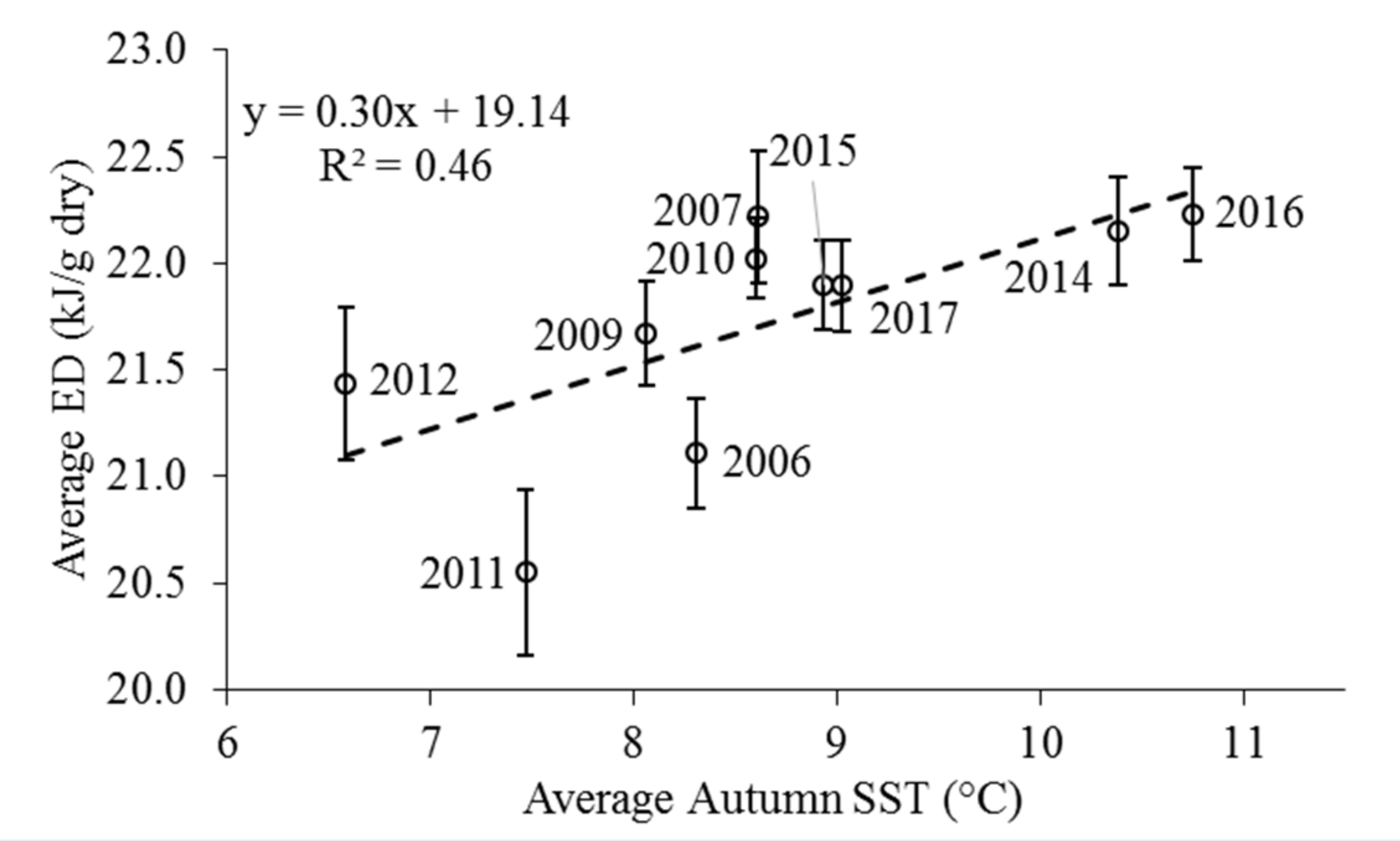

Figure 9.–Annual mean energy density (kJ/g) of dry tissue mass by average autumn sea surface temperature for juvenile Chinook salmon caught during surface trawl surveys in the northeastern Bering Sea, 2006–2017.

Note: Simple linear regression model fit shown by dashed line (n = 10 years). Error bars represent 95% confidence intervals. Data unavailable for 2008 and 2013.

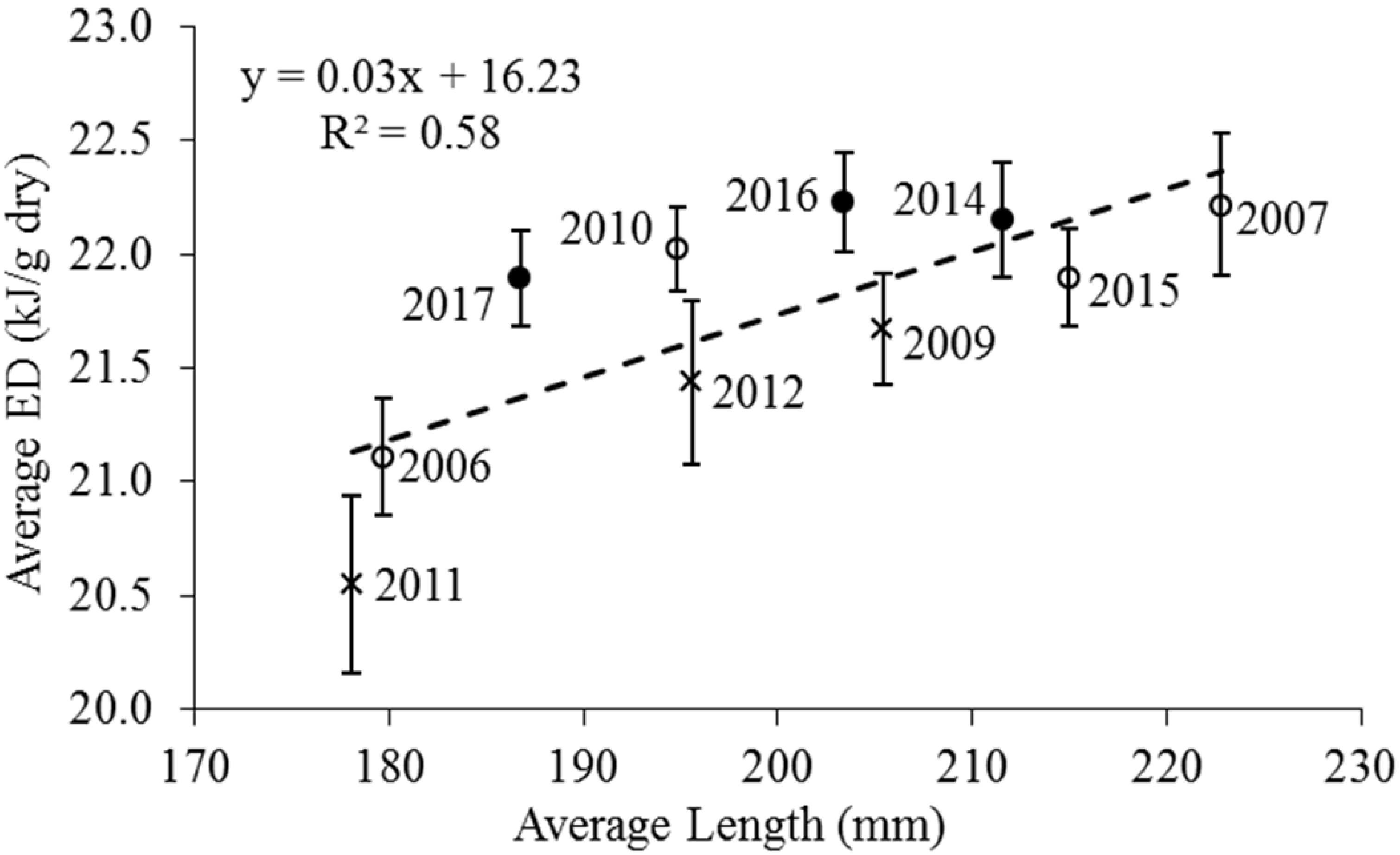

Figure 10.–Annual mean energy density (kJ/g) of dry tissue mass by fork length (mm) of juvenile Chinook salmon caught during surface trawl surveys in the northeastern Bering Sea, 2006–2017.

Note: Simple linear regression model fit shown by dashed line (*n* = 10 years). Error bars represent 95% confidence intervals. Data unavailable for 2008 and 2013. Symbols indicate 3 coldest years (x; autumn SST <8.1°C), 3 warmest years (●; autumn SST > 9.0°C) and 4 intermediate years (○).

APPENDIX A

Appendix A1.–Prey items contained within the other fish, decapod, and other invertebrate categories used for reporting juvenile Chinook salmon stomach content data.

Other fish
Liparidae (snailfish)
Pleuronectidae (righteye flounders)
Limanda spp. (Pleuronectidae)
Reinhardtius hippoglossoides (Greenland halibut)
Agonidae (poachers)
Anisarchus medius (Stout Eelblenny)
Clupea pallasii (Pacific Herring)
Gadidae (cods)
Eleginus gracilis (Safrron Cod)
Hexagrammos stelleri (Whitespotted greenling)
Hippoglossoides robustus (Bering flounder)
Osmerus mordax (Rainbow smelt)
Osmerus spp.
Teleostei spp.
Elongate larvae
Unidentifiable digested fish
Decapods
Anomura
Brachyura
Chionoecetes opilio (Snow crab)
Chionoecetes spp.
Hyas (Oregoniidae)
Paguridae (hermit crabs)
Pandalidae (shrimp)
Caridea (shrimp)
Other invertebrates
Zooplankton
Amphipoda
Copepoda
Cumacea
Diastylis
Euphausiacea
Gammaridae
Hyperiidae
Hyperia galba
Hyperia medusarum
Hyperoche

-continued-

Appendix A1.–Page 2 of 2.

Other invertebrates
Zooplankton
Isopoda
Mysidae
Neomysis rayii
Themisto libellula
Themisto spp.
Thysanoessa raschii
Insects
Aphididae
Coleoptera (bettles)
Corixidae
Diptera (true flies)
Muscidae (house flies)
Tachinidae
Ichneumonidae (parasitoid wasps)
Trichoptera (caddisflies)
Other
Cephalopoda
Gonatus spp.
Nereididae (polychaete worms)
Platyhelminthes (flatworms)
Polychaete (bristle worms)